

Growth, fecundity, and egg size of least brook lamprey, *Lampetra aepyptera*

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Synopsis

Eight geographically-diverse (33° 11' N to 39° 14' N) populations of least brook lamprey varied significantly in density of larvae and mean length of metamorphosing and adult lampreys (101–152 mm). Absolute fecundity (503–5900 eggs) did not change significantly with stage of post-larval development, suggesting little post-metamorphic atresia; egg dry weight increased to stage 6, the penultimate stage of metamorphosis. Absolute fecundity increased with the cubic power of total length. Relative fecundity (250–1124 eggs per gram total body weight) decreased significantly with increasing length within two streams. Relative fecundity, adjusted to a common length, increased with mean length of the population. Conversely, mean egg dry weight (0.09–0.24 mg, stages 6–8) increased with maternal length within three streams, and decreased with length among streams. In populations where spawning occurs at a small body size, females produce comparatively fewer but larger eggs. Large eggs may be required to counter the effects of an unproductive environment and the accompanying reduction in relative fecundity is compensatory. No relationship was evident between latitude, annual thermal units, or density and relative fecundity or egg size. Mean length of a population was also unrelated to these environmental factors.

Introduction

Interpopulational and interannual variations in fecundity and egg size have been reported for a number of teleost species (Messieh 1976, Velikanov 1986, Tanasichuk & Ware 1987, Volodin 1988). Such intraspecific differences in egg number and size have been attributed to fluctuations in temperature (Tanasichuk & Ware 1987), latitude (Paulson & Smith 1975), and food availability (Wootton 1979).

Population density has also been cited as a factor regulating fecundity, thus establishing an effective negative feedback mechanism for regulating population numbers (Bagenal 1973). Lett et al. (1975), for example, found the number of eggs produced

by Atlantic cod, *Gadus morhua*, to decrease with increasing stock size. These differences in fecundity may be related to corresponding changes in body size (Lett et al. 1975, Bailey & Almatar 1989). Growth is often reduced at high densities (e.g. Jones 1976, Trzebiatowski et al. 1981) and absolute fecundity in many species is positively correlated with female size (Bagenal 1966, 1973). Relative fecundity (eggs per gram total body weight), however, has also been found to decrease at high densities (Kipling & Frost 1969, Craig & Kipling 1983), suggesting that a compensatory effect of density on reproductive effort transcends a simple effect on maternal size.

In lampreys, studies to date have focused on differences in relative fecundity among species

(Hardisty 1964, 1971), or intraspecific variations which are size-related (Kott 1971, Beamish & Thomas 1983). The present study investigates interpopulational differences in fecundity. We examine the effects of population density, latitude, annual thermal units, and female body size on egg size and number among populations of the non-parasitic least brook lamprey, *Lampetra aepyptera*.

Materials and methods

Metamorphosing and adult *L. aepyptera* were electrofished from the substrate of eight geographically-diverse streams of the eastern United States (Table 1). Relative density was estimated from the number of larvae collected per m² of substrate (Docker et al. unpublished data), and ranked on a scale of 1 (lowest) to 5 (highest) to allow for the inclusion of streams where sampling area was imprecisely known. Annual thermal units, expressed as °C days, were estimated for these or nearby

streams (US Department of Commerce, National Technical Information Service; Water resources data for Alabama, Delaware, Kentucky, Maryland and Tennessee water year 1987).

After capture, lampreys were killed by an overdose of methane tricaine sulfonate (> 100 mg l⁻¹). In 1988, total length (± 1 mm) of each freshly killed lamprey and total body weight (± 0.01 g) of a subsample were measured prior to freezing. Thawed length (± 1 mm) and weight (± 0.001 g) were subsequently measured. The relationship between fresh and thawed length is described by the regression (± 95% confidence limits):

$$L_F = 0.87 \pm 0.04 L_T + 23.10 \pm 8.92$$

(n = 161, r = 0.957, p < 0.001),

where L_F is fresh length and L_T is thawed length, both in mm. Similarly,

$$W_F = 0.88 \pm 0.11 W_T + 0.87 \pm 1.08$$

(n = 74, r = 0.878, p < 0.001),

Table 1. Sampling sites for metamorphosing and adult *Lampetra aepyptera*. Density was estimated from the number of larvae collected per m² of substrate (Docker et al. unpublished data), and ranked as follows: 1 = fewer than 0.01 larvae m⁻²; 2 = 0.01–0.05; 3 = 0.05–0.10; 4 = 0.10–0.30; 5 = 0.30–0.50 larvae m⁻².

Stream	Date	No. females	Latitude and longitude	Annual thermal units (°C days)	Density	
					larvae m ⁻²	ranking
Chapel Branch, DE	22.2.1980	5	38° 38'–38° 40' N 75° 39' E	5480	–	4*
Blackwater Creek, DE	2.2.1980	5	38° 25' N 75° 40' E	5480	–	**
Unicorn Branch, MD	15.12.1988	5	39° 13'–39° 15' N 75° 50'–75° 51' E	6275	0.044	2
Garey Mill Pond Branch, DE	15.12.1988	10	38° 56' N 75° 43'–75° 46' E	5088	0.078	3
Jay Creek, AL	2.2.1988	13	33° 14' N 87° 26' E	5850	0.148	4
Cane Creek, TN	30.1.1988	9	36° 03'–36° 10' N 85° 31'–85° 37' E	5012	0.462	5
Harid Creek, AL	13.10.1988	5	33° 11' N	5850	0.072	3
	2.2.1988	9	87° 39'–87° 41' E			
Little Whippoorwill Creek, KY	13.10.1988	14	36° 44'–36° 46' N 86° 50'–86° 53' E	5775	0.003	1

* qualitative estimate only; sampling area imprecisely known.

** number of larvae and area unknown.

where W_F and W_T are fresh and thawed weight, respectively, both in g.

Lampreys collected in 1980 were preserved in 5% formalin. Conversion formulae for preserved-to-fresh length and weight were not available for *L. aepyptera* adults. Fresh length and weight of adults were predicted from the following regressions, calculated for large *L. aepyptera* larvae preserved to constant length and weight (7 days):

$$L_F = 1.12 \pm 0.09 L_P - 9.73 \pm 4.04$$

$$(n = 15, r = 0.992, p < 0.001),$$

where L_F and L_P are fresh and preserved length (mm), respectively, and:

$$W_F = 0.82 \pm 0.27 W_P + 0.29 \pm 1.06$$

$$(n = 15, r = 0.873, p < 0.001),$$

where W_F and W_P are fresh and preserved weight (g). Predicted fresh length estimated in this manner varied by less than 0.5 mm, or 0.6%, from length predicted according to a relationship determined for 35 mature adult southern brook lamprey, *Ichthyomyzon gagei* (Beamish 1982).

Stages of metamorphosis (stages 1–7) and a stage for the adult interval (stage 8; stage 9 represents spent adults) were assigned according to criteria described for the related *Lampetra planeri* (Bird & Potter 1979). Sex was determined by visual inspection of the gonad under a dissecting microscope. After removal from the body cavity, the ovary was blotted to remove excess moisture, weighed to the nearest mg, and dried at 60°C (Hislop 1988) to constant weight. Fecundity was determined by counting, under a dissecting microscope, all eggs within the gonad. Mean egg dry weight for each individual was approximated as ovary dry weight divided by total egg number. Preservation in 5% formalin, relative to freezing, was found to have no effect on tissue protein or lipid levels (Beamish unpublished data), and presumably little effect on tissue dry weight.

While metamorphosis has not been described for *L. aepyptera*, some reduction in body size during the post-larval, nontrophic period has been reported in *I. gagei* (Beamish 1982). Assuming the timing

of metamorphosis to be similar in the two species (Beamish unpublished data), weight of least brook lampreys captured in October was adjusted according to the relationship described by Beamish (1982) to correspond to those collected in February. Length of metamorphosing *I. gagei* changed little prior to February (Beamish 1982).

Total length, rather than body weight, is used in this study as the measure of size to relate to fecundity. Body weight is presumably affected by egg number, and the ovary-free weight prior to preservation was not obtained. Further, weight corrections for stage of development did not take into account the disparate changes in somatic and ovarian weight during the months prior to spawning (Beamish 1982).

Statistical procedures applied included one-way ANOVA, Duncan's new multiple range test, simple linear regression, and analysis of covariance (Steel & Torrie 1980).

Results

Length and weight of the post-larval lampreys, mean egg weight, and absolute and relative fecundity varied significantly among streams (one-way ANOVA, $p < 0.05$; Table 2). The two Harid Creek samples, differing in their time of collection and stage of development, demonstrated significant differences in egg size only. Mean fecundity was greater in October than in February, but the differences were not significant (Duncan's new multiple range test). Where population means are subsequently described, with the exception of egg size, the two Harid Creek samples are combined.

Absolute and relative fecundity

Absolute fecundity increased significantly with female size. Total number of eggs (F) was related to the cubic power of fresh length (L_F in mm), according to the regression ($\pm 95\%$ CL):

$$\log F = 3.46 \pm 0.55 \log L_F - 4.03 \pm 0.30$$

$$(n = 75, r = 0.824, p < 0.001).$$

Within individual populations, with the exception of Little Whippoorwill Creek, absolute fecundity similarly increased with total length. The logarithmic relationship was statistically significant, however, in only Garey Mill Pond Branch and Jay Creek.

Log relative fecundity within a population decreased with log length, significantly so in Jay and Little Whippoorwill Creeks (Fig. 1). Using analysis of covariance, with log length as the covariate, log relative fecundity differed significantly ($p < 0.05$) among populations. Log relative fecundity at the overall mean length of 133.3 mm (R_M , eggs g^{-1}), calculated according to the individual regressions for each stream, increased with log mean length of the population (L_M in mm):

$$\text{Log } R_M = 2.41 \pm 1.93 \log L_M - 2.38 \pm 4.07 \\ (n = 8, r = 0.780, p = 0.022).$$

Similarly, among individuals from all populations, the logarithmic relationship between relative fecundity and length was significantly positive (Fig. 1).

Egg weight and gonadosomatic index

Mean egg dry weight and ovarian weight as a per-

centage of body weight (gonadosomatic index), varied significantly with stage of development (one-way ANOVA, $p < 0.01$). Within a given stream, however, neither changed significantly after stage 6 of metamorphosis (Duncan's new multiple range test, $p > 0.05$; Fig. 2a, b).

Log mean egg dry weight of stage 6–8 lampreys increased with log length among females within a population (Fig. 3). Analysis of covariance, with log length as the covariate, indicated significant differences ($p < 0.05$) in log egg weight among streams. Log mean egg dry weight at the overall mean length (E_M in mg) decreased with log mean length of the population (L_M in mm):

$$\text{Log } E_M = -3.47 \pm 2.36 \log L_M + 6.44 \pm 4.92 \\ (n = 7, r = 0.861, p = 0.013).$$

The relationship between mean egg dry weight and body length among all females (stages 6–8) was also significantly negative (Fig. 3).

Gonadosomatic index of females from stages 6 to 8 did not vary significantly with length among individuals within a population ($p > 0.05$). Overall, gonadosomatic index decreased with length:

$$\text{GSI} = -0.09 \pm 0.06 L_F + 27.81 \pm 8.18 \\ (n = 56, r = -0.346, p = 0.009),$$

Table 2. Mean (\pm 95% confidence limits) size and stage of metamorphosing and adult *Lampetra aepyptera*, egg dry weight, and absolute and relative fecundity. Weights of metamorphosing lampreys collected in October were adjusted to correspond to those captured in February (see text).

Stream	Stage	Fresh		Egg	Fecundity	
		total length (mm)	weight (g)	dry weight (mg)	number of eggs	eggs g^{-1}
Chapel	7.8 \pm 0.5	101 \pm 8	1.7 \pm 0.4	0.19 \pm 0.04	681 \pm 152	395 \pm 53
Blackwater	6.0 \pm 0.0	108 \pm 14	2.0 \pm 0.4	0.24 \pm 0.05	691 \pm 121	360 \pm 63
Unicorn	6.0 \pm 1.1	113 \pm 20	2.9 \pm 0.4	0.14 \pm 0.04	997 \pm 377	344 \pm 66
Garey Mill	7.4 \pm 0.4	127 \pm 8	3.5 \pm 0.5	0.09 \pm 0.01	2265 \pm 239	641 \pm 50
Jay Creek	6.9 \pm 0.3	136 \pm 28	4.1 \pm 1.0	0.09 \pm 0.02	2240 \pm 387	563 \pm 140
Cane Creek	8.0 \pm 0.0	137 \pm 6	5.3 \pm 0.8	0.16 \pm 0.01	2485 \pm 436	476 \pm 77
Harid (Feb)	7.6 \pm 0.5*	143 \pm 9	4.8 \pm 0.7	0.11 \pm 0.02*	2220 \pm 312	473 \pm 92
Harid (Oct)	3.0 \pm 0.8*	144 \pm 9	4.9 \pm 0.9	0.01 \pm 0.00*	3340 \pm 1564	649 \pm 200
Little Whippoorwill	4.1 \pm 0.5	152 \pm 5	6.1 \pm 0.6	0.03 \pm 0.01	3721 \pm 841	641 \pm 174

* February and October values significantly different ($p < 0.05$).

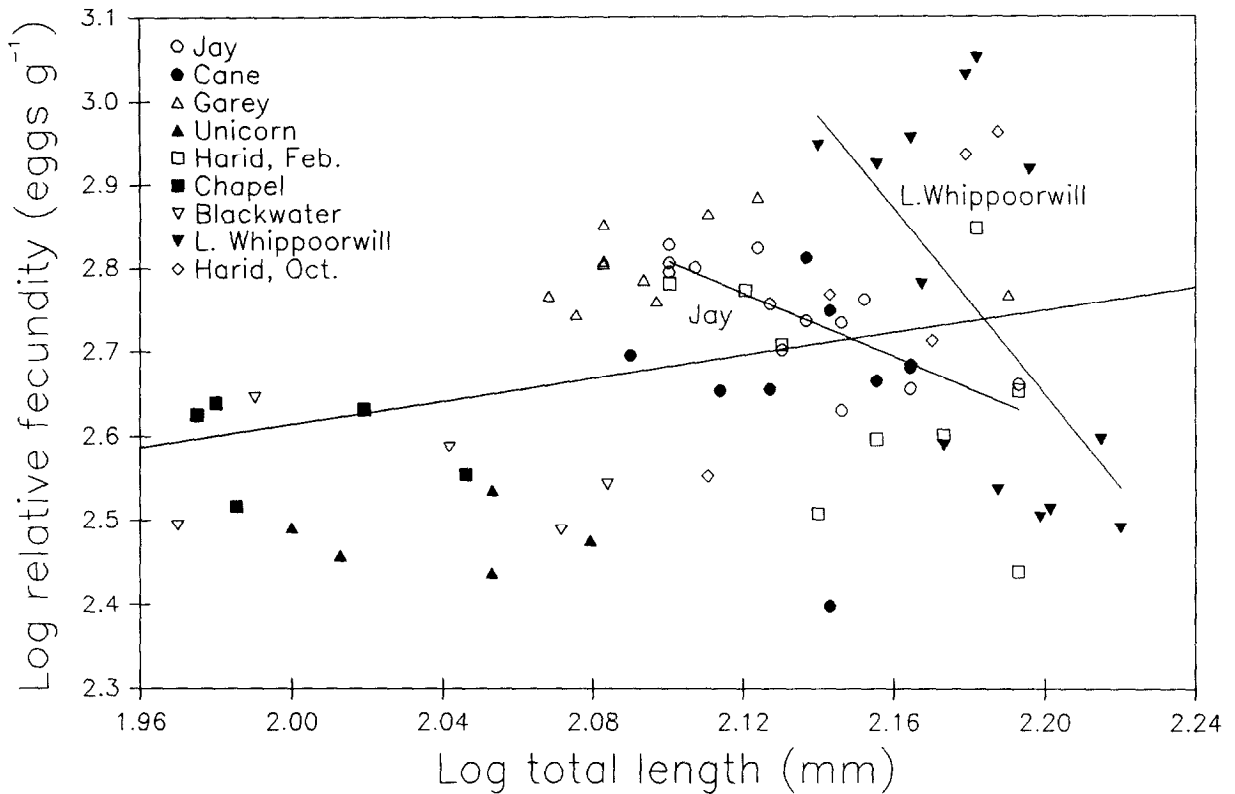


Fig. 1. Logarithmic relationship between relative fecundity (R , eggs g^{-1}) and fresh total length (L_F , mm). The regression for individuals from all streams ($\pm 95\%$ confidence limits) is: $\log R = 0.68 \pm 0.56 \log L_F + 1.25 \pm 0.30$ ($n = 75$, $r = 0.275$, $p = 0.016$). For individual populations, the significant regressions are: Jay Creek: $\log R = -1.89 \pm 0.97 \log L_F + 6.77 \pm 0.09$ ($n = 13$, $r = 0.792$, $p = 0.001$); L. Whippoorwill: $\log R = -5.93 \pm 4.72 \log L_F + 15.70 \pm 0.39$ ($n = 14$, $r = 0.621$, $p = 0.018$).

where GSI is thawed ovarian weight, as a percentage of thawed body weight, and L_F is fresh length (mm). Among populations, however, mean gonadosomatic index and mean length were not significantly related ($p = 0.068$).

Latitude, temperature, and density

Neither log relative fecundity nor log mean egg dry weight, calculated at a common length for each population as described above, were significantly related to density of larvae, latitude, or annual thermal units ($0.147 < p < 0.952$).

Log mean length did not vary significantly with either density, latitude, or annual thermal units ($0.064 < p < 0.985$).

Discussion

The positive relationship, observed in *L. aepyptera*, between absolute fecundity and female size is well-known in teleosts (e.g. Bagenal 1966, Docker et al. 1986, Hay & Brett 1988) and in other species of lampreys (Hardisty 1964, Kott 1971, Walsh & Burr 1981, McAllister et al. 1981). A similar cubic relationship has been noted in a number of teleosts (Bagenal 1966, DeMartini 1987, Herrera et al. 1988, Wright & Shoesmith 1988).

That fecundity at a given length was comparable between early metamorphosis and the late or adult stages suggests that there is little post-metamorphic atresia in *L. aepyptera*. Atresia occurring immediately after the onset of metamorphosis, however, cannot be ruled out in this study. Data for other non-parasitic lampreys both support (Beamish &

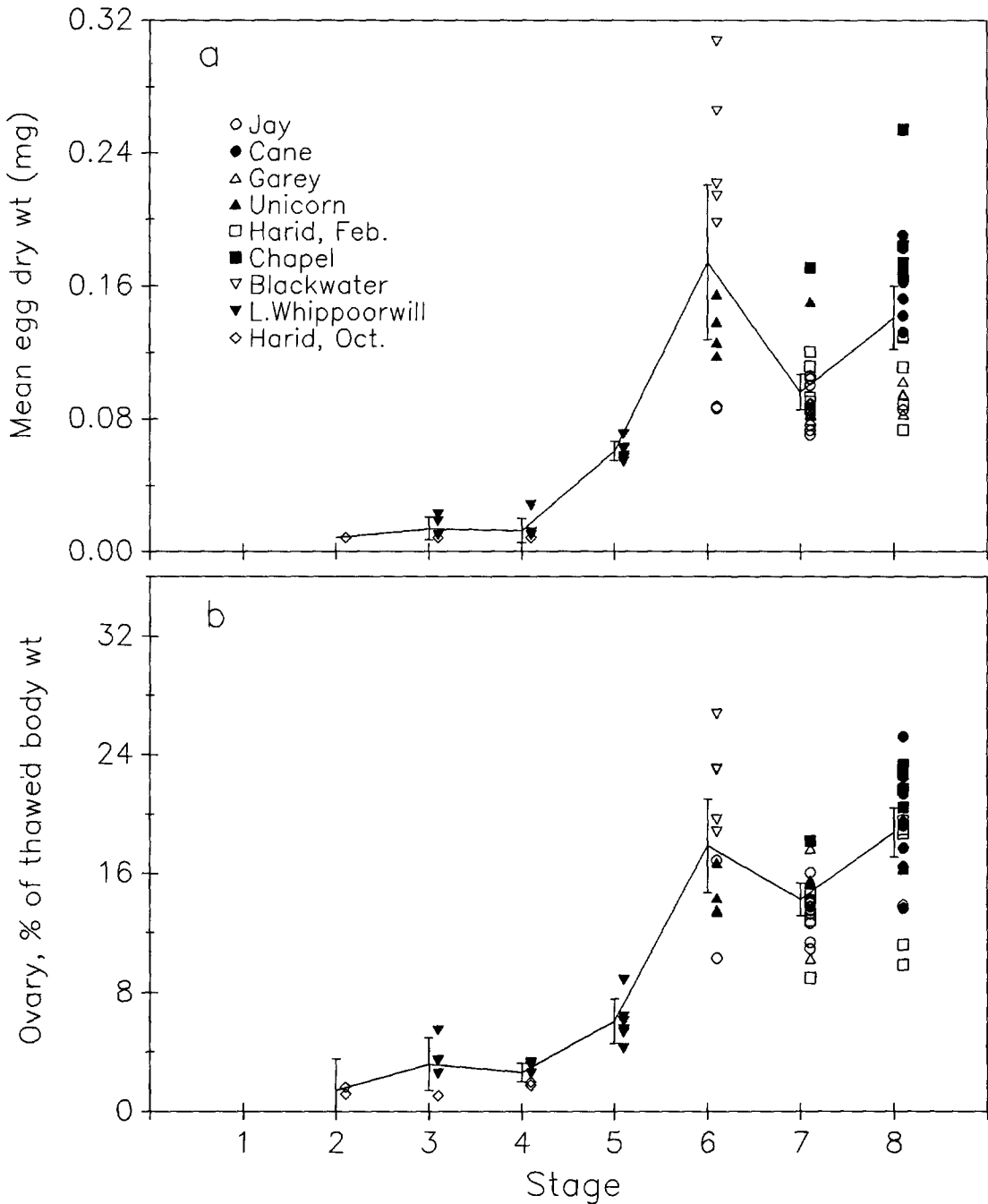


Fig. 2. Egg dry weight (a) and ovarian weight in percent of thawed body weight (b), in relation to stage of development from early metamorphosis (stage 2) to maturity (stage 8). Means \pm 95% confidence limits are indicated.

Thomas 1983) and counter (Hardisty 1964, Hughes & Potter 1969) this assumption of limited post-metamorphic atresia.

A minor adjustment of egg number following metamorphosis would imply that fecundity, as ob-

served in the present study, would be little affected by density or temperature at this time. Craig & Kipling (1983) and Tanasichuk & Ware (1987), respectively, found relative fecundity of Northern pike, *Esox lucius*, and Pacific herring, *Clupea ha-*

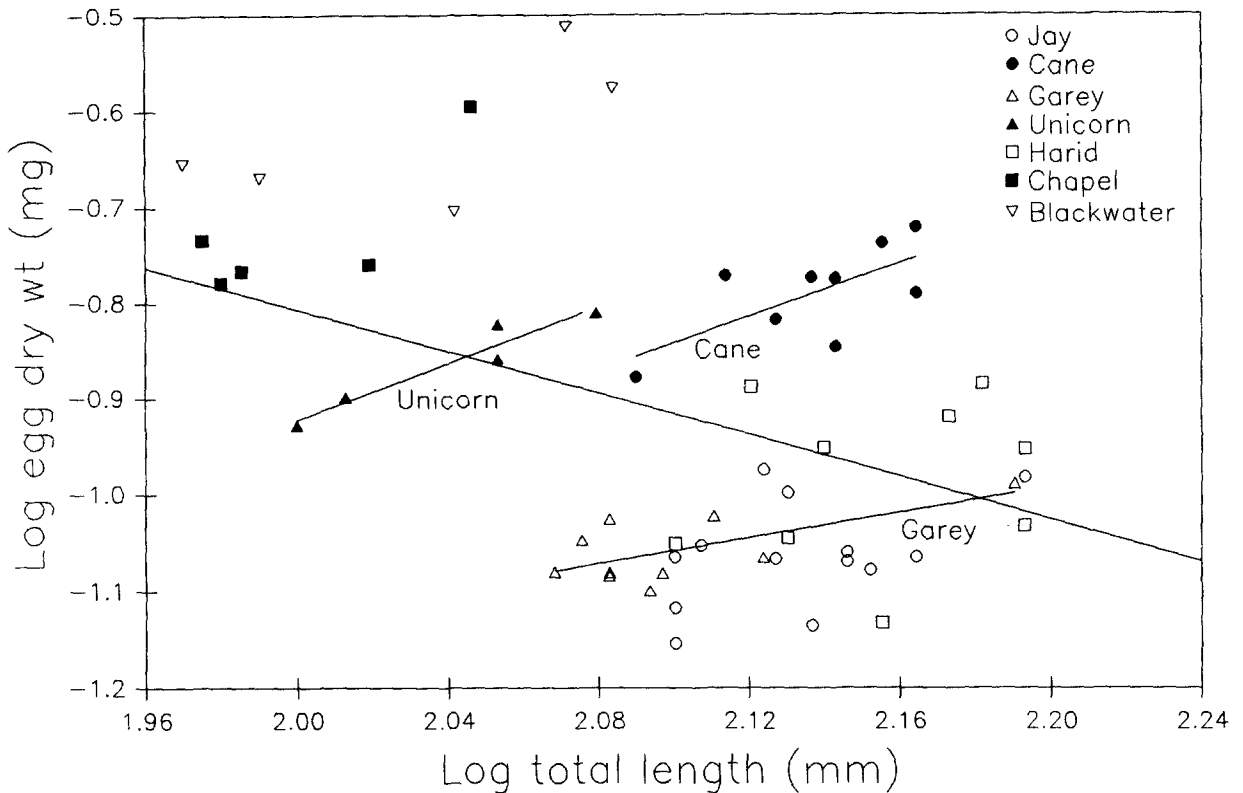


Fig. 3. Logarithmic relationship between mean egg dry weight (E , mg) and fresh total length (L_F , mm). The overall regression (stages 6–8) is: $\log E = -1.09 \pm 0.69 \log L_F + 1.38 \pm 0.30$ ($n = 56$, $r = -0.399$, $p = 0.002$). For individual populations, the significant regressions are: Unicorn: $\log E = 1.48 \pm 0.78 \log L_F - 3.89 \pm 0.07$ ($n = 5$, $r = 0.961$, $p = 0.009$); Cane: $\log E = 1.39 \pm 0.57 \log L_F - 3.75 \pm 0.09$ ($n = 14$, $r = 0.621$, $p = 0.046$); Garey: $\log E = 0.66 \pm 0.61 \log L_F - 2.44 \pm 0.07$ ($n = 10$, $r = 0.661$, $p = 0.038$).

rengus pallasi, to be most affected by stock biomass or mean sea temperature during a decisive period up to two years prior to spawning. In least brook lamprey, fecundity may be regulated by conditions acting during oogenesis in larvae.

The decrease in relative fecundity with female length, observed within the Jay and Little Whipoorwill Creek populations, was anticipated based on similar inverse relationships in other lamprey species (Kott 1971, Beamish 1982, Beamish & Thomas 1983). That the relationship was not significant in the other streams was presumably due to their small sample sizes and limited length ranges.

Among populations, the opposite trend between relative fecundity and length was observed. In populations in which spawning occurred at smaller sizes, females yielded fewer eggs per gram than where lampreys were large. Regardless of the factors

which affect growth, it may be body size that ultimately regulates relative egg number. Slow growth or small body size may reduce the initial number of oocytes formed or maintained.

The interpopulational differences in length of metamorphosing and adult lampreys observed in the present study were presumably due to differential growth. The age structure of larval stocks collected in the streams was similar, regardless of their differences in body size (Docker et al. unpublished data). Further, the length-frequency curves for each stock show similar distributional patterns within each age class, indicating that size-specific mortality does not vary among streams (Docker et al. unpublished data); that is, body size is not greater in some streams simply because smaller animals die preferentially. That least brook lamprey length was not related to density of larvae,

latitude, or annual thermal units may be due to modifying effects of other environmental factors, such as variations in stream discharge (Beamish 1982) or water chemistry (Docker et al. unpublished data).

The expected positive relationship between egg size and body length (Bagenal 1973, Docker et al. 1986, DeMartini 1987) was significant among females within three of the streams examined. In contrast, concomitant with the increase in a population's relative fecundity, mean egg weight decreased with female length among streams. While large egg size may compensate for low relative fecundity by increasing survival (Bagenal 1969, Wallace & Aasjord 1984), it may be that under conditions of poor growth large eggs are necessary to 'provide a better start in life' (Beattie 1987) and the corresponding reduction in relative fecundity is itself compensatory. Marsh (1984, 1986) suggests that large eggs of the orangethroat darter, *Etheostoma spectabile*, are advantageous where food is scarce. Similarly, Koskela & Pasenan (1975) found fewer and larger eggs in the common frog, *Rana temporaria*, from northerly latitudes and higher altitudes, where the growing season is short. Messieh (1976) and Tanasichuk & Ware (1987) also report an inverse relationship between relative fecundity and egg size over a latitudinal gradient. Gonadosomatic index, however, was constant among the Pacific herring populations (Messieh 1976, Tanasichuk & Ware 1987). Gonadosomatic index of the least brook lamprey decreased slightly with increasing body size, indicating the lack of a complete trade-off between egg number and size.

In summary, in populations of least brook lamprey where spawning occurs at small sizes, there are comparatively fewer but larger eggs than in streams where growth is high and females are large. Large eggs may function in countering the effects of an unproductive environment, and the reduction in relative fecundity is compensatory. Density, annual temperature, and latitude had little or no effect on either egg number or size.

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References cited

- Bagenal, T.B. 1966. The ecological and geographical aspect of fecundity of plaice. *J. Mar. Biol. Assoc. U.K.* 46: 161-186.
- Bagenal, T.B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. *J. Fish Biol.* 1: 349-353.
- Bagenal, T.B. 1973. Fish fecundity and its relations with stock and recruitment. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.* 164: 186-198.
- Bailey, R.S. & S.M. Almatar. 1989. Variation in the fecundity and egg weight of herring (*Clupea harengus* L.). Part II. Implications for hypotheses on the stability of marine fish populations. *J. Cons. int. Explor. Mer* 45: 125-130.
- Beamish, F.W.H. 1982. Biology of the southern brook lamprey, *Ichthyomyzon gagei*. *Env. Biol. Fish.* 7: 305-320.
- Beamish, F.W.H. & E.J. Thomas. 1983. Potential and actual fecundity of the 'paired' lampreys, *Ichthyomyzon gagei* and *I. castaneus*. *Copeia* 1983: 367-374.
- Beattie, R.C. 1987. The reproductive biology of common frog (*Rana temporaria*) populations from different altitudes in northern England. *J. Zool., Lond.* 211: 387-398.
- Bird, D.J. & I.C. Potter. 1979. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 1. A description of the timing and stages. *J. Linn. Soc. London, Zool.* 65: 127-143.
- Craig, J.F. & C. Kipling. 1983. Reproduction effort versus the environment; case histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. *J. Fish Biol.* 22: 713-727.
- Demartini, E.E. 1987. Tests of ovary subsampling options and preliminary estimates of batch fecundity for two *Paralabrax* species. *Calif. Coop. Oceanic Fish. Invest. Rep.* 28: 168-170.
- Docker, M.F., T.E. Medland & F.W.H. Beamish. 1986. Energy requirements and survival in embryo mottled sculpin (*Cottus bairdi*). *Can. J. Zool.* 64: 1104-1109.
- Hardisty, M.W. 1964. The fecundity of lampreys. *Arch. Hydrobiol.* 60: 340-367.
- Hardisty, M.W. 1971. Gonadogenesis, sex differentiation and

- gametogenesis. pp. 295–359. In: M.W. Hardisty & I.C. Potter (ed.) *The Biology of Lampreys*, Volume 1, Academic Press, London.
- Hay, D.E. & J.R. Brett. 1988. Maturation and fecundity of Pacific herring (*Clupea harengus pallasii*): an experimental study with comparisons to natural populations. *Can. J. Fish. Aquat. Sci.* 45: 399–406.
- Herrera, M., J.A. Hernando, C. Fernandez-Delgado & M. Bellido. 1988. Age, growth and reproduction of the barbel, *Barbus sclateri* (Gunther, 1868), in a first-order stream in southern Spain. *J. Fish Biol.* 33: 371–381.
- Hislop, J.R.G. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. *J. Fish Biol.* 32: 923–930.
- Hughes, R.L. & I.C. Potter. 1969. Studies on gametogenesis and fecundity in the lampreys *Mordacia praecox* and *M. mordax* (Petromyzonidae). *Aust. J. Zool.* 17: 447–464.
- Jones, R. 1976. Growth of fishes. pp. 251–279. In: D.H. Cushing & J.J. Walsh (ed.) *The Ecology of the Seas*, Blackwell Scientific Publications, Oxford.
- Kipling, C. & W.E. Frost. 1969. Variations in the fecundity of pike *Esox lucius* L. in Windermere. *J. Fish Biol.* 1: 221–237.
- Koskela, P. & S. Pasanen. 1975. The reproductive biology of the female common frog, *Rana temporaria* L., in northern Finland. *Aquilo (Zool.)* 16: 1–12.
- Kott, E. 1971. Characteristics of pre-spawning American brook lamprey from Big Creek, Ontario. *Ont. Field-Nat.* 85: 235–240.
- Lett, P.F., A.C. Kohler & D.N. Fitzgerald. 1975. Role of stock biomass and temperature in recruitment of southern Gulf of St. Lawrence Atlantic cod, *Gadus morhua*. *J. Fish. Res. Board Can.* 32: 1613–1628.
- Marsh, E. 1984. Egg size variation in central Texas populations of *Etheostoma spectabile* (Pisces: Percidae). *Copeia* 1984: 291–301.
- Marsh, E. 1986. Effects of egg size on offspring fitness and maternal fecundity in the orangethroat darter, *Etheostoma spectabile* (Pisces: Percidae). *Copeia* 1986: 18–30.
- McAllister, C.T., M.C. Wooten & T.L. King. 1981. Observations of size and fecundity of the least brook lamprey, *Lampetra aepyptera* (Abbott), from northcentral Arkansas. *Proc. Ark. Acad. Sci.* 35: 86–87.
- Messieh, S.N. 1976. Fecundity studies of Atlantic herring from the southern Gulf of St. Lawrence and along the Nova Scotia coast. *Trans. Amer. Fish. Soc.* 105: 384–394.
- Paulson, A.C. & R.L. Smith. 1975. Latitudinal variations of Pacific herring fecundity. *Trans. Amer. Fish. Soc.* 106: 244–247.
- Steel, R.G.D. & J.H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill, New York. 633 pp.
- Tanasichuk, R.W. & D.M. Ware. 1987. Influence of interannual variations in winter sea temperature on fecundity and egg size in Pacific herring (*Clupea harengus pallasii*). *Can. J. Fish. Aquat. Sci.* 44: 1485–1495.
- Trzebiatowski, R., J. Filipiak & R. Jakubowski. 1981. Effect of stock density on growth and survival of rainbow trout (*Salmo gairdneri* Rich.). *Aquaculture* 22: 289–295.
- Velikanov, A.Ya. 1986. Fecundity of the far east capelin, *Malotus villosus socialis*, in the coastal water of Sakhalin. *J. Ichthyol.* 27: 87–96.
- Volodin, V.M. 1988. Fecundity as a possible natural marker in the study of the intrapopulational structure and interpopulational differences of the bream, *Abramis brama*. *J. Ichthyol.* 28: 93–97.
- Wallace, J.C. & D. Aasjord. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). *J. Fish Biol.* 24: 427–436.
- Walsh, S.J. & B.M. Burr. 1981. Distribution, morphology and life history of the least brook lamprey, *Lampetra aepyptera* (Pisces: Petromyzontidae), in Kentucky. *Brimleyana* 6: 83–100.
- Wootton, R.J. 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symp. Zool. Soc. Lond.* 4: 133–159.
- Wright, R.M. & E.A. Shoemith. 1988. The reproductive success of pike, *Esox lucius*: aspects of fecundity, egg density and survival. *J. Fish Biol.* 33: 623–636.