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The influence of environmental variables on the density of larval lampreys in different seasons

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Summary. The objective of the study was to identify a subset of a set of twenty environmental variables which could explain variations in the density of larval lampreys (*Geotria australis*) in a south-western Australian stream. Generalised linear modelling, assuming Poisson distributions for the larval counts, led to a different model for each of the four seasons, with variations in larval density being explained in each season by a combination of between five and eight environmental variables. The influence of stream region also had to be taken into account in the model for winter.

Four environmental variables (substrate organic material and chlorophyll *a*, macrophyte roots and low-angle shading) were present in three of the four seasonal models. A further six variables (water depth, substrate depth and profile, medium-sized sands, light intensity, and the presence of an eddy) were each found useful for two models. Two variables (current velocity and substrate profile) were each retained in one model. Eight of the twenty variables were not required for any of the seasonal models. The importance of organic material, shade, eddies, current velocity substrate particle size and a sufficient depth of substrate in our models agree with the largely subjective assessments of larval lamprey habitats made in the field by many previous workers for other lamprey species in diverse geographical localities.

Our finding that larval density increased with increases in organic material and unicellular algae in the substrate and with shade, contrasts with the results of a different model based on data collected in a northern European stream. These differences can be related to our use of a more rigorous and comprehensive sampling regime and a more appropriate form of statistical analysis.

Key words: Ammocoetes – Lamprey – Environmental variables – Density – *Geotria*

Larval lampreys (ammocoetes) are relatively sedentary animals which spend most of their time in burrows in the substrate of streams and rivers (Potter 1980). They feed by filtering unicellular algae, detritus and microorganisms from the overlying water and substrate surface (Moore and Beamish 1973; Potter et al. 1975; Moore and Potter 1976a, b; Rogers et al. 1980). Ammocoetes have a relatively slow rate of growth and typically take between three and six years to reach the mean lengths of 90–150 mm at which metamorphosis normally takes place (e.g. Hardisty and Huggins 1970; Potter 1970, 1980; Beamish and Potter 1975; Purvis 1979; Beamish 1980; Potter et al. 1980; Potter and Hilliard 1986).

Many workers have listed such features as shallow water, low current velocity, shade, small substrate particle size and the presence of organic detritus, as important components of those areas where large numbers of ammocoetes are found (e.g. Schultze 1930; Enequist 1937; Hardisty 1944; Churchill 1947; Applegate 1950; Schroll 1959; Sterba 1962; Thomas 1962; Potter 1970; Manion and McLain 1971; Manion and Smith 1978). More recently, Malmqvist (1980) has used both univariate and multivariate statistics in an attempt to ascertain the effects of eighteen environmental variables on the density distribution of larval *Lampetra planeri* (Bloch) in a Swedish stream. While Malmqvist's conclusions regarding the important components of larval habitats agreed in some respects with those of previous studies, they also diverged in several important ways. However, these differences could have been produced both by the high degree of environmental heterogeneity that must have arisen from the large area of Malmqvist's sampling sites and to the restriction of sampling to a short period when stream conditions differed from those typically occurring in more stable times of the year. Moreover, since Malmqvist's attempt to identify important environmental variables using stepwise discriminant analysis involved a separation of his thirty-seven sites into arbitrarily defined density groups, some information must have been lost in applying this rather artificial approach. Malmqvist also determined which of the simple correlation coefficients between each environmental variable and larval density were significant. Since variables which appear to be unimportant alone can turn out to be important in the presence of other variables (McKay and Campbell 1982), such correlations can be misleading in identifying influential variables.

In the current study, numbers of larval *Geotria australis* Gray were counted in small quadrats in a south-western Australian stream. Records were made of twenty environmental variables considered likely to affect larval abundance and a linear modelling technique used to determine which of these variables could be used to account for variations in larval density. The sampling regime and method of analysis allowed any seasonal effects of environmental variables on density to be investigated.

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Materials and methods

Description of stream and sampling regime

Sampling was carried out in the middle of each season from the winter of 1981 to the autumn of 1982 (5–10 July; 21–25 October; 5–9 February; and 22–26 April) at six well-separated sites along Carey Brook, a 26 km tributary of the Donnelly River in south-western Australia (Lat. 34° S, Long. 116° E; see Potter et al. (1980) for precise location). Carey Brook flows from its source through 12 km of the southernmost part of the lateritic Darling Plateau, before falling approximately 105 m over a further 7 km down a south-west face of the Darling Scarp. The final 7 km of the stream crosses gently sloping ground from the foot of the main scarp to the coastal plain, where it empties into the Donnelly River. Two of the sampling sites were located on the plateau section (upper region), two on the scarp section (middle region) and two along the stream's lower reaches (lower region). Since the three regions differed in the above respects, stream region was considered as a possible factor in our modelling.

The entire length of the stream flows through relatively undisturbed eucalypt forest and lies within an area having an average annual precipitation of 1,400 mm (Hydrography Section, Western Australia Public Works Dept. records). Most of this rainfall typically falls between May and early September (records provided by the Commonwealth Bureau of Meteorology). The catchment areas of the upper, middle and lower regions of Carey Brook are 20, 40 and >110 km^2 respectively (Western Australia Public Works Dept. records). The respective means of the maximum instantaneous flow rate in these three regions for recent winters were 0.36, 1.73 and >10 m^3 s^{-1}, while for recent summers they were 0.011, 0.094 and 0.25 m^3 s^{-1} (values derived from data provided by the Western Australia Public Works Dept.).

A total of 137 randomly positioned 0.25 m^2 quadrats were sampled. These did not include those that lay on bedrock or other impenetrable surfaces such as submerged logs. Six quadrats were sampled at each site in summer and autumn, and in all but two of the six sites in spring. A lower number of quadrats (4 or 5) was sampled at some sites in the winter, as a result of the problems posed by the effects of high discharge. This was partly compensated for by an increased number of quadrats at the other site in the same stream region.

The quadrats were enclosed by a rectangular aluminium frame measuring 40 cm in width, 62 cm in length and 50 cm in height. The lower 10 cm of each side of the frame was enclosed with sheet aluminium and sharpened to allow penetration of the substrate, while the upper 40 cm was sheathed by a fine mesh plastic screen. The aluminium frame acted as the cathode of an electric fish shocker. The ammocoetes were stimulated to emerge from the substrate by passing interrupted bursts of pulsed direct current down a pointed anode which was moved slowly across the substrate surface inside the quadrat. The frame prevented the larvae escaping laterally through the substrate or water column before they were collected by dip net. Previous tests, involving repeated electric shocking of single quadrats for one hour and examinations of the swept substrate, demonstrated that only very rarely was a larva able to remain within its burrow for longer than two minutes of exposure to the short but frequent bursts of current. For this reason, the sampling of all quadrats was restricted to a stimulatory period of five min or until all the emerged larvae had been captured.

The following measurements were made after the position of each quadrat had been delineated but before the frame was inserted. (i) The average current velocity across the substrate surface, using a Marsh-McBirney M201 impellorless current meter (ii) The average depth of the water column over the substrate. (iii) The intensity of light above the substrate, using a Gooseman's Luxmeter and expressed as a percentage of the light measured at the nearest unshaded open area.

After inserting the frame, the extent of both the fine particulate and macrodetritus overlying the substrate were each recorded as a percentage of the surface area within the quadrat. Using a forester's optical densiometer aligned to the northern horizon, estimates were made of the percentage cover provided by the surrounding vegetation and forest canopy at angles of 0–45° and 45–90° to provide values for low-angle and high-angle shading respectively.

Following the collection of larvae, the average depth of the softer sediments was determined by recording the depths to which a sharpened and graduated steel rod would penetrate the substrate. Large cores (200 × 60 mm diameter) and small cores (50 × 30 mm diameter) of substrate were taken for the analysis of particle size and chlorophyll *a* respectively. The small cores were frozen and kept in the dark. During core sampling, a note was made of whether macrophyte roots were present within the substrate and if the sediment profile was uniform or stratified. Finally, the position of the quadrat (in relation to the centre and nearest edge of the stream) and whether the quadrat was in an eddy were recorded.

The small core samples were defrosted in the laboratory and the top 10 mm ground with 90% aqueous acetone in a pestle and mortar, prior to spectrophotometric determination of chlorophyll *a* using the acidification technique of Lorenzen (1967). Since the readings were required to reflect relative amounts of microalgae in the surface substrate of the quadrats, care was taken to ensure that no macrophyte tissue was ground up with the core samples.

The sediment from the top 60 mm of the large cores was divided into two vertical halves and air-dried overnight at 60° C. The top 20 mm of one half was weighed, heated to 600° C for 15 h and reweighed to determine the amount of organic material within the top part of the substrate. The other 60 mm half was weighed, boiled with H_2O_2 to remove the organic material and deflocculated with a low-speed round blade mixer and dispersing solution, before being wet-sieved to enable the weights of the gravels (particles >2 mm) and coarse (0.6–2.0 mm) and medium (0.2–0.6 mm) sands to be calculated (Standards Association of Australia 1977). The remaining fine sands (0.06–0.2 mm) were washed, dried and weighed after the filtrates had been sedimented to determine the weights of the silts (2–60 μm) and clays (<2 μm) (Briggs 1977). Each of the above weights was expressed as a percentage of the total weight of all these components.

The nonparametric Kruskal-Wallis test (Siegel 1956) was used to identify which of the quantitative environmental variables measured at the quadrat positions altered with season.

Generalised linear modelling

Multiple regression models have been used successfully to explain and predict organism density in terms of environmental variables (e.g. Davidson and Andrewartha 1948; Lakhani and Davis 1982; Turnpenny 1983; Booth and Usher 1984). Where the mean number of organisms per sample is high and zero counts are rare, the usual assumption of normality associated with multiple regression techniques is often approximately met or can be adequately attained through a simple logarithmic transformation of the data. However, if the mean number of organisms per sample is low and zero counts occur more frequently in the data, it is difficult to apply this method satisfactorily because arbitrary weights have to be assigned to the zero counts. Slightly different weighting factors can result in large changes to regression coefficients. An alternative approach is to make the more correct assumption that, if there are no significant associative or dispersive 'intrinsic' interactions between animals, counts of organisms in random quadrats will follow a Poisson distribution. The natural logarithm of the mean counts can then be modelled as a linear combination of explanatory or predictor variables. This approach falls into the framework of the generalised linear model described by Nelder and Wedderburn (1972) and Baker and Nelder (1978).

The Numerical Algorithms Group (Oxford) Generalised Linear Interactive Modelling (GLIM) system of Baker and Nelder (1978) enables the construction of models with a variety of error distributions in an interactive manner. Since a Poisson distribution can be assumed, no arbitrary weighting decision need be taken and the presence of zero counts in the data should not cause major difficulties. The techniques of model fitting are essentially the same as in multiple regression. The goodness-of-fit of a model is indicated by the deviance which, if the model fits the data and the expected counts are not too small, is approximately chi-squared distributed. If the expected counts are small, the chi-squared approximation may be poor and should be used with caution. Nevertheless, the deviance, along with various residual plots, may still be used informally to assess goodness-of-fit (Bishop et al. 1977). However, the chi-squared approximation holds much better for changes in the deviance than the deviance itself (Baker and Nelder 1978). The change in the deviance on the deletion of a single variable or a subset of variables gives an indication of the contribution of that explanatory variable or subset. The analysis of deviance is very similar to the more familiar analysis of variance (Aitkin 1979).

In the current study, the data were analysed using version 3.12 of Baker and Nelder's (1978) GLIM package. The logarithm of the mean organism count was modelled initially as a linear combination of the twenty environmental variables (the covariates). Season and stream region (factors) and their associated interaction effects were added only if lack of fit was apparent. It should be noted that four of the environmental variables, namely presence of an eddy and macrophytes, quadrat position and whether the profile of the soft substrate was uniform, were qualitative, each with two levels. These were treated for convenience and discussion purposes as single dummy environmental variables, each taking values 0 and 1.

Stepwise backward elimination was then used to remove environmental variables (and associated interaction terms if present) until the elimination of a term produced a significant increase in the deviance of the model. At each step, the variable which produced the least change in deviance was eliminated. While some bias is introduced into the statistical tests by this procedure, this can be overcome to some extent by using smaller significance levels for the retention tests. Variables retained on the basis of tests at the conventional level (0.05) should be treated cautiously (see McKay and Campbell 1982). Residual plots (see e.g., Draper and Smith 1966) were used to check the adequacy of the fit and the assumptions of the model. In particular, plots of ordered residuals against expectations of normal order statistics were used to check the Poisson assumption.

Results

Larval density and environmental variables

The total number of larvae sampled in the 137 quadrats was 411, giving an overall mean of 3.0 larvae per quadrat. Values ranged from 0 to 32. The latter value, equivalent to a density of 128 m^{-2}, is slightly larger than the maximum density recorded by Malmqvist (1980) in his study of larval *L. planeri* in a Swedish stream.

The mean values for five of the quantitative environmental variables measured in the quadrats differed significantly ($P<0.01$) among seasons (Table 1). For example, the mean chlorophyll *a* concentration in the top 10 mm of the substrate ranged from 0.6 μg cm^{-2} in winter to 9.2 μg cm^{-2} in the autumn, while the mean current velocity over the substrate in the winter was over three times greater than that of the summer. The amount of light at the water surface relative to the amount falling on a nearby open area (% light intensity) was lowest in summer. This feature was related to the development of the forest canopy during the latter season, which in turn was reflected by the greatest value for high-angle shading. There was a conspicuous tendency for the fine sands, silts and organic material to be higher in the spring and summer than in the autumn and winter, whereas the reverse was true for the gravels and medium and coarse sands (Table 1).

The models

The variations in larval density in the stream throughout the year could not be explained by a model that took only the twenty environmental variables into account, i.e. the deviance for this model (304.3, 116 df) was large. Where appropriate, conventional logarithmic and arcsine transformations of environmental variables led to some improvement. However, the addition of season as a simple effect markedly enhanced the fit. Extensive investigation pointed to interactions between many of the environmental variables and season, and also indicated that stream region could be important. Consequently, the data were examined in more detail by season. The twenty environmental variables produced a well-fitting full model for each season except winter. Subsequent elimination of variables led to the final models summarised in Tables 2 and 3. Only the model for winter required the inclusion of the factor stream region to explain the variations in larval density. This addition reflected differences among the contributions of four of the retained covariates in the final winter model (presence

Table 1. The mean and range for the quantitative environmental variables in each season

Variable	Units	Winter		Spring		Summer		Autumn	
Chlorophyll *a*	$\mu g\ cm^{-2}$	0.60	(0– 3)	8.1	(0– 39)	4.9	(0– 18)	9.2	(2– 26)***
Low-angle shading	%	82	(40–100)	75	(50–100)	84	(45–100)	81	(50–100)
High-angle shading	%	47	(10– 80)	40	(10– 70)	54	(15– 90)	50	(8– 88)*
Light Intensity	%	55	(11– 97)	51	(5– 98)	34	(2– 93)	51	(11– 98)**
Current velocity	$cm\ s^{-1}$	9.1	(0– 39)	5.4	(0– 21)	2.8	(0– 10)	4.1	(0– 17)***
Water depth	cm	22	(2– 71)	18	(1– 43)	14	(1– 45)	18	(1– 55)
Substrate depth	cm	15	(4– 20)	16	(8– 40)	17	(7– 40)	15	(5– 36)
Gravels	%	6.3	(0– 65)	3.2	(0– 26)	2.7	(0– 24)	4.9	(0– 36)
Coarse sands	%	14	(0– 43)	8.4	(0– 28)	15	(0– 45)	15	(0– 51)**
Medium sands	%	50	(13– 86)	45	(6– 92)	41	(3– 79)	46	(0– 89)
Fine sands	%	17	(3– 69)	23	(2– 60)	24	(3– 62)	20	(2– 61)
Silts	%	2.2	(0– 4)	2.5	(0– 8)	2.9	(0– 10)	1.8	(0– 10)
Clays	%	4.5	(1– 17)	5.8	(1– 21)	4.2	(1– 22)	4.0	(1– 15)
Organic material	%	6.5	(0– 30)	12	(0– 65)	10	(0– 71)	8.4	(0– 60)*
Fine detritus cover	%	46	(0– 95)	73	(0–100)	79	(5–100)	77	(2–100)***
Macrodetritus cover	%	14	(0– 95)	22	(0– 90)	14	(0– 90)	12	(0– 82)

Significant differences between seasons at $P<0.05$, 0.01 and 0.001 are denoted by *, ** and *** respectively

Table 2. The four seasonal models. The estimated coefficients (with standard errors) of the retained environmental variables and the constant are given for the linear predictor of the logarithm of larval density for each season. The deviance and degrees of freedom are shown for the null model, the full model (with all variables) and the final model for each season. The deviance resulting from the exclusion of each retained variable from the final model is also given, while + denotes those variables whose inclusion might be treated cautiously (see text for details)

Spring

	Deviance	DF	Variable	Coefficient	S.E.	Deviance (after removal)
Null Model	: 148.7	33	Organic material	4.217	0.603	93.1
Full Model	: 22.1	13	Chlorophyll *a*	0.855	0.185	66.0
Final Model	: 40.8	28	Light Intensity	−1.729	0.382	63.8
Constant	: −1.19	(SE=0.69)	Macrophyte roots	−1.035	0.415	48.7
34 Quadrats			Substrate Profile	1.103	0.478	46.5+

Summer

	Deviance	DF	Variable	Coefficient	S.E.	Deviance (after removal)
Null Model	: 136.0	35	Organic material	4.830	0.929	63.7
Full Model	: 24.0	15	Low-angle shading	3.027	1.095	45.2
Final Model	: 37.6	27	Macrophyte roots	0.788	0.276	45.1
Constant	: −5.45	(SE=1.82)	Chlorophyll *a*	0.664	0.271	43.8
36 Quadrats			Medium sands	1.998	0.855	43.3
			Presence of Eddy	−0.592	0.264	42.9+
			Water depth	−0.357	0.162	42.5+
			Light Intensity	−1.475	0.726	42.2+

(continuation – see next page)

of an eddy, water depth, fine detritus and medium sands) in different regions of the stream. This feature was probably related to the more severe effects of the higher water flow in the middle and lower stream regions at this time and reflected an increased importance of eddies and suitable substrates for the larvae to maintain their position in these reaches of the stream.

Table 2 gives the coefficients (with standard errors) of the retained environmental variables in a linear predictor (including a constant term) of the logarithm of larval density for each season. Relevant deviances and corresponding degrees of freedom are given. For example, larval counts from 34 quadrats in the spring led to a final model involving five environmental variables, the deviance for which was 40.8 (28 df). The deviance for the null model (one with no explanatory variables) is 148.7 (33 df). The difference between these deviances (107.9, 5 df) is very significant, indicating a strong association between the larval counts and the retained environmental variables. The difference between the deviances for the full and final models is only 18.6 (15 df), indicating that the eliminated variables provide no additional information about variations in the larval counts beyond that given by the retained variables. An indication of the individual contribution of each retained vari-

Table 2 (continued)

Autumn

	Deviance	DF	Variable	Coefficient	S.E.	Deviance (after removal)
Null Model	: 234.2	35	Chlorophyll a	1.853	0.262	81.8
Full Model	: 4.3	15	Current Velocity	−1.408	0.221	64.5
Final Model	: 16.3	30	Low-angle shading	3.677	0.821	40.8
Constant	: −12.9	(SE=2.21)	Substrate depth	1.822	0.672	24.2
36 Quadrats			Organic material	1.747	0.804	20.7+

Winter

	Deviance	DF	Variable	Lower Region Coeff.	Lower Region S.E.	Middle Region Coeff.	Middle Region S.E.	Upper Region Coeff.	Upper Region S.E.	Deviance – after removal
Null Model	: 134.8	30	Presence of Eddy	5.329	1.052	14.80	6.502	−3.477	1.271	55.7
Full Model	: 4.6	2	Medium sands	21.67	5.998	37.92	18.88	–		48.6
Final Model	: 19.3	15	Water depth	2.165	0.776	3.778	1.891	–		41.9
31 Quadrats			Fine detritus	1.799	0.921	7.679	4.193	–		27.9
			Low-angle shading	2.976	0.822	2.976	0.822	2.976	0.822	35.6
			Macrophyte roots	1.114	0.322	1.114	0.322	1.114	0.322	31.7
			Substrate profile	2.066	0.817	2.066	0.817	2.066	0.817	26.6
			Substrate Depth	0.841	0.408	0.841	0.408	0.841	0.408	23.1+
			Constant	−37.43	9.842	−59.30	25.80	−8.085	2.245	

able in the presence of the others is given by the increase in deviance accompanying its exclusion. For example, if chlorophyll *a* is removed form the spring model, the deviance increases to 66.0 (27 df), a change of 25.2 (1 df) which is highly significant ($P<0.0005$). The change in the deviance on the deletion of substrate profile (5.7, 1 df), although significant ($P<0.025$), is less dramatic and might be viewed with caution.

Eight of the twenty environmental variables were not retained by any of the seasonal models (gravels, coarse and fine sands, silts, clays, macrodetritus, quadrat position and high-angle shading). This suggests that their relationship with the larval counts, if any, could be explained by the other variables. Two variables (fine detritus and current velocity) were selected for only one model. While none of the remaining eleven variables were selected by all four models, four of them were each retained for three of the seasonal models (organic material, chlorophyll *a*, low-angle shading and the presence of macrophyte roots in the substrate). Organic material appears to be a very useful explanator in both spring and summer models. The remaining six covariates (medium sands, light, depth of substrate, water depth, substrate profile and the presence of an eddy) were each retained in two of the seasonal models.

The number of covariates present in each seasonal model ranges from five in the spring and autumn to eight in the winter and summer (Table 3). Although the majority of selected variables have positive coefficients in the predictions for log mean larval density, the current velocity and light intensity coefficients are negative. The coefficients of three of the covariates (water depth and the presence of an eddy and macrophyte roots) are not consistently positive or negative in the seasonal models in which they were retained.

Residual plots examined at various stages throughout the analysis and, in particular, for the final models, gave no cause to doubt the Poisson assumption or the adequacy of the models.

Table 3. A résumé of the environmental variables retained in the seasonal models

Variable	Winter 1	Winter 2	Winter 3	Spring	Summer	Autumn
Organic material				+	+	+
Chlorophyll *a*				+	+	+
Low-angle shading	+	+	+		+	+
Macrophyte roots	+	+	+	−	+	
Substrate depth	+	+	+			+
Light Intensity				−	−	
Substrate Profile	+	+	+	+		
Medium sands	+	+			+	
Water Depth	+	+			−	
Presence of Eddy	+	+	−		−	
Current velocity						−
Fine detritus	+	+				

+ and − denote a positive and negative contribution to the logarithm of the mean larval density. 1, 2 and 3 refer to the lower, middle and upper regions of Carey Brook

Discussion

The models constructed in this study using the GLIM system employ a different combination of environmental variables for each season to explain the variations in larval density of *Geotria australis* in a south-western Australian stream. Only in winter did stream region appear to have an influence beyond that which could be explained by the environmental variables considered. In placing a biological interpretation on the models, it is important to recog-

nise that a model coefficient indicates the influence of the corresponding covariate on (the logarithm of) the mean larval density when all other covariates are treated as being fixed. In practice, changes to one covariate will be accompanied by changes to the others, according to the correlations between them in the stream. It is also worth emphasising that the exclusion of an environmental variable from a model does not necessarily imply that it is unassociated with variations in larval density, but that its association may have been explained by other (retained) variables.

Virtually all the environmental variables retained by the spring, summer and autumn models are related to the density of larval *G. australis* in the manner described by earlier workers, whose descriptions were often based on where they had collected large numbers of ammocoetes during more stable periods of the year when current velocities were low (for references, see Introduction). While our results and the conclusions of the previous studies agree with some of those of Malmqvist (1980), they also differ in a number of important ways.

The models for spring, summer and autumn highlight the importance of the amount of organic material in the substrate for explaining variations in larval density. Allowing for the effect of other environmental variables, an increase in the amount of organic material corresponded to an increase in larval density. While these findings contrast with those of Malmqvist (1980), who did not find a significant correlation between organic material and larval density, they do agree with the accounts of Enequist (1937); Hardisty (1944); Applegate (1950) and Sterba (1962) for populations from widely differing geographical localities.

The contribution of substrate chlorophyll *a* to the models for spring, summer and autumn is not surprising in view of the fact that the chlorophyll *a* levels were reflecting relative amounts of diatoms and other microalgae, which are known to be an important component of the diet of larval lampreys (Creaser and Hann 1929; Schroll 1959; Manion 1967; Moore and Beamish 1973; Potter et al. 1975; Moore and Potter 1976a, b). Since Malmqvist (1980) also found that algae were very abundant in the gut of larval *L. planeri*, it is surprising that he found an inverse relationship between larval density and chlorophyll *a*.

The positive and negative coefficients in the summer model for the relationships between the density of larval *G. australis* and the degree of low-angle shading and light intensity respectively, agree with the observations that ammocoetes are photophobic (Young 1935; Harden-Jones 1955; Reynolds and Casterlin 1979) and are more stressed in shallow artificial burrows exposed to light than to dark regimes (Potter and Rogers 1972). Moreover, on the basis of extensive field studies, Schroll (1959) concluded that shade was an important factor influencing the distribution of larval *L. planeri*. This view conflicts with Malmqvist's (1980) results, which did not find a significant correlation between this variable and the larval density of the same species. However, since Malmqvist sampled only in early April, close to the time when photographs show little or no development of the beech and alder canopy in the woodland through which his stream ran (Malmqvist 1978), the amount of shade provided by these deciduous trees must have been very small compared with the situation in summer and early autumn.

The negative relationship between the density of larval *G. australis* and current velocity in the autumn model can be attributed to the behaviour of ammocoetes during the periods of increasing flow rates found in this season. Thus, when larvae are flushed out by the effects of increased discharge on the substrate, their method of re-entry into other substrates (Sawyer 1959) are best suited to areas of soft sediments where currents are slacker. Such places would be prevalent in eddies, the presence of which was shown to be accompanied by increased larval abundance in the middle and lower regions of the stream in winter. Since maximum discharge occurs during this season and leads to the entrainment and suspension in the water column of particularly the smaller-sized substrate particles, many areas of the stream bed contain less of the fine sands, silts and organic material which characterise larval habitats in the spring and summer. The reduction during the autumn and winter of much of these important components of potential ammocoete beds may explain why organic material is not present in the winter model and why the depth of the substrate is retained as an explanator for both seasonal models.

The importance of current velocity and eddies can be readily equated with the study of Schroll (1959), which showed that areas of high larval abundance were normally found in regions of the river where current velocity was less than 0.03 m s^{-1}. They also agree with the conclusions of Hardisty (1944), Applegate (1950), Sterba (1962), Thomas (1962) and Potter (1970), as well as with the discriminant analysis of Malmqvist (1980). The positive coefficients of the proportional amount of medium sands (particle size 0.2–0.6 mm) in the winter and summer models for *G. australis* also parallel the results recorded for holarctic ammocoetes (Schroll 1959; Manion and McClain 1971).

The negative coefficient for the depth of the water column in the summer model agrees with the situation described for the same species in New Zealand (Maskell 1929) and for *Mordacia mordax* (Richardson) in eastern Australia (Potter 1970), as well as for various species in Europe (Hardisty 1944) and North America (Schultze 1930; Churchill 1947; Manion pers. comm). While two of the last workers also found ammocoetes to be prevalent along or near the water line in winter, there is a positive relationship between water depth and the density of larval *G. australis* in the middle and lower regions of Carey Brook at this time of year. This apparent anomaly can be explained by the fact that in these regions the stream has no flood plain but is contained within a steep sided, U-shaped gutter. Thus in winter, when the water level and flow are high, areas of substrate suitable for larval colonization tend not to become deposited along the edges of the stream but are found in deeper water. The winter model also indicates that higher numbers of larvae occurred where macrophyte roots were present. The presence of macrophytes and eddies help reduce the erosion of the substrate, and are features which have been regarded as important components of other larval habitats (Hardisty 1944; Applegate 1950; Schroll 1959; Sterba 1962; Thomas 1962; Potter 1970). The more stable areas of the stream bed also tend to accumulate deposits of detritus, and this may account for the positive relationship between larval density and the amount of fine detrital material overlying the substrate in winter.

The negative coefficient for the presence of macrophytes in the model for spring, when stream flow and water levels had fallen, reflects the movement of larvae towards the now shallow edges of the stream where finer particles and

organic material are being deposited. However, as the water levels continue to fall in the summer, thereby exposing these areas, the ammocoetes have to move back towards those regions which they occupied in winter. This explains the return in the summer model to a positive relationship between larval density and macrophytes.

Since the results of the spring, summer and autumn models explaining larval density in a Western Australian stream closely agree with those reported by previous workers for several lamprey species during stable periods in other parts of the world, the main characteristics of a larval lamprey habitat at such times are apparently universal. It is also worth re-emphasising that the absence in Malmqvist's (1980) results of correlations between larval density and several environmental variables considered important by other workers and our models, may be attributed to a sampling regime restricted to early April and to the use of an inappropriate statistical analysis. Certainly Malmqvist's selection of sampling areas occupying two metre-long sections of the stream must have led to a high level of environmental heterogeneity within these 'quadrats', while in early April features such as stream stability, woodland canopy and chlorophyll *a* levels would have differed markedly from those found in the summer and autumn of northern Europe.

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References

Aitkin M (1979) A simultaneous test procedure for contingency table models. Appl Stat 28:233–242

Applegate VC (1950) Natural history of the sea lamprey, *Petromyzon marinus* in Michigan. U.S. Dep Int Fish Wildl Serv Spec Sci Rep 55

Baker RJ, Nelder JA (1978) The GLIM System Release 3 Manual. Numerical Algorithms Group, Oxford

Beamish FWH, Potter IC (1975) The biology of the anadromous sea lamprey (*Petromyzon marinus*) in New Brunswick. J Zool 177:57–72

Beamish RJ (1980) Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can J Fish Aquat Sci 37:1906–1923

Bishop YMM, Fienberg SE and Holland PW (1977) Discrete Multivariate Analysis: Theory and Applications. MIT Press, Cambridge, Massachusetts

Booth RG, Usher MB (1984) Arthropod communities in a maritime antarctic moss-turf habitat: effects of the physical and chemical environment. J Anim Ecol 53:879–893

Briggs D (1977) Particle size analysis. Sources and methods in Geography: Sediments. Butterworths, London

Churchill WS (1947) The brook lamprey in the Brule River. Trans Wisconsin Acad Sci Arts Lett 37:337–346

Creaser CW, Hann CS (1929) The food of larval lampreys. Occas Pap Michigan Acad Sci 10:433–437

Davidson J, Andrewartha HG (1948) The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). J Anim Ecol 17:200–222

Draper NR, Smith H (1966) Applied Regression Analysis. John Wiley and Sons, New York

Enequist P (1937) Das Bachneunauge als ökologische Modification des Flüsseneunauges Über die Fluss- und Bachneunaugen Schwedens. Ark Zool 29:1–22

Harden Jones FR (1955) Photokinesis in the ammocoete larva of the brook lamprey. J Exp Biol 32:492–503

Hardisty MW (1944) The life history and growth of the brook lamprey (*Lampetra planeri*). J Anim Ecol 13:110–122

Hardisty MW, Huggins RJ (1970) Larval growth in the river lamprey *Lampetra fluviatilis*. J Zool 161:549–559

Lakhani KH, Davis BNK (1982) Multiple regression models of the distribution of *Heleanthemum chamaecistis* in relation to aspect and slope at Bornack, England. J Appl Ecol 17:621–629

Lorenzen CJ (1967) Determination of chlorophyll and pheo-pigments: Spectrophotometric equations. Limnol Oceanogr 12:343–346

McKay RJ, Campbell NA (1982) Variable selection techniques in discriminant analysis. I Description. Br J Math Stat Psychol 35:1–29

Malmqvist B (1978) Population structure and biometry of *Lampetra planeri* (Bloch) from three different watersheds in South Sweden. Arch Hydrobiol 84:65–86

Malmqvist B (1980) Habitat selection of larval brook lampreys (*Lampetra planeri*, Bloch) in a South Swedish stream. Oecologia (Berlin) 45:35–38

Manion PJ (1967) Diatoms as food of larval sea lampreys in a small tributary of northern Lake Michigan. Trans Am Fish Soc 96:224–226

Manion PJ, McLain AL (1971) Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Tech Rep Great Lakes Fish Comm 16:1–35

Manion PJ, Smith BR (1978) Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II 1966–1972. Tech Rep Great Lakes Fish Comm 30:1–35

Maskell F (1929) On the New Zealand lamprey, Geotria australis Gray 1. Biology and life history. Trans Proc N.Z. Inst 60:167–210

Moore JW, Beamish FWH (1973) Food of larval sea lamprey (*Petromyzon marinus*) and American brook lamprey (*Lampetra lamottei*) J Fish Res Board Can 30:7–15

Moore JW, Potter IC (1976a) A laboratory study on the feeding of larvae of the brook lamprey *Lampetra planeri* (Bloch). J Anim Ecol 45:81–90

Moore JW, Potter IC (1976b) Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J Anim Ecol 45:699–712

Nelder JA, Wedderburn RHW (1972) Generalized Linear Models. J R Stat Soc A 135:370–384

Potter IC (1970) The life cycles and ecology of Australian lampreys of the genus *Mordacia*. J Zool 161:487–511

Potter IC (1980) Ecology of larval and metamorphosing lampreys. Can J Fish Aquat Sci 37:1641–1657

Potter IC, Hilliard RW (1986) Growth and the average duration of larval life in the southern hemisphere lamprey, *Geotria australis* Gray. Experientia (in press)

Potter IC, Rogers MJ (1972) Oxygen consumption in burrowed and unburrowed ammocoetes of *Lampetra planeri* (Bloch). Comp Biochem Physiol A 41:427–432

Potter IC, Cannon D, Moore JW (1975) The ecology of algae in the Moruya River, Australia. Hydrobiologia 47:415–430

Potter IC, Hilliard RW, Bird DJ (1980) Metamorphosis in the Southern Hemisphere lamprey, *Geotria australis*. J Zool 190:405–430

Purvis H (1979) Variations in growth, age at transformation and sex ratio of sea lampreys reestablished in chemically treated tributaries of the upper Great Lakes. Tech Rep Great Lakes Fish Comm 35:1–36

Reynolds WW, Casterlin ME (1979) Photokinetic responses and diel activity of sea lamprey *Petromyzon marinus* ammocoete larvae. J Fish Biol 14:425–428

Rogers PA, Glenn AR, Potter IC (1980) The bacterial flora of the gut contents and environment of larval lampreys. Acta Zool (Stockholm) 61:23–27

Sawyer HW (1959) Burrowing activities of the larval lampreys. Copeia 1959:256–257

Schroll F (1959) Zur Ernährungsbiologie der steirischen Ammocöten *Lampetra planeri* (Bloch) und *Eudontomyzon danfordi* (Regan). Int Rev Gesamten Hydrobiol Hydrogr 44:395–429

Schultze LP (1930) The life history of *Lampetra planeri* Bloch, with a statistical analysis of the rate of growth of the larvae from western Washington. Occas Pap Zool Mus Univ Michigan 221:1–35

Siegel S (1956) Nonparametric statistics for the behavioural sciences. McGraw Hill Book Company, New York

Standards Association of Australia (1977) Methods of testing soil for engineering purposes: Part C – Soil Classification Tests. Tech Sheets Standards Ass Aust AS.1289.C6.1–3

Sterba G (1962) Die Neunaugen (Petromyzonidae). In Handbuch der Binnenfischerei Mitteleuropas, Vol 3, Demoll R et al. (eds) E Schwizerbart Stuttgart, pp 263–352

Thomas MLH (1962) Observations on the ecology of ammocoetes of *Petromyzon marinus* L and *Entosphenus lamottei* (Le Sueur). Unpubl M.Sc. thesis, University of Toronto, Canada

Turnpenny AWH (1983) Multiple regression analysis for forecasting critical fish influxes at power station intakes. J Appl Ecol 20:133–142

Young JZ (1935) The photoreceptors of lampreys. 1. Light sensitive fibres in the lateral line nerves. J Exp Biol 12:229–238

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