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Follicular Atresia in Atlantic Salmon (*Salmo salar* L.) in Newfoundland Rivers

by

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Abstract

Follicular atresia is a degenerative process which can occur at any stage of oocyte development, resulting in a reduction in the number of mature eggs available for spawning. Fecundity values used in the calculation of Atlantic salmon egg depositions for most Newfoundland rivers are derived from ovaries collected in the recreational fishery during the summer. Eggs are in early stages of development at this time. In this study, the fecundity of small salmon (<63 cm in fork length) determined from ovaries collected during the summer was compared to that derived from fish sampled during broodstock stripping in the fall for the same river. The rivers involved were Indian River, Exploits River, Conne River, and Little Salmonier River. A reduction in the number of eggs between summer and fall was attributed to atresia. Fecundity expressed in terms of length (eggs/cm) was a better indicator of atresia than weight (eggs/kg). There was a decrease in the number of eggs/cm between summer and fall for Indian River in 1984 (11.2%) and 1985 (5.0%); the average was 8.2%. Decreases for Exploits River in 1985 and 1986 were 16.6 and 14.2% with an average of 13.7%. The greatest reduction (28.5%) occurred in the case of Conne River in 1987. The onset of atresia has been attributed to adverse environmental conditions resulting in stress, among which is water temperature. During the summer of 1987, severe drought conditions affected most rivers in Newfoundland, including Conne River. Sustained low water levels and high water temperatures in 1987 could explain the high rate of atresia observed for this river. An increase was noted for Little Salmonier River in 1985 (16.9%) but this result might have been due to the small sample sizes involved. Results show that atresia can occur to varying degrees depending on environmental conditions. Fecundity values derived from ovaries collected in the recreational fishery therefore have to be regarded as potential and their use could result in underestimates of conservation spawner requirements and overestimates of egg depositions.

Résumé

L'atrésie folliculaire est un processus dégénératif qui peut survenir à n'importe quel stade de croissance de l'ovocyte. Il entraîne une diminution du nombre d'oeufs à pondre. On se sert des ovaires recueillis pendant la pêche récréative de l'été pour établir les valeurs de fécondité utilisées dans le calcul de la ponte d'oeufs de saumons de l'Atlantique dans la plupart des rivières de Terre-Neuve. Pendant l'été, les oeufs en sont à leurs premiers stades de croissance. Dans le cadre de la présente étude, la fécondité de petits saumons (<63 cm de longueur à la fourche) déterminée à partir des ovaires recueillis pendant l'été a été comparée à celle qui a été établie à l'automne pendant l'extraction des oeufs des stocks de géniteurs de la même rivière. L'étude a été menée dans la rivière Indian, la rivière des Exploits, la rivière Conne et la rivière Little Salmonier. On a attribué à l'atrésie la diminution du nombre d'oeufs survenue de l'été à l'automne. La fécondité établie en fonction de la longueur (oeufs/cm) était un meilleur indice d'atrésie que celle déterminée en fonction du poids (oeufs/kg). Dans la rivière Indian, il y a eu une diminution du nombre d'oeufs/cm à l'automne par rapport à l'été en 1984 (11,2 p. 100) et en 1985 (5 p. 100). La diminution moyenne était de 8,2 p. 100. La diminution la plus marquée (28,5 p. 100) est survenue dans la rivière Conne en 1987. On attribue la manifestation de l'atrésie à des conditions environnementales défavorables (notamment la température de l'eau) entraînant un stress chez le poisson. Pendant l'été de 1987, la plupart des rivières de Terre-Neuve, y compris la rivière Conne, ont été touchées par des conditions de sécheresse intense. L'incidence élevée d'atrésie observée dans la rivière Conne en 1987 pourrait être attribuable aux bas niveaux d'eau continus et à la température élevée de l'eau. On a observé une augmentation de l'atrésie dans la rivière Little Salmonier en 1985 (16,9 p. 100), mais ce résultat pourrait être imputable à l'échantillonnage restreint de l'étude alors menée. Les résultats de diverses études montrent que le degré d'atrésie peut varier en fonction des conditions environnementales. Les valeurs de fécondité établies à partir des ovaires recueillis dans le cadre de la pêche récréative doivent donc être considérées comme des données potentielles. Leur utilisation pourrait donner lieu à des sous-estimations des besoins en géniteurs pour assurer la conservation et des surestimations de la ponte.

Introduction

Atresia is a degenerative process which can occur at any stage of oocyte development and differentiation, resulting in a loss of oocytes from the ovary and ultimately affecting the number of mature eggs available for spawning (Guraya 1986; Tyler and Sumpter 1996). For salmonids, atresia has been reported to occur in Atlantic salmon, *Salmo salar* L., (Melnikova 1964; Prouzet *et al.* 1984), brook trout, *Salvelinus fontinalis* (Mitchill), (Vladykov 1956; Tyler and Sumpter 1996), and rainbow trout, *Oncorhyhchus mykiss* (Walbaum), (Scott 1962; Tyler and Sumpter 1996).

Fecundity is an important parameter used in the calculation of Atlantic salmon conservation spawner requirements (O'Connell and Dempson 1995) and egg depositions (e.g., O'Connell *et al.* MS 1996; Dempson and Furey MS 1996) for rivers in the Newfoundland Region. Fecundity is usually determined from ovaries collected in the recreational fishery, which occurs from mid-June to early September each year, with most of the catch typically being taken in July-early August. The possibility of atresia results in uncertainty in calculations of conservation spawner requirements and egg depositions using fecundity values derived from such ovaries.

In this paper, the extent of atresia is determined for small salmon (< 63 cm in fork length) in three rivers in Newfoundland that were involved in Atlantic salmon enhancement programs (Indian River, Exploits River, and Little Salmonier River) and for one river (Conne River) that provided broodstock for an aquaculture operation. Fecundity determined from ovaries collected from the recreational fishery in each river is compared to that derived by sampling broodstock during egg stripping procedures at incubation facilities in the fall. It is implied that a decrease in the number of eggs between summer and fall is due to atresia (Vladykov 1956; Scott 1962; Melnikova 1964; Prouzet *et al.* 1984). Change in fecundity as oocyte development progresses from early stages through to maturity is also examined.

Materials and Methods

Fig. 1 is a map showing the locations of the rivers studied. Indian and Exploits rivers are in Salmon Fishing Area (SFA) 4, Notre Dame Bay, Little Salmonier River is in SFA 9, St. Mary's Bay, and Conne River flows into Bay D'Espoir on the south coast (SFA 11).

Sampling in the recreational fishery was conducted throughout the adult run in each river. Broodstock was collected throughout the run for all rivers except Conne River where fish were taken from a staging pool in the lower river in September, after the run was over.

Eggs collected in the recreational fishery were stored in Gilson's fluid until ovarian tissue had broken down, after which time they were transferred to 10% formalin. Eggs were counted directly. At egg incubation facilities, eggs were counted directly following manual stripping, fertilization, and a water hardening period of approximately 3 hours. Each fish was then killed and retained eggs were counted and added to the number stripped to give the total number of eggs. Egg stripping occurred from mid-October to early November. All fish were measured for fork length (cm) and whole weight (kg).

Average egg diameter was based on 10 sets of measurements of the total length (measured to the nearest 0.01 mm with a Helios mechanical or a Mitutoyo Digimatic electronic caliper) of 10 randomly-selected eggs placed side by side in a V-notch polyethylene trough. In order to determine if there was a progressive loss of eggs as development advanced, fecundity was calculated for several increasing egg size groups (Vladykov 1956). These size groups (mm) were constructed according to the following limits: group 1 (< 2); group 2 (≥ 2 and < 3); group 3 (≥ 3 and < 4); group 4 (≥ 4 and < 5); group 5 (≥ 5 and < 6); group 6 (≥ 6 and < 7).

Individual regressions of number of eggs on fork length (both variables ln transformed) for ovaries collected in the summer typically displayed wide scatter, were not significant ($P > 0.05$) in some instances, and had low r^2 values. Also, there were wide differences in sample sizes. This precluded the use of a general linear model for comparisons between years and seasons using fecundity with length as a covariate, such as employed by Winters *et al.* (1993). Therefore, non-parametric comparisons [Wilcoxon two-sample test (Z)] were performed on individual values of fecundity (number of eggs per female, number of eggs per kg of body weight, and number of eggs per cm of body length) using the NPAR1WAY procedure of SAS (SAS Institute 1985). Mean number of eggs per kg or cm and associated standard deviations were estimated using the ratio estimator techniques of Cochran (1977).

Results

The relationship between fecundity and fork length for Indian River (Fig. 2) for the summers of 1984 and 1985 separately and for years combined were significant, but r^2 values were low and there was wide scatter. Corresponding plots for the fall were much tighter and r^2 values were considerably improved. Regressions for Exploits River (Fig. 3) for the summer period were not significant for 1985 and 1986 separately but the regression for years combined was significant. Regressions for the fall period improved in a manner similar to Indian River but with lower r^2 values. Regressions for summer versus fall for Conne River in 1987 behaved similarly (Fig. 4) and there is a suggestion that the same might be true for Little Salmonier River (Fig. 4), although sample sizes (N) for the latter river were comparatively very small (Table 1).

Mean weight, mean length, mean number of eggs per female, and sample sizes for all analyses are shown in Table 1. There were overall reductions in the numbers of eggs per female from summer to fall for Indian, Exploits, and Conne rivers. The greatest reduction occurred for Conne River while the least was for Indian River. The differences were significant for Conne and Exploits rivers (Table 2); differences for Indian River were not significant for individual years but for years combined the difference was close to significance at the 5% level of confidence. In contrast, there was an increase in the number of eggs per female from summer to fall for Little Salmonier River. There was no significant difference between years in number of eggs per female for either summer or fall for Indian

River (Table 3). There was a significant difference between years for fall but not for summer for Exploits River.

There was an increase in fecundity expressed in terms of body weight from summer to fall for Indian River for both 1984 and 1985 while the reverse was true for fecundity in terms of body length (Table 4). The difference in terms of weight was significant for 1985 and years combined but not for 1984 (Table 2). The difference in terms of length was significant only for years combined. There were significant reductions in fecundity in terms of both weight and length for Exploits (years separately and combined) and Conne rivers, the magnitude of which was greatest for length. There was an increase (not significant) in fecundity for both the weight and length designations for Little Salmonier River. There was a significant difference between years for fecundity expressed as weight for summer for Indian River but not for fall; there was no significant difference between years in terms of length for either season (Table 3). The only significant difference between years for Exploits River was in terms of length for summer.

The relationship between fecundity and egg size group for Indian, Exploits, Little Salmonier, and Conne rivers is shown in Table 5 and Figs. 5-7. Size groups 2-4 were poorly represented on an individual river and yearly basis, being absent entirely from Conne and Little Salmonier rivers. Size groups 4-6 were encountered only in the fall. There was an increase in fecundity expressed in terms of weight for size groups 4 and 5 compared to smaller size groups for Indian River, which is consistent with the summer versus fall comparison presented above. Information on the relationship between fecundity and egg size has been collected for several other rivers in Newfoundland (Table 6). These data were also obtained from the recreational fishery and are for all years combined for a given river. Except for a single specimen in size group 3 for Gander River and 1 specimen in each of size groups 3 and 4 for Biscay Bay River, size group 2 was the highest encountered. Size groups 3 and 4 for Biscay Bay River were for mortalities sampled in the fall. Overall, there was a decrease in fecundity from size group 1 to size group 2 for all rivers both in terms of weight and length. When data for all rivers and years are combined (Table 6 and Fig. 7), there is a suggestion that the reduction in number of eggs in terms of length occured mainly between size groups 1 and 2 and remained relatively stable after that. The situation in terms of weight was more obscure.

Discussion

There was a reduction in fecundity from summer to fall in terms of length for all rivers except Little Salmonier River, which showed an increase. The result for Little Salmonier River might be due to the small numbers of fish in both summer and fall samples and may not be a real effect. The increase in fecundity for Indian River in terms of weight appears to be a function of the magnitude of total body weight loss between summer and fall, compared to the other rivers. Melnokova (1964) observed a similar result for Atlantic salmon in the Varguza River, Russia. The decrease in weight was attributed to the lack of feeding and diversion of energy into the gonads. This author cautioned against comparing fecundity in terms of body weight for specimens collected at different times of the year. Length was a more constant value for Varguza River which also applies to the present study.

The onset and regulation of atresia has been attributed to adverse environmental conditions resulting in stress (Guraya 1986; Tyler and Sumpter 1996). Among the factors considered to influence atresia are food availability, captivity, crowding, and temperature. It is not anticipated that food availability is a factor for pre-spawning Atlantic salmon in the present study, since feeding ceases shortly after entery into freshwater. However, specimens sampled in the fall for Indian River, Exploits River, and Little Salmonier River were held in captivity from the time they entered freshwater until stripping. Broodstock was collected throughout the summer. The goal of broodstock collection and holding techniques employed in Newfoundland is to minimize stress and maximize egg production, controlling such factors as temperature (this also applies to the transport of fish by tank truck from collection sites to holding sites), flow rate, and crowding. In the case of Indian and Exploits rivers, broodstock was held in pools in controlled flow spawning channels (O'Connell *et al.* (1983). Fish from Little Salmonier River were held in a cage in a lake just upstream from the site of collection and transferred to a controlled flow spawning channel by helicopter in September. Typically, mortality during transport and at holding facilities in these rivers was very low or none at all, an indication that stress was not a significant concern. In Conne River, broodstock were collected from a natural staging pool in the river in September and transported by helicopter to the brood-holding facility. Like most rivers in Newfoundland in 1987, Conne River was affected by the worst drought conditions in 40 years (O'Connell *et al.* MS 1988). At the pool from which broodstock was collected, fish were delayed in their upstream migration from mid-summer to early fall due to low water levels, and endured prolonged periods of abnormally high water temperatures. This could help explain the high level of atresia recorded for Conne River compared to the other rivers, where more or less normal environmental conditions prevailed during the years studied. The fish sampled in the recreational fishery in Conne River in the summer of 1987 were not exposed to drought conditions since they were caught soon after entering the river from the sea. The total number of eggs stripped from broodstock at the Exploits River incubation facility in 1987 was lower than taken from a comparable number of fish in previous years (C. E. Bourgeois, personal communication).

Upon entering freshwater, Atlantic salmon have a great number of oocytes that do not develop to maturation, since the number is greater than can be supported by the metabolic reserves of the fish (Melnikova 1964; Prouzet *et al.* 1984). Similar comments have been made in relation to brook trout (Vladykov 1956) and rainbow trout (Scott 1962). This could account in part for the wide scatter and low r^2 values characteristic of fecundity-length relationships for summer fish compared to the much tighter fits exhibited by relationships for fall fish.

Atresia can occur throughout successive stages of oocyte development, right up to ovulation (Tyler and Sumpter 1996). Vladykov (1956) reported that atresia was at its height early in the season for brook trout. A goal of examining change in fecundity with increase in egg size in the present study was to see if there was a size during the summer, using samples collected from the recreational fishery, when fecundity was close to that observed in the fall when eggs were at full maturation.

Because of the relative scarcity of intermediate egg size groups in summer samples, it is difficult to determine the form of any decline in fecundity with egg size. There was an overall tendency for egg sizes of 2-3 mm to be encoutered from late July through August, a time when only 10-20% of the total season angling catch is normally taken. The low number of intermediate size groups appears to be related to the fact that fish were angled for the most part right after entry into freshwater when very little oocyte development was in progress. A greater intensity of sampling in August could yield more of the larger egg sizes. The decline observed for fecundity in terms of length when all data for all rivers were pooled is consistent with the observation for brook trout reported by Vladykov (1956).

The present study shows that atresia can occur in small salmon in Newfoundland, and can vary depending on environmental conditions, as inferred by the results for Conne River, which might be an extreme case. However, the level of atresia recorded for Conne River is similar to that reported for the Elorn River in France (Prouzet *et al.* 1984). A confounding element is the fact that broodstock was captured shortly after entry into freshwater and held in captivity until stripping. The fact that fish for Indian and Exploits rivers were held under conditions designed to minimize stress suggests that atresia might be more severe under natural conditions. The artificial holding period for Conne River was much shorter than for the other rivers. Fecundity values based on ovaries collected in the recreational fishery have to be regarded as potential and their use could result in underestimates of conservation spawner requirements and overestimates of egg depositions.

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Table 1. Mean length, mean whole weight, and mean number of eggs per female in summer and fall for all rivers. N = no. of specimens.

River	Year	N		Mean Weight (SD) kg		Mean Length (SD) cm		Mean no. of eggs/female (SD)		
		Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	% change
Indian River	1984	78	9	1.44 (0.38)	1.15 (0.37)	49.5 (3.63)	49.8 (4.51)	2604 (830.5)	2325 (764.7)	-10.7
	1985	154	10	1.56 (0.21)	1.22 (0.22)	50.1 (2.10)	49.0 (2.91)	2663 (689.2)	2442 (620.9)	-8.3
	1984 & 85 combined	232	19	1.52 (0.28)	1.19 (0.29)	50.3 (2.77)	49.4 (3.67)	2643 (738.4)	2386 (675.5)	-9.7
Exploits River	1985	145	22	1.48 (0.28)	1.30 (0.23)	53.4 (3.07)	51.3 (2.45)	2802 (688.7)	2246 (558.4)	-19.8
	1986	39	20	1.44 (0.27)	1.43 (0.26)	52.8 (4.08)	52.8 (3.08)	2985 (858.6)	2559 (532.5)	-14.3
	1985 & 86 combined	184	42	1.47 (0.28)	1.36 (0.25)	53.3 (3.31)	52.0 (2.82)	2841 (729.3)	2395 (562.3)	-15.7
Little Salmonier River	1985	13	5	2.01 (0.33)	2.11 (0.25)	55.6 (3.12)	57.3 (2.91)	2903 (1069.7)	3497(185.1)	+20.5
Conne River	1987	136	30	1.45 (0.25)	1.27 (0.17)	51.1 (2.36)	50.7 (2.37)	3424 (635.2)	2430 (402.8)	-29.0

Table 2. Results of statistical comparisons of fecundity in terms of weight and length between summer and fall for each river.

River	Year	Fecundity					
		Eggs/female		Eggs/kg		Eggs/cm	
		Z	P	Z	P	Z	P
Indian River	1984	-1.44	0.1502	1.15	0.2502	-1.67	0.0958
	1985	-1.16	0.2441	2.02	0.0437	-0.89	0.3735
	1984 & 85 combined	-1.91	0.0566	2.50	0.0125	-1.93	0.0535
Exploits River	1985	-3.99	0.0001	-2.62	0.0087	-3.87	0.0001
	1986	-2.43	0.0153	-2.41	0.0160	-2.60	0.0093
	1985 & 86 combined	-4.23	0.0001	-3.27	0.0011	-4.38	0.0000
Little Salmonier River	1985	1.08	0.2782	0.59	0.5542	0.39	0.6934
Conne River	1987	-6.95	0.0001	-5.52	0.0000	-7.14	0.0000

Table 3. Results of statistical comparisons of fecundity in terms of weight and length between years for summer and fall for Indian River and Exploits River.

River	Season	Year	Fecundity					
			Eggs/female		Eggs/kg		Eggs/cm	
			Z	P	Z	P	Z	P
Indian River	Summer	1984 vs. 1985	-1.16	0.2437	1.95	0.0510	-0.29	0.7727
	Fall	1984 vs. 1985	-0.61	0.5403	-0.05	0.9674	-0.86	0.3913
Exploits River	Summer	1985 vs. 1986	1.55	0.1213	1.64	0.1019	1.92	0.0544
	Fall	1985 vs. 1986	2.03	0.0426	0.67	0.5045	1.73	0.0845

Table 4. Fecundity in terms of weight and length in summer and fall for each river and percent change in fecundity from summer to fall.

River	Year	Fecundity					
		Mean no. of eggs/kg (SD)			Mean no. of eggs/cm (SD)		
		Summer	Fall	% change	Summer	Fall	% change
Indian River	1984	1808 (61.1)	2019 (50.2)	+11.7	52.6 (1.71)	46.7 (3.85)	-11.2
	1985	1708 (36.1)	1998 (106.9	+17.0	52.5 (1.05)	49.9 (3.48)	-5.0
	1984 & 85 combined	1740 (31.4)	2008 (60.6)	+15.4	52.7 (0.90)	48.3 (2.53)	-8.2
Exploits River	1985	1899 (42.6)	1731 (54.9)	-8.9	52.5 (1.06)	43.7 (2.07)	-16.6
	1986	2074 (98.2)	1787 (60.0)	-13.8	56.5 (2.47)	48.5 (1.87)	-14.2
	1985 & 86 combined	1935 (39.7)	1759 (40.3)	-9.1	53.3 (0.99)	46 (1.43)	-13.7
Little Salmonier River	1985	1442 (174.6	1659 (66.7)	+15.0	52.2 (5.62)	61.0 (1.05)	+16.9
Conne River	1987	2364 (50.1)	1906 (36.6)	-19.4	67.0 (1.06)	47.9 (1.21)	-28.5

Table 5. Fecundity in terms of weight and length in relation to egg size for Indian River, Exploits River, Little Salmonier River, and Conne River. Number of specimens in parentheses.

River	Year	Egg size group (mm)											
		1		2		3		4		5		6	
		Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm
Indian River	1984	1885(73)	54.5(73)	687(2)	25.1(2)	873(3)	25.0(3)	1907(3)	36.9(3)	2059(6)	51.1(6)		
	1985	1736(145)	53.5(145)	1231(9)	36.5(9)			2592(1)	69.9(1)	1923(9)	47.6(9)		
	1984 & 85 combined	1784(218)	53.9(218)	1111(11)	34.4(11)	873(3)	25.0(3)	2135(4)	45.6(4)	1980(15)	49.0(15)		
Exploits River	1985	1934(137)	53.3(137)	1425(7)	41.2(7)	564(1)	14.2(1)			1731(22)	43.7(22)		
	1986	2074(39)	56.5(39)							1809(19)	49.0(19)	1388(1)	38.1(1)
	1985 & 86 combined	1965(176)	54.0(176)	1425(7)	41.2(7)	564(1)	14.2(1)			1769(41)	46.2(41)	1388(1)	38.1(1)
Little Salmonier River	1985	1490(12)	54.7(12)							1659(5)	61.0(5)		
Conne River	1987	2363(136)	67.0(136)							1915(29)	47.7(29)	1712(1)	53.2(1)

Table 6. Fecundity in terms of weight and length in relation to egg size for Gander River, Middle Brook, Terra Nova River, Biscay Bay River, Northeast River, Placentia, and for all rivers and years combined. Number of specimens in parentheses.

River	Egg size group (mm)											
	1		2		3		4		5		6	
	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm	Eggs/kg	Eggs/cm
Gander River	1798(409)	57.1(409)	1446(59)	51.1(59)	873(1)	26.4(1)						
Middle Brook	2014(263)	60.8(263)	1423(15)	44.6(15)								
Terra Nova River	1859(70)	57.7(70)	1285(14)	40.1(14)								
Biscay Bay River	2100(332)	67.3(332)	1709(40)	53.3(40)			1415(1)	47.7(1)	1840(1)	44.4(1)		
Northeast River, Placentia	2365(182)	70.6(182)	1852(4)	63.3(4)								
All rivers and years combined*	2002(2120)	60.4(2120)	1484(150)	48.7(150)	861(6)	30.4(6)	1920(5)	46.1(5)	1836(91)	48.0(91)	1563(2)	45.8(2)

* Also includes data presented in Table 5 and additional years for Conne River.

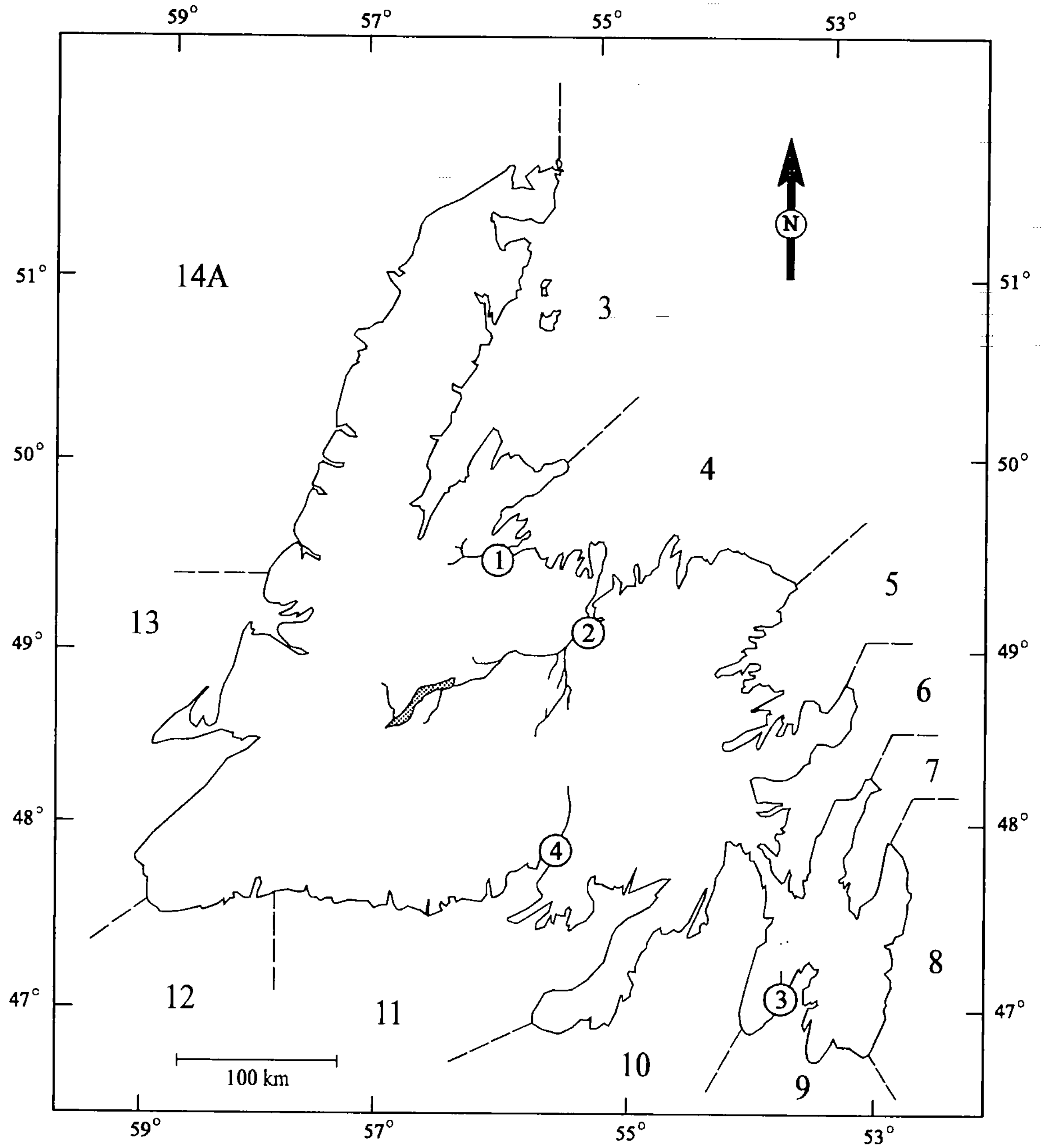

Fig 1. Map showing the Salmon Fishing Areas of Newfoundland and the location of the four rivers mentioned in the text: (1) Indian River; (2) Exploits River; (3) Little Salmonier River; (4) Conne River.

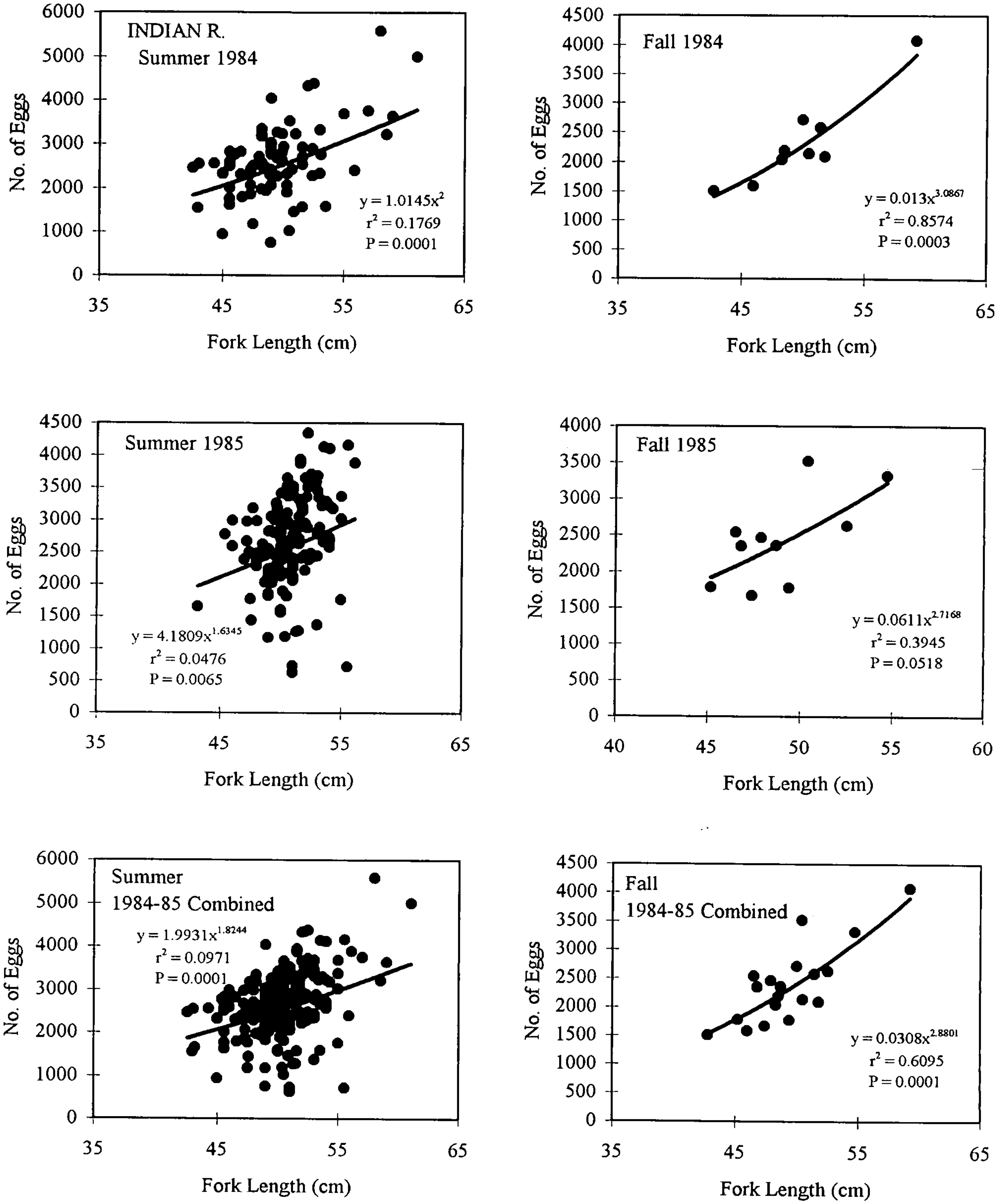

Fig. 2. Fecundity-length relationships for summer and fall of 1984 and 1985 for Indian River.

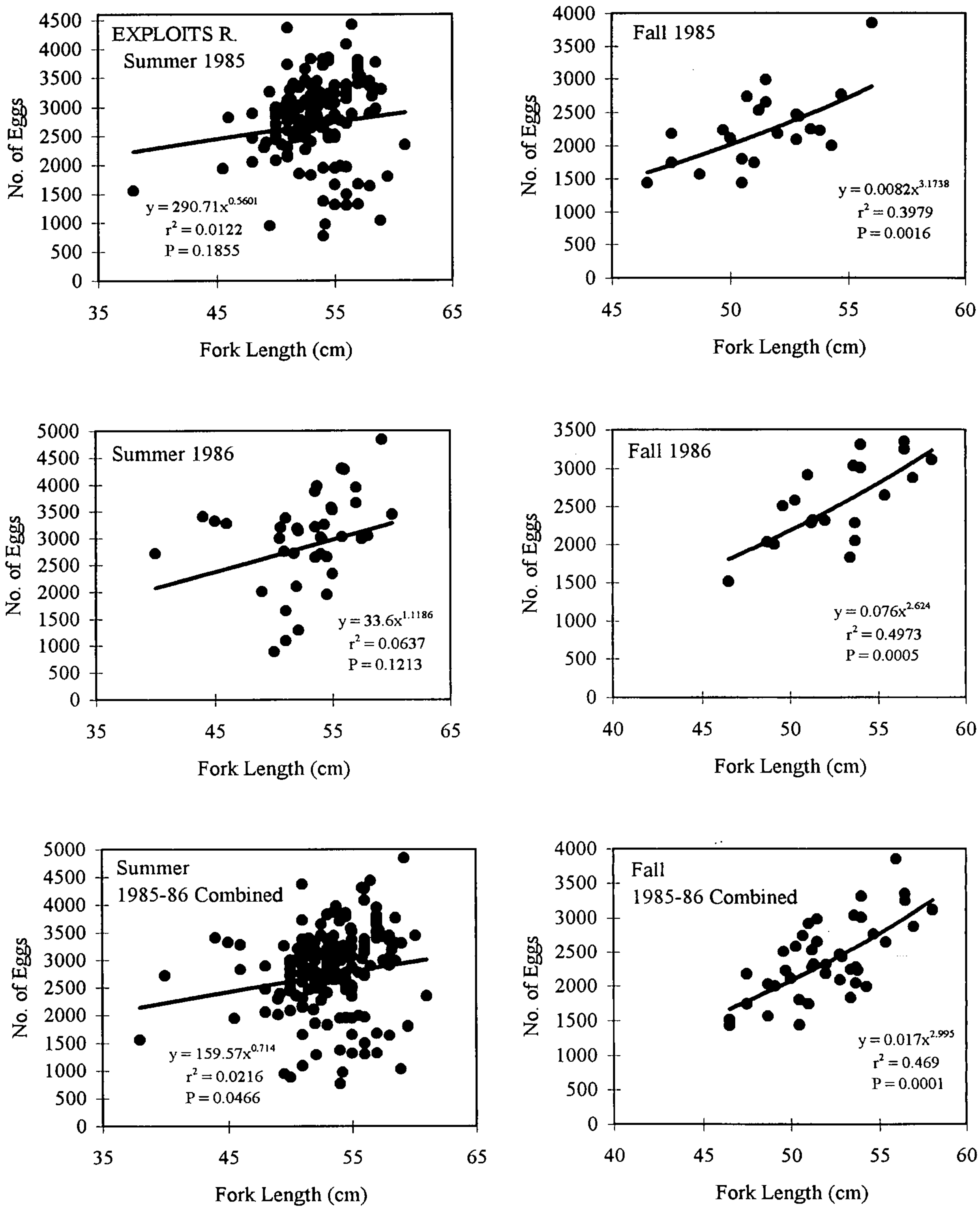

Fig. 3. Fecundity-length relationships for summer and fall of 1985 and 1986 for Exploits River.

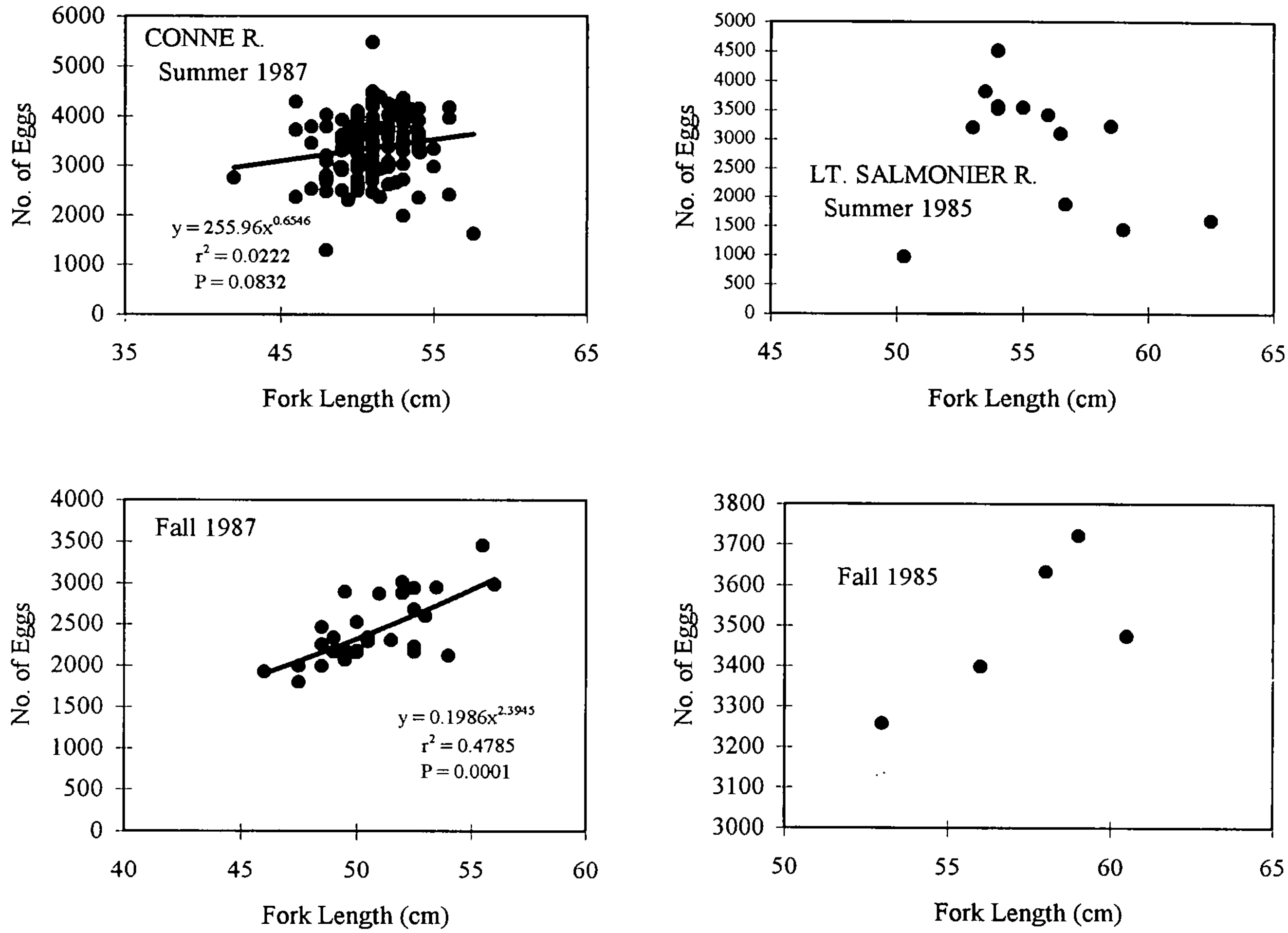

Fig. 4. Fecundity-length relationships for summer and fall for Little Salmonier River (1985) and Conne River (1987).

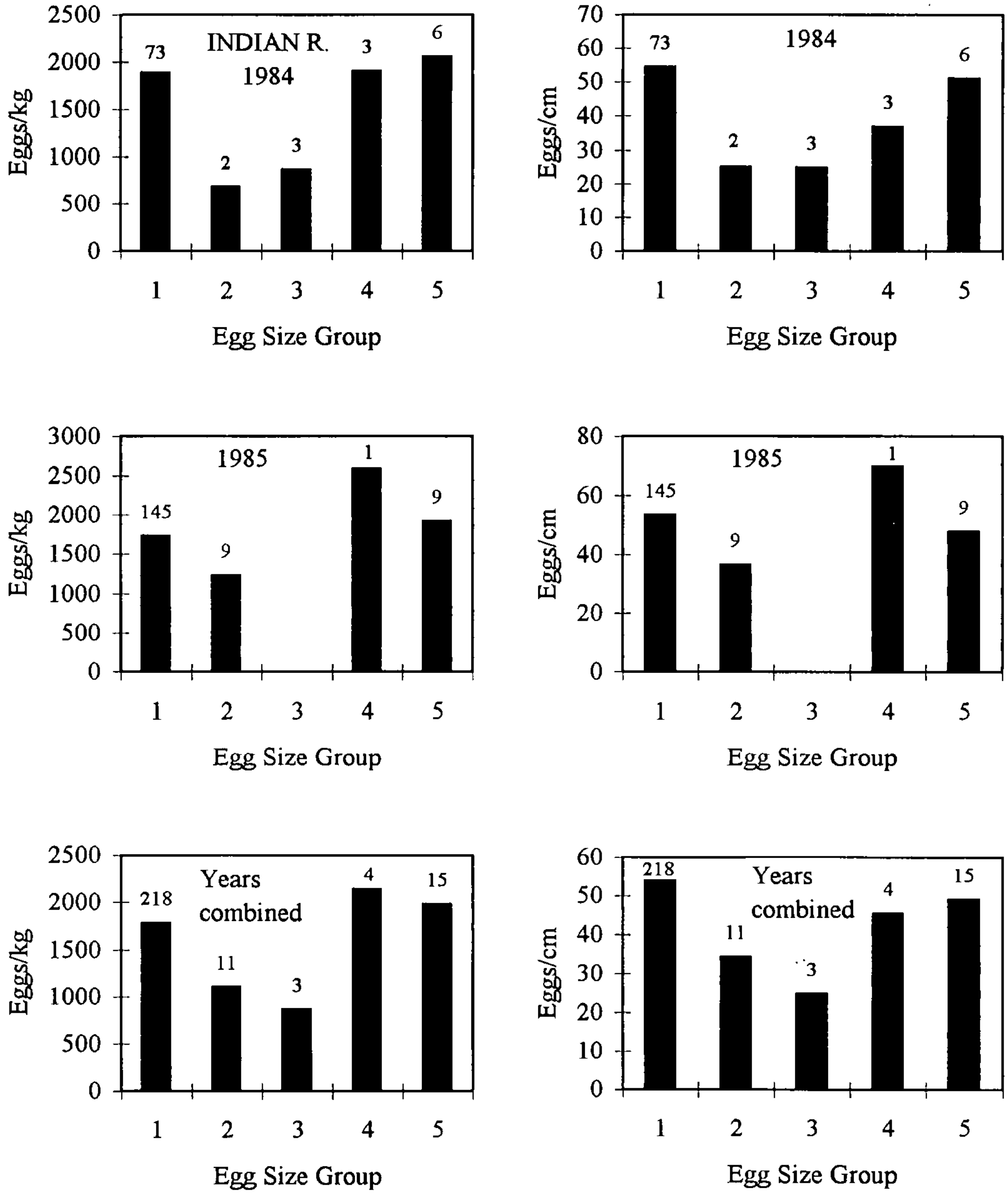

Fig. 5. Fecundity in terms of weight and length in relation to egg size for Indian River.

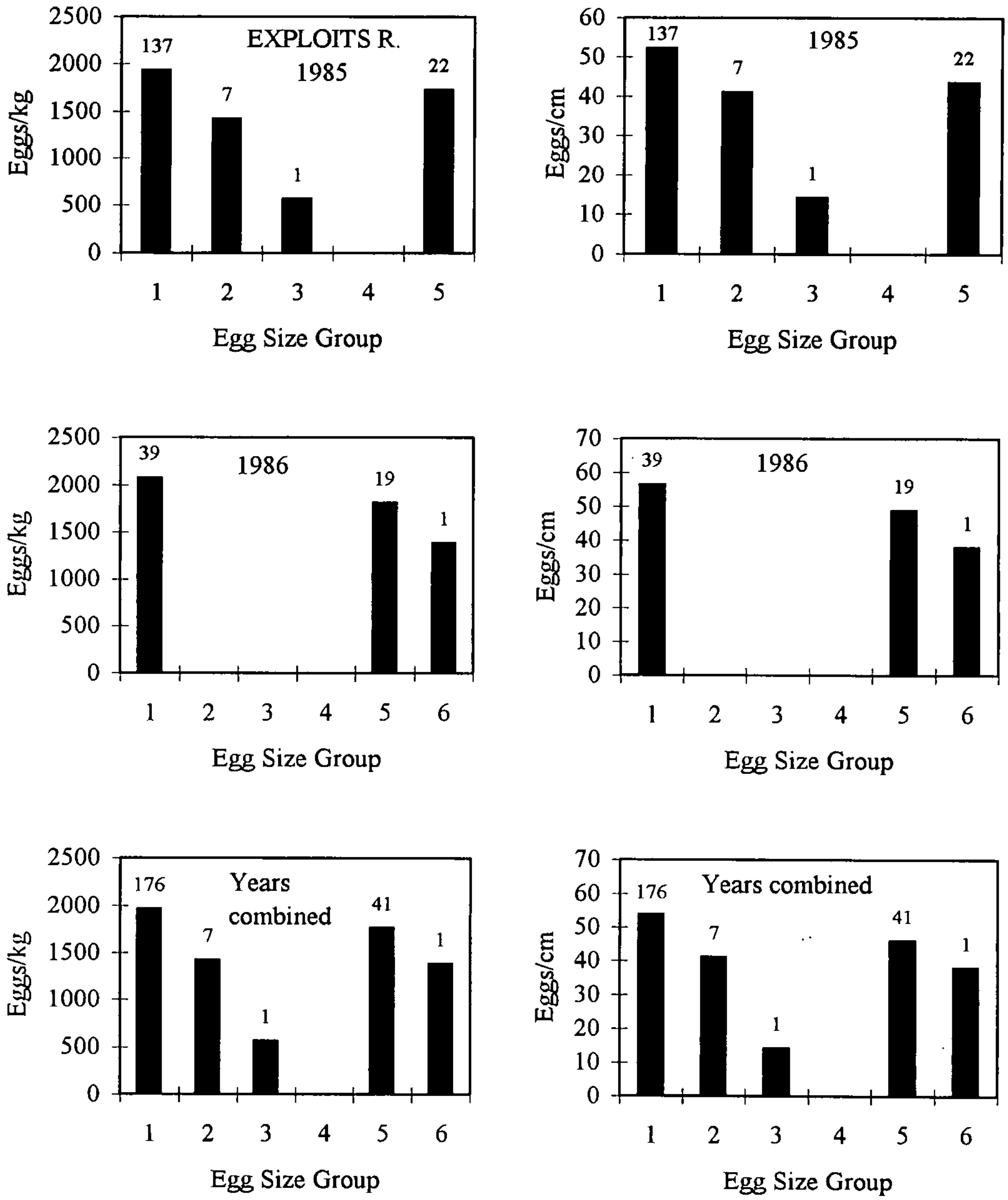

Fig. 6. Fecundity in terms of weight and length in relation to egg size for Exploits River.

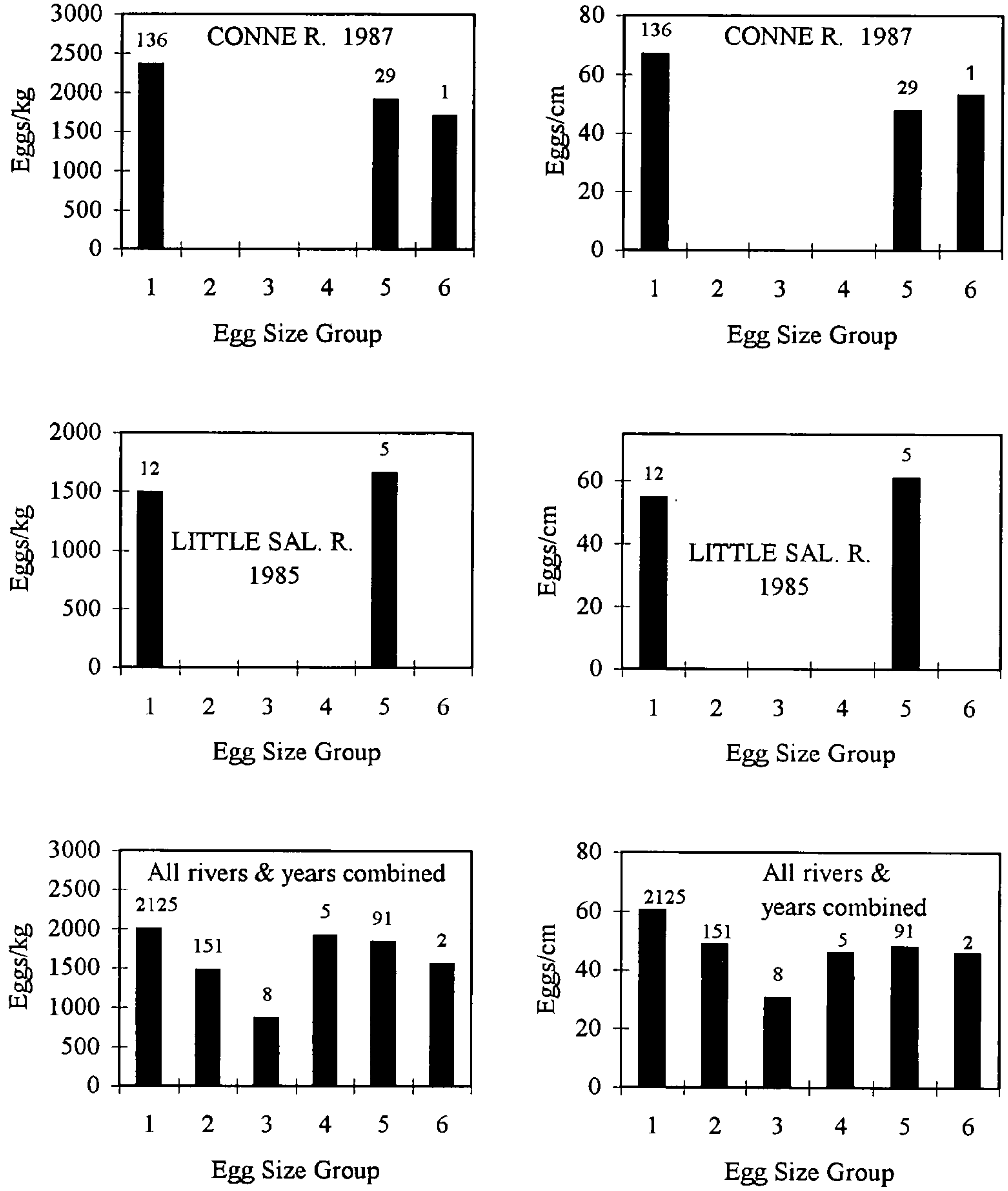

Fig. 7. Fecundity in terms of weight and length for Little Salmonier River, Conne River and for all rivers and years combined (see text and Table 6).