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Testing and Extension of a Lamprey Feeding Model

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Testing and extension of a sea lamprey **feeding model**

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Abstract:

A previous model of feeding by sea **lamprey** Petromyzon marinus predicted energy intake and growth by lampreys as a function of **lamprey** size, host size, and duration of feeding attachments, but it was applicable only to lampreys feeding at 10 degrees C and it was tested against only a single small data set of limited scope. We extended the model to other temperatures and tested it against an extensive data set (more than 700 feeding bouts) accumulated during experiments with captive sea lampreys. Model predictions of instantaneous growth were highly correlated with observed growth, and a partitioning of mean squared error between model predictions and observed results showed that 88.5% of the variance was due to random variation rather than to systematic errors. However, deviations between observed and predicted values varied substantially, especially for short feeding bouts. Predicted and observed growth trajectories of individual lampreys during multiple feeding bouts during the summer tended to correspond closely, but predicted growth was generally much higher than observed growth late in the year. This suggests the possibility that large overwintering lampreys reduce their feeding rates while attached to hosts. Seasonal or size-related shifts in the fate of consumed energy may provide an alternative explanation. The **lamprey** feeding model offers great flexibility in assessing growth of captive lampreys within various experimental protocols (e.g., different host species or thermal regimes) because it controls for individual differences in feeding history.

KeyWords Plus:

PETROMYZON-MARINUS, BIOENERGETICS MODEL, PARASITIC LAMPREYS, LARGEMOUTH BASS, GROWTH, SURVIVAL, CONSUMPTION, SIZE

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Abstract.--A previous model of sea lamprey Petromyzon marinus feeding predicted energy intake and growth by lampreys as a function of lamprey size, host size, and duration of feeding attachments, but it was applicable only to lampreys feeding at 10° C and it was tested against only a single small data set of limited scope. We extended the model to other temperatures and tested it against an extensive data set (over 700 feeding bouts) accumulated during experiments with captive sea lampreys. Model predictions of instantaneous growth were highly correlated with observed growth, and a partitioning of mean squared error between model predictions and observed results showed that 88.5% of the variance was due to random variation rather than systematic errors. However, deviations between observed and predicted values varied substantially, especially for short feeding bouts. Predicted and observed growth trajectories of individual lampreys over multiple feeding bouts during the summer tended to correspond closely, but predicted growth was generally much higher than observed growth late in the year. This suggests the possibility that large overwintering lampreys reduce their feeding rates while attached to hosts. Seasonal or size-related shifts in the fate of consumed energy may provide an alternative explanation. The lamprey feeding model offers great flexibility in assessing growth of captive lampreys under various experimental protocols (e.g., different host species or thermal regimes) because it permits individual differences in feeding history to be controlled for.

Evaluating alternatives for management of sea lamprey Petromyzon marinus in the Great Lakes requires an understanding of the effect on hosts of parasitic-phase lampreys that evade the control process. This effect should be assessed not only at the population level, but also at the level of the individual lamprey and its host. Variation in feeding behavior among individual lampreys, and among the feeding bouts of a single lamprey, can affect lamprey growth, the probability of host death, and the fitness of hosts that survive attacks. Moreover, the sum of feeding "decisions" by individual lampreys is reflected in observed variation among host species in marking rates and mortality.

Despite the importance of understanding the interaction between individual lamprey and host, relatively little recent research has been mounted at this level, with two notable exceptions. First, Cochran and Kitchell (1986, 1989) developed a model of feeding by parasitic lampreys as a vehicle to apply ecological and evolutionary theory to the prediction of lamprey feeding behavior. Second, Swink and colleagues at the Lake Huron Biological Station (LHBS) have staged lamprey attacks in laboratory tanks to investigate such issues as size selectivity, temperature, and the effects of host size and species on host survival (Swink and Hanson 1986, 1989; Swink 1990, 1991, 1993). The present study resulted from an interaction between these two lines of research.

The model of lamprey feeding detailed by Cochran and Kitchell (1986, 1989), derived largely from the experimental work of Farmer (1974), quantifies energy intake by a sea lamprey as a function of lamprey size, host (trout) size, interval between feedings, and duration of the feeding attachment. It is similar to the bioenergetics model of Kitchell and Breck (1980) in that both are energetics-based, but the feeding model accounts for changes in host blood quality during a feeding bout and allows for differences among feeding episodes with respect to the lamprey's feeding behavior and its effects on the host. The feeding model was tested quantitively by Cochran and Kitchell (1989), who found no significant difference between observed instantaneous growth rates of 14 captive sea lampreys with known feeding histories and growth rates predicted independently by the model. The model has proven useful for examining qualitatively such facets of lamprey feeding behavior as duration of attachment, size selectivity, host species selectivity, and the potential role of buffer species in sea lamprey management (Cochran and Kitchell 1986, 1989; Cochran 1994). It can help generate testable hypotheses and aid in the design of reasonable experiments to test those hypotheses (Cochran and Kitchell 1986). Although the model has been used mostly to examine the lamprey in lamprey-host interactions, the feeding model could also help focus on the host by estimating the energy diverted to the lamprey from the host's normal physiological functions and by accounting for changes in host blood quality.

Limitations of the lamprey feeding model as presented by Cochran and Kitchell (1989) include (a) its restriction to lamprey feeding at 10°C, based on the laboratory feeding experiments of Farmer (1974), and (b) a need for further validation. In addition to being limited to 10°C, the test of model predictions by Cochran and Kitchell (1989) involved only 14 lampreys, and both lampreys and hosts were restricted to small sizes. Accordingly, the objectives of the present study were to extend the lamprey feeding model to temperatures other than 10°C and test it against the extensive independent data set accumulated at the LHBS.

Methods

The original lamprey feeding model was described in detail by Cochran and Kitchell (1986, 1989). It was expanded to temperatures other than 10°C by incorporating a Model 2 equation (Hewett and Johnson 1992) using the parameters applied by Kitchell and Breck (1980) to sea lampreys. This dome-shaped function, which has a value of 0.67 at 10°C and a peak value of 1.0 at 18°C, is used to adjust the rate of blood removal calculated at 10°C from the ratio of lamprey biomass to host biomass in Cochran and Kitchell's (1989) model:

$$V(T) = (f(T)/0.67) \times V(10)$$

where $V(T)$ is the percentage of the host's blood volume removed daily at water temperature T (°C), $f(T)$ is the model 2 function of Hewett and Johnson (1992) evaluated at T, and $V(10)$ is the rate of blood removal at 10°C from Cochran and Kitchell's (1989) model.

We tested the feeding model in the manner of Cochran and Kitchell (1989) by comparing predicted and observed instantaneous growth rates over feeding bouts by individual captive lampreys. Requisite data for each feeding bout include initial and final lamprey mass, host mass, duration of the non-feeding interval prior to attachment, duration of the feeding attachment, and daily water temperature. The data sets collected at the LHBS (Swink and Hanson 1986, 1989; Swink 1990, 1993) include many feeding histories that satisfy these requirements (Table 1). In the LHBS experiments, tanks containing lampreys were supplied continuously with Lake Huron water pumped from about 8 m below the surface. During summer, it was refrigerated before being introduced into the study tanks. For the few dates when water temperature was not recorded, we estimated water temperature by linear interpolation.

To evaluate the validity of the feeding model, we used Theil's (1961) decomposition of mean squared error (*MSE*), which provides an indication of the degree and sources of error in model predctions (Mincer and Zarnowitz 1969; Rice and Cochran 1984). If P_i and A_i represent series of n predicted and actual values, respectively, then

$$MSE = \frac{1}{n} \sum_{i=1}^{n} (P_i - A_i)^2$$

and

$$1 = \frac{(\bar{P}-\bar{A})^2}{MSE} + \frac{(S_P-rS_A)^2}{MSE} + \frac{(1-r^2)S_A^2}{MSE} = MC + SC + RC,$$

where $\bar{P}$, $\bar{A}$, S_P, and S_A are the means and standard deviations of the P_i and A_i and r is the correlation between them. In an ideal case, all paired P_i and A_i fall on the 1:1 line, a least squares regression of A_i on P_i has a slope of one and an intercept of zero, and MSE=0 (*MSE* is the variance of the points around the 1:1 line). When predictions are not perfect (MSE>0), *MC* is the proportion of *MSE* representing bias due to the difference in means of the actual and predicted values (the "mean component"), *SC* is the error resulting from the slope differing from unity (the "slope component"), and *RC* is the proportion of *MSE* due to random error (the "residual component"). The more closely that the decomposition of *MSE* approaches the distribution of MC=0, SC=0, RC=1, the less that errors between observed and predicted values are due to systematic biases.

Deviations between observed and predicted instantaneous growth rates over feeding bouts were also used to search for specific systematic biases in model predictions. We examined plots of deviations versus such variables as lamprey mass, host mass, attachment time, mean water temperature during the feeding bout, and calendar date.

In the analyses described above, we considered each feeding bout as a separate event. As another way to depict model performance, we compared observed and predicted trajectories of growth by individual lampreys over the course of multiple feeding bouts.

Results

We present here results for the entire data set pooled over all years. In all cases, trends were consistent among years. In no case, for example, was a correlation between two variables significantly positive in one year and significantly negative in another (Appendix).

Over all feeding bouts, predicted final lamprey mass was highly correlated with observed final mass (r=0.97, N=733, P<0.001; Figure 1). However, given that both observed and predicted growth over a feeding bout begin at the same initial lamprey mass and are correlated with time, and given that initial lamprey mass varied widely among feeding bouts, this result is not unexpected. A more rigorous test compares observed and predicted instantaneous growth rates over feeding bouts (Figure 2). These two variables were significantly correlated (r=0.45, N=733, P<0.0001), and decomposition of MSE revealed that most of the variance was due to random variation rather than systematic errors (MC=0.083, SC=0.032, RC=0.885). However, a paired t-test revealed that the mean deviation between observed and predicted values (observed minus predicted) was significantly less than zero (t= -8.16, P<0.001). Predicted growth rates tend to exceed observed values.

Deviations between observed and predicted instantaneous growth rates over feeding bouts were highly variable, but especially so for short feeding bouts (Figure 3). Deviations were negatively correlated with initial lamprey mass (r= -0.24, P<0.001; Figure 4) and with the initial date of feeding bouts (*r*= -0.15, $P<0.001$; Figure 5), and they were positively correlated with average temperature over the feeding bouts (*r*=0.11, $P<0.005$; Figure 6). Because of significant intercorrelation among initial lamprey mass, initial date of feeding bout, and average temperature (all pairwise correlations significant at $P<0.001$), we examined partial correlations between deviations and each of these variables, holding each or both of the other variables constant. Partial correlations between deviations and initial lamprey mass remained significant ($P<0.001$) when initial date (*r*= -0.19), average temperature (*r*= -0.22), or both (*r*= -0.19) were held constant. Of the other possible combinations, only the partial correlation between deviations and initial date, holding average temperature constant, remained significant (*r*= -0.11, $0.001<P<0.002$).

We compared deviations between observed and predicted instantaneous growth rates of sea lampreys among the various host types used in the original laboratory experiments (Table 1). Significant differences among host types ($F_{6,726}=5.39$, $P<0.001$; Figure 7) were due to differences among lampreys feeding on small, medium, and large lake trout Salvelinus namaycush used in 1986 and 1987 (Swink 1990), but differences in host mass in these years were confounded with trends in water temperature and initial date of feeding bouts. The mean deviations for lampreys feeding on rainbow trout Oncorhynchus mykiss (-0.0053, *SE*=0.0019, *N*=78) and for those feeding on lake trout pooled over all years (-0.0065, *SE*=0.0008, *N*=655) were not significantly different (*t*=0.58, *P*=0.56). However, the mean deviation for rainbow trout was marginally different (*t*=1.98, *P*=0.05) from that for lake trout used by Swink and Hanson (1989) in the same study (-0.0109, *SE*=0.0021, *N*=77).

We compared trajectories of observed and predicted body mass of individual lampreys with feeding histories consisting of multiple consecutive feeding bouts. Concordance between observed and predicted growth trajectories tended to be good early in the year (Figure 8). Later in the year, observed and predicted trajectories often, but not always, diverged (Figure 9). Whereas observed growth tended to decline late in the year, predicted growth did not.

Discussion

We provide here a much more extensive test of the lamprey feeding model than did Cochran and Kitchell (1989). In addition to the greater number of lampreys (272 vs 14) and feeding bouts (733 vs 28), the current study involved lampreys of a greater size range (initial mass of 2-365 g vs 5-11 g) and hosts of a greater size range (217-6022 g vs 49-95 g). The mean water temperature averaged over feeding bouts in the present study (10.5°C) was similar to the constant temperature (10±0.5°C) used by Cochran and Kitchell (1989), but the range in temperature in the present study (0-21°C) was much greater.

We are encouraged that model predictions of final lamprey mass (Figure 1) and instantaneous growth rate (Figure 2) are highly correlated with observed values and that most of the error between observed and predicted values (88.5%) is due to random variation rather than systematic effects. Nevertheless, the model tended to predict higher growth than was actually observed, and the plot of predicted versus observed instantaneous growth rates shows a great deal of scatter (Figure 2). Our consideration of these apparent shortcomings suggests ways for the model to be refined.

A priori, we might expect a greater likelihood for the feeding model to overestimate rather than underestimate lamprey energy consumption. It is assumed when modeling a feeding bout that a lamprey is actively feeding during the entire time it is attached to a host (or at least that the equations used to estimate host blood removal rates adequately average over periods of feeding activity and inactivity). To the extent that any lampreys delay or suspend feeding during attachments, this assumption is violated, and both energy consumption and resulting growth will be overestimated. Farmer (1980) observed that 37% of attacks by sea lampreys were terminated before feeding was initiated, with attachment times ranging from 0.5 to 18 days. Similar periods of nonfeeding attachment might also occur after feeding is initiated. Because active feeding is difficult to identify from external cues, it may be desirable to assess the continuity of feeding with neurophysiological techniques (e.g., Kawasaki and Rovainen 1988).

A posteriori, our examination of deviations between observed and predicted instantaneous growth rates suggests that the tendency for the feeding model to overestimate energy consumption is due at least in part to a seasonal effect. Predicted instantaneous growth tended to exceed observed growth late in the year (Figure 5), when lampreys were large (Figure 4) and water temperatures were low (Figure 6). Admittedly, these trends are based on correlations of relatively small magnitude, which may be statistically significant primarily by virtue of the large sample size involved. Nevertheless, they are consistent with a tendency late in the year for divergence between predicted and observed trajectories of growth by individual lampreys over multiple feeding bouts (Figure 9). We suspect that the seasonal effect may represent a "slowing down" by large overwintering lampreys, i.e., even lower rates of blood removal than would be expected at low winter water temperatures. This slowing down apparently occurred in the laboratory as early as the end of September, when sea lampreys in the Great Lakes are entering their period of greatest growth (Bergstedt and Swink 1995). This difference may be an artifact of the shallow depth (~8m) of the LHBS water intake, which exposed the laboratory animals to more rapidly declining autumn water temperatures than lampreys living at greater depths in the lakes.

The tendency for predicted instantaneous growth to exceed observed growth by large lampreys late in the year possibly reflects not - or not only - a seasonable change in blood removal rate but rather changes in the metabolism of energy once it is consumed. Either a shift to production of more energy-rich tissue or an increase in metabolic rate could lead to reduced growth in mass. For example, Beamish et al. (1979) found that lipid content (% wet mass) increased dramatically during the trophic phase of the anadromous sea lamprey, and Claridge and Potter (1975) associated an increase in metabolic rate with gonadal maturation in the river lamprey Lampetra fluviatilis. Bioenergetics models for other fish species have sometimes yielded poor fits between observed and predicted growth by failing to account for seasonal metabolic shifts (Minton and McLean 1982; Wahl and Stein 1991).

In some cases, the feeding model severely underestimated growth (e.g., the three isolated points just above the horizontal axis in Figure 1). This can happen especially with relatively long attachments during which lampreys achieve substantial growth, as shown in the lower left panel of Figure 8. This result was anticipated by Cochran and Kitchell (1989), who pointed out that the feeding model incorporates no feedback effect of a lamprey's growth on its ability to extract blood from its host.

The more variable deviations between observed and predicted instantaneous growth rates associated with short feeding bouts (Figure 3) might be expected for several reasons. Both experimental error and true variability in lamprey feeding rates might contribute to deviations between observed and predicted growth rates, and both should have greater effect for short feeding bouts. Conversely, the effects of any experimental error in measurement of lamprey mass or of the duration of nonfeeding or feeding intervals would be masked when averaged over a long feeding bout.

Farmer (1980) reported feeding rates for sea lampreys that varied from 2.9% to 29.8% wet weight per day at 10°C, but the lamprey feeding model is based on a mean rate of 11.9%. Using average values from the present study (temperature - 10°C; initial lamprey mass - 84 g; host mass - 1859 g; nonfeeding interval - 6 days; feeding interval - 9 days), we calculated deviations between the instantaneous growth rate predicted by the feeding model when the feeding rate was set at the mean value (11.9%) and the instantaneous growth rates predicted at the extreme feeding rates (2.9% and 29.8%) reported by Farmer (1980). These deviations (-0.018 and 0.018) bracket 68% of the deviations we calculated for the LHBS data set.

Variability in lamprey feeding rates may result in part from variation in attachment site on the host (Farmer 1974). Short feeding bouts with relatively large positive or negative deviations between observed and predicted instantaneous growth rates may result respectively from attachments to sites with relatively high or low rates of blood removal. Attachments at sites that result in high blood removal rates are more likely to result in short feeding bouts due to earlier host death or earlier depletion of host blood quality. Attachments at sites with low blood removal rates may also result in short feeding bouts if the lampreys involved are prone to detach and seek new hosts. The lamprey feeding model currently applies the same estimate of blood removal rate regardless of attachment site. Separate laboratory measurements of blood removal rates at different attachment sites would permit more precise parameterizations of the feeding model.

In the original application of the lamprey feeding model (Cochran and Kitchell 1989), blood removal rates were estimated in two ways: (1) from the ratio of lamprey to host biomass, and (2) when applicable, from the length of time a lamprey took to kill its host. The latter alternative is preferable because it allows for variation in blood removal rates (Cochran and Kitchell 1989). However, we did not use option 2 in generating the results we present here because we have no data on the relation between host survival time and percentage blood volume removal rates at temperatures other than 10°C. When we did attempt to use this method without adjusting for temperature, we observed much greater variability in deviations between observed and predicted instantaneous growth rates and a greater tendency to overestimate instantaneous growth rate. Although experiments to measure blood removal rates and host survival times at temperatures other than 10°C would be labor intensive, they would help refine the model to provide more precise predictions of lamprey energy consumption and growth.

The lamprey feeding model is potentially useful for comparing the growth of lampreys maintained under different experimental conditions (e.g., different host species) while controlling for individual variations in feeding history (number and durations of attachments, water temperature, etc.). Much as the residual between an individual's actual body mass and the mass predicted by a regression of body mass on length can indicate whether that individual is relatively plump or lean while controlling for its body length, the deviation between observed and model-predicted instantaneous growth rates can indicate whether an individual lamprey has grown more or less than expected on the basis of its particular feeding history. Our comparison of deviations for lampreys feeding on rainbow trout and lake trout (pooled over all years) suggested that lamprey performed equally well in terms of growth when feeding on either species. Restricting the data set to lake trout used in the same study as the rainbow trout (Swink and Hanson 1989) suggested instead that lampreys grew relatively more quickly when attached to rainbow trout, a conclusion also reached by Swink and Hanson (1989). Swink and Hanson (1989) suggested that because rainbow trout were better adapted than lake trout to the thermal regime used in their study and fed more readily on the dry pelleted food that they used, the rainbow trout remained healthier and provided greater nourishment to lampreys per unit time attached.

In conclusion, use of a large independent data set validated the general utility of the lamprey feeding model. Most of the error between model predictions and actual results was due to random variation rather than systematic errors (88.5% in this case versus 76% in a comparable model validation by Rice and Cochran [1984]). Our search for sources of systematic bias suggested several potential refinements for fine-tuning model predictions. Morever, model results suggest additional investigations into lamprey biology, including the assessment of overwinter feeding and growth for both newly metamorphosed and pre-spawning animals.

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References

Beamish, F.W.H., I.C. Potter, and E. Thomas. 1979. Proximate composition of the adult anadromous sea lamprey, Petromyzon marinus, in relation to feeding, migration and reproduction. Journal of Animal Ecology 48:1-19.

Bergstedt, R.A., and W.D. Swink. 1995. Seasonal growth and duration of the parasitic life stage of the landlocked sea lamprey (Petromyzon marinus). Canadian Journal of Fisheries and Aquatic Sciences 52:1257-1264.

Claridge, P.N., and I.C. Potter. 1975. Oxygen consumption, ventilatory frequency and heart rate of lampreys (Lampetra fluviatilis) during their spawning run. Journal of Experimental Biology 63:192-206.

Cochran, P.A. 1994. Why lampreys and humans "compete" (and when they don't): toward a predictive theory of host species selection by parasitic lampreys. Pages 329-345 in D.J. Stouder, K.L. Fresh, and R.J. Feller, editors. Theory and application in fish feeding ecology. Belle W. Baruch Library in Marine Science, No. 18. University of South Carolina, Columbia.

Cochran, P.A., and J.F. Kitchell. 1986. Use of modelling to investigate potential feeding strategies of parasitic lampreys. Environmental Biology of Fishes 16:219-223.

Cochran, P.A. and J.F. Kitchell. 1989. A model of feeding by parasitic lampreys. Canadian Journal of Fisheries and Aquatic Sciences 46:1845-1852.

Farmer, G.J. 1974. Food consumption, growth, and host preferences of the sea lamprey, Petromyzon marinus L. Doctoral dissertation, University of Guelph, Guelph, Ontario, Canada.

Farmer, G.J. 1980. Biology and physiology of feeding in adult lampreys. Canadian Journal of Fisheries and Aquatic Sciences 37:1751-1761.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute, Technical Report WIS-SG-92-250, Madison.

Kawasaki, R., and C.M. Rovainen. 1988. Feeding behavior by parasitic phase lampreys, Ichthyomyzon unicuspis. Brain, Behavior and Evolution 32:317-329.

Kitchell, J.F., and J.E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (Petromyzon marinus). Canadian Journal of Fisheries and Aquatic Sciences 37:2159-2168.

Mincer, J. and V. Zarnowitz. 1969. The evaluation of economic forecasts. Pages 3-46 in J. Mincer, editor. Economic forecasts and expectations. National Bureau of Economic Research, New York.

Minton, J.W., and R.B. McLean. 1982. Measurement of growth and consumption of sauger (Stizostedion canadense): implications for fish energetics studies. Canadian Journal of Fisheries and Aquatic Sciences 39:1396-1403.

Rice, J.A. and P.A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65:732-739.

Swink, W.D. 1990. Effect of lake trout size on survival after a single sea lamprey attack. Transactions of the American Fisheries Society 119:996-1002.

Swink, W.D. 1991. Host-size selection by parasitic sea lampreys. Transactions of the American Fisheries Society 120:637-643.

Swink, W.D. 1993. Effect of water temperature on sea lamprey growth and lake trout survival. Transactions of the American Fisheries Society 122:1161-1166.

Swink, W.D., and L.H. Hanson. 1986. Survival from sea lamprey (Petromyzon marinus) predation by two strains of lake trout (Salvelinus namaycush). Canadian Journal of Fisheries and Aquatic Sciences 43:2528-2531.

Swink, W.D., and L.H. Hanson. 1989. Survival of rainbow trout and lake trout after sea lamprey attack. North American Journal of Fisheries Management 9:35-40.

Theil, H. 1961. Economic forecasting and policy. North-Holland, Amsterdam, The Netherlands.

Wahl, D.H., and R.A. Stein. 1991. Food consumption and growth of three esocids: field tests of a bioenergetics model. Transactions of the American Fisheries Society 120:230-246.

Table 1.-Summary of data sets used in the present study. These data sets consist of feeding histories resulting from experiments with captive sea lampreys at the Lake Huron Biological Station. Number of lampreys, number of feeding bouts, host types, and resulting publications are indicated. When not specifically indicated, lake trout were of the Marquette strain.

Year	**Number of lamprey**	**Number of feeding bouts**	**Host types**	**Reference**
1983	37	63	lake trout	Swink, unpublished data
1984	57		<u>lake trout</u>	Swink and Hanson 1986
		88	Seneca strain	
		84	Marquette strain	
1985	42	77	lake trout	Swink and Hanson 1989
		78	rainbow trout	
1986	44		<u>lake trout</u>	Swink 1990
		66	small (469-557 mm)	
		46	medium (559-643 mm)	
		47	large (660-799 mm)	
1987	52		<u>lake trout</u>	Swink 1990
		55	medium (559-650 mm)	
		52	large (660-825 mm)	

1989	42		lake trout	Swink 1993
		45	high temperature	
		32	low temperature	

FIGURE 1.-Final lamprey mass predicted by the lamprey feeding model versus observed final mass. The diagonal identity line (y=x) is provided for comparison. *N*=733.

FIGURE 2.-Instantaneous growth rate of sea lampreys (G, per day) predicted by the lamprey feeding model versus observed instantaneous growth rate. The diagonal identity line (y=x) is provided for comparison. *N*=733.

FIGURE 3.-Deviation between observed and model-predicted instantaneous growth rates of sea lampreys (per day) versus duration of feeding. *N*=733.

FIGURE 4.-Deviations between observed and model-predicted instantaneous growth rates of sea lampreys (per day) versus initial lamprey mass (g). *N*=733.

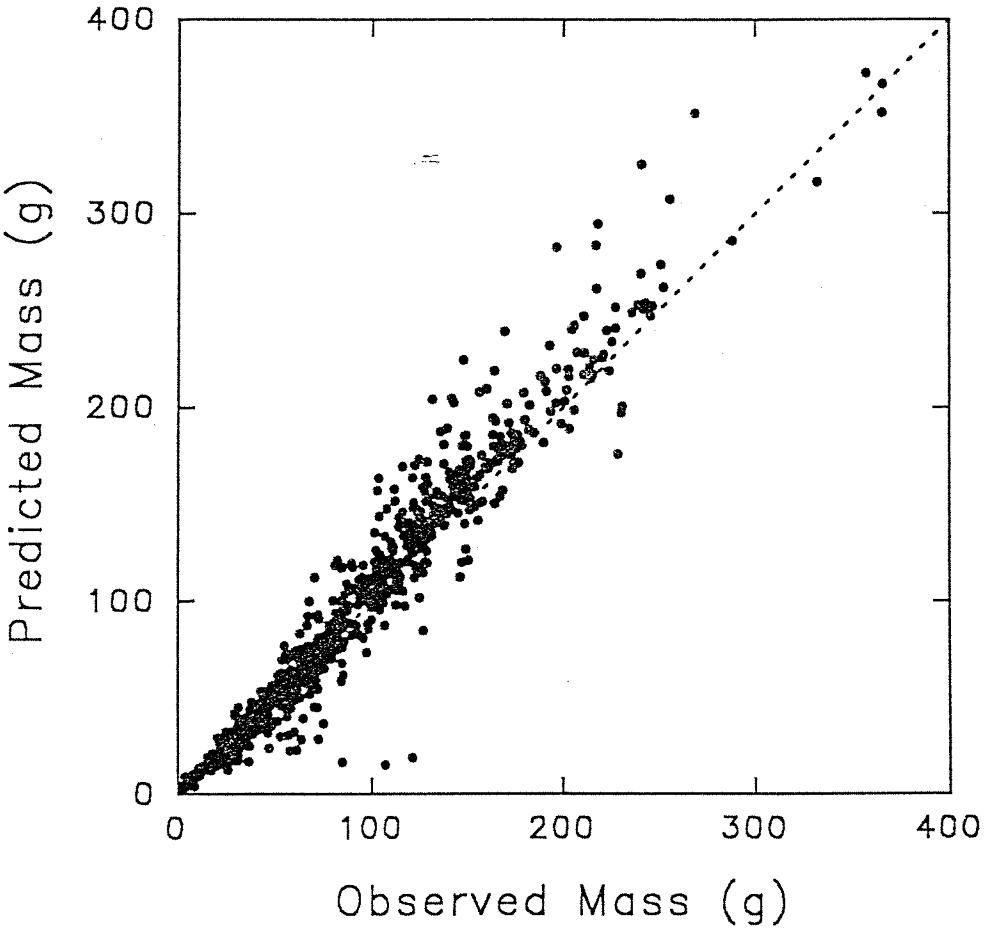
FIGURE 5.-Deviation between observed and model-predicted instantaneous growth rates of sea lampreys (per day) versus initial date of feeding bout (day of the year). *N*=733.

FIGURE 6.-Deviation between observed and model-predicted instantaneous growth rates of sea lampreys (per day) versus daily water temperature (°C) averaged over feeding bouts. *N*=733.

FIGURE 7.-Deviations between observed and model-predicted instantaneous growth rates of sea lampreys (per day) for various host types. 1=lake trout, Marquette strain; 2 and 3 = Seneca and Marquette strain lake trout used by Swink and Hanson (1986); 4, 5, and 6= small, medium and large Marquette strain lake trout used by Swink (1990); 7=rainbow trout used by Swink and Hanson (1989). Refer to Table 1 for sample sizes.

FIGURE 8.-Examples of observed (O) and model-predicted (P) lamprey mass (g) versus time (day of the year) for lampreys with feeding histories consisting of multiple consecutive feeding bouts early in the year. Each panel represents an individual lamprey.

FIGURE 9.-Examples of observed (O) and model-predicted (P) lamprey mass (g) versus time (day of the year) for individual lampreys with feeding histories consisting of multiple consecutive feeding bouts late in the year. Each panel represents an individual lamprey.



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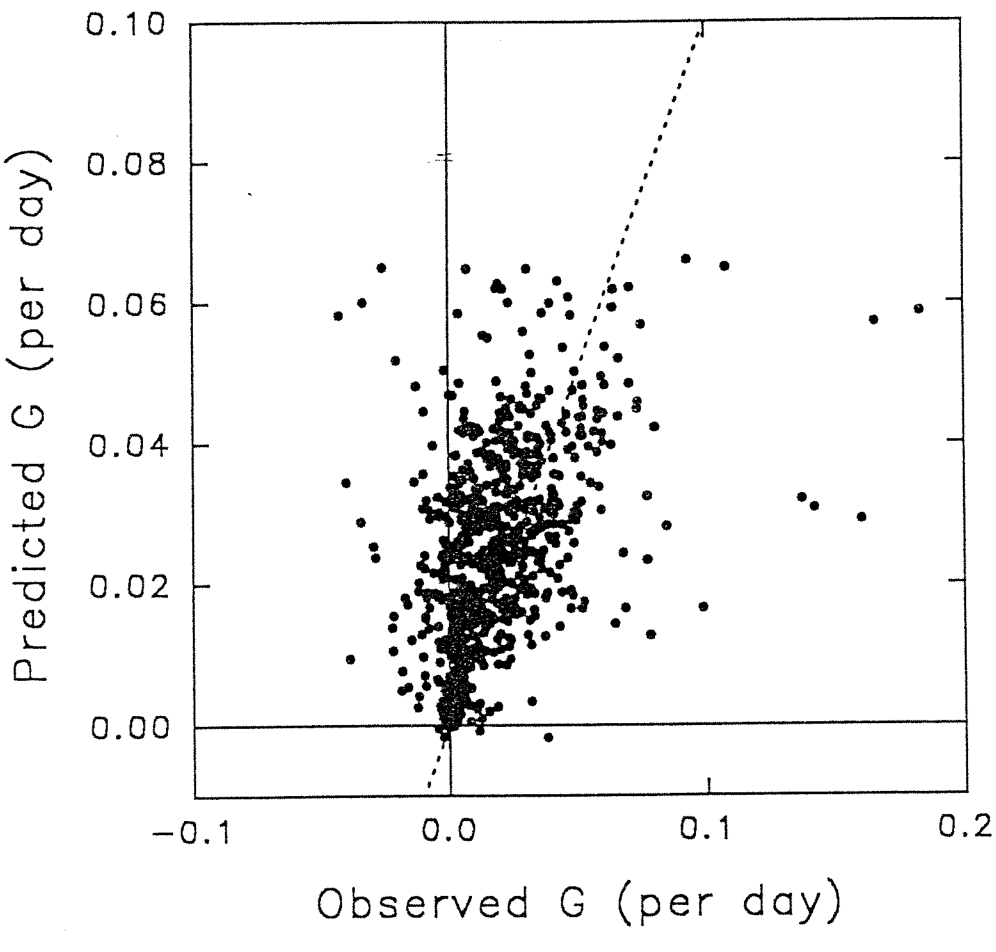
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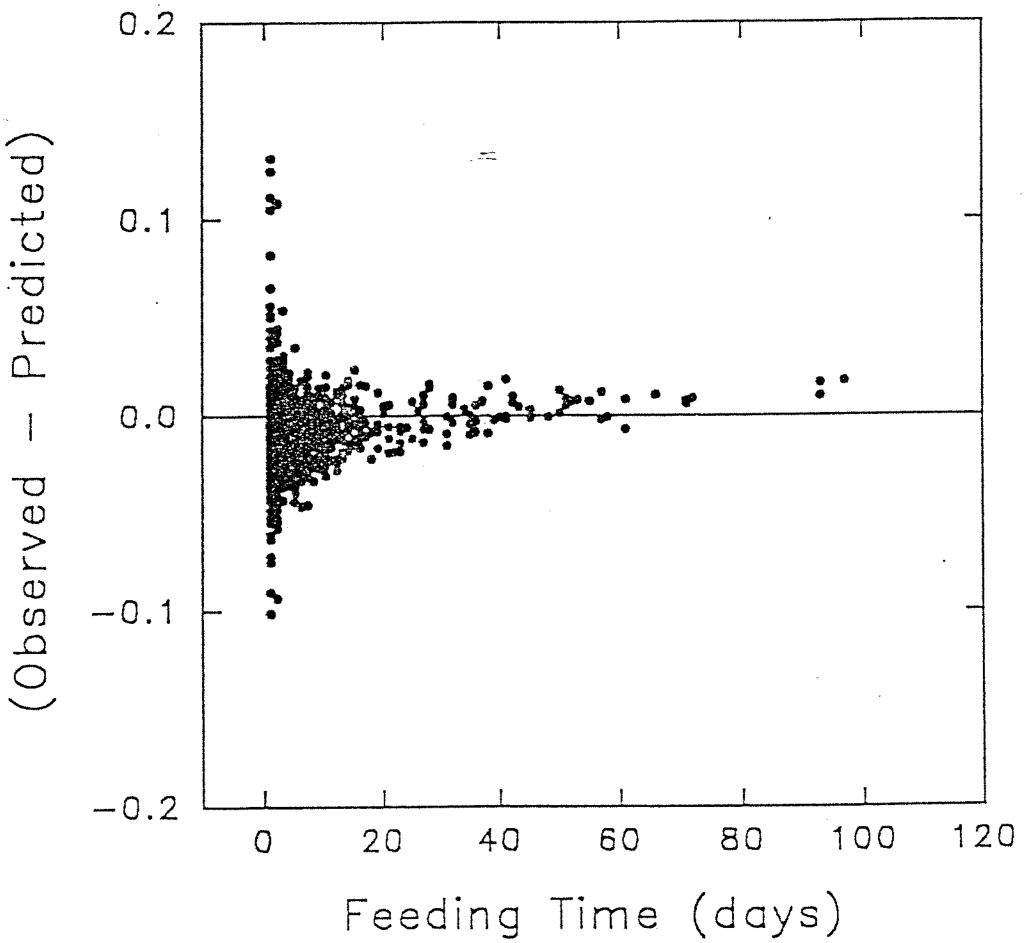
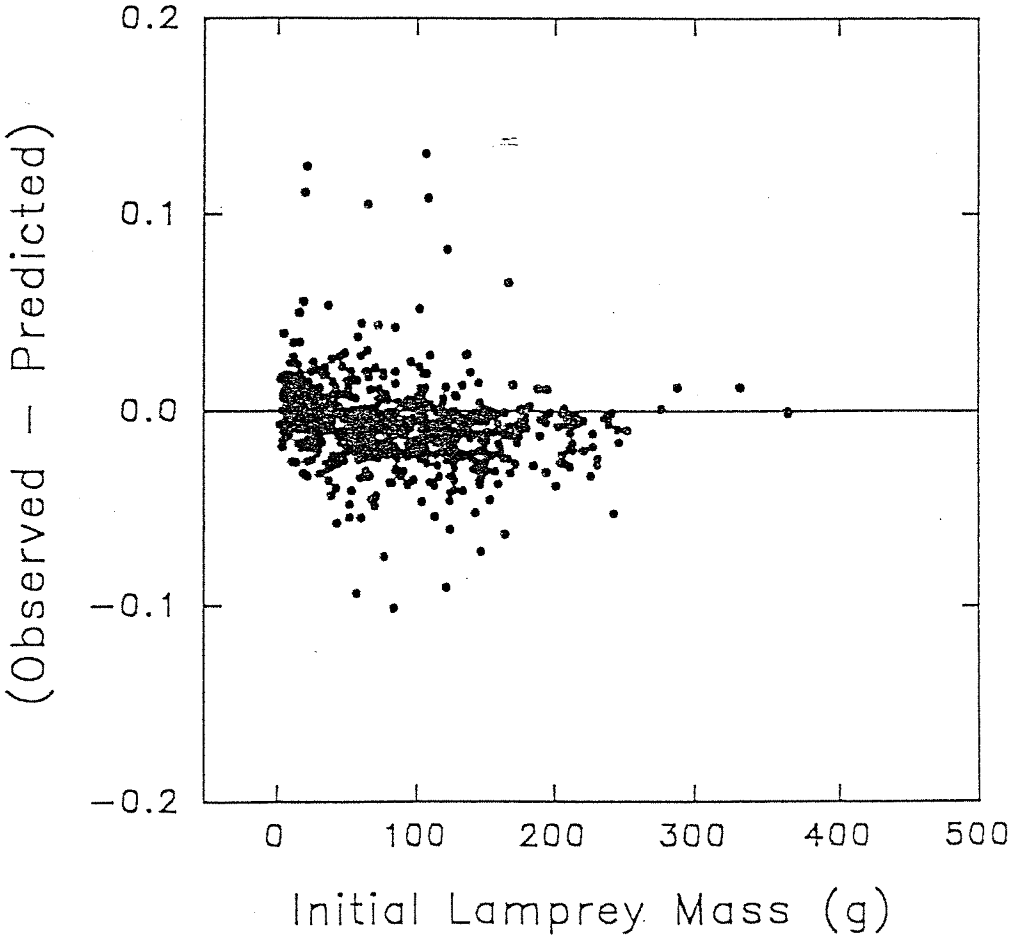
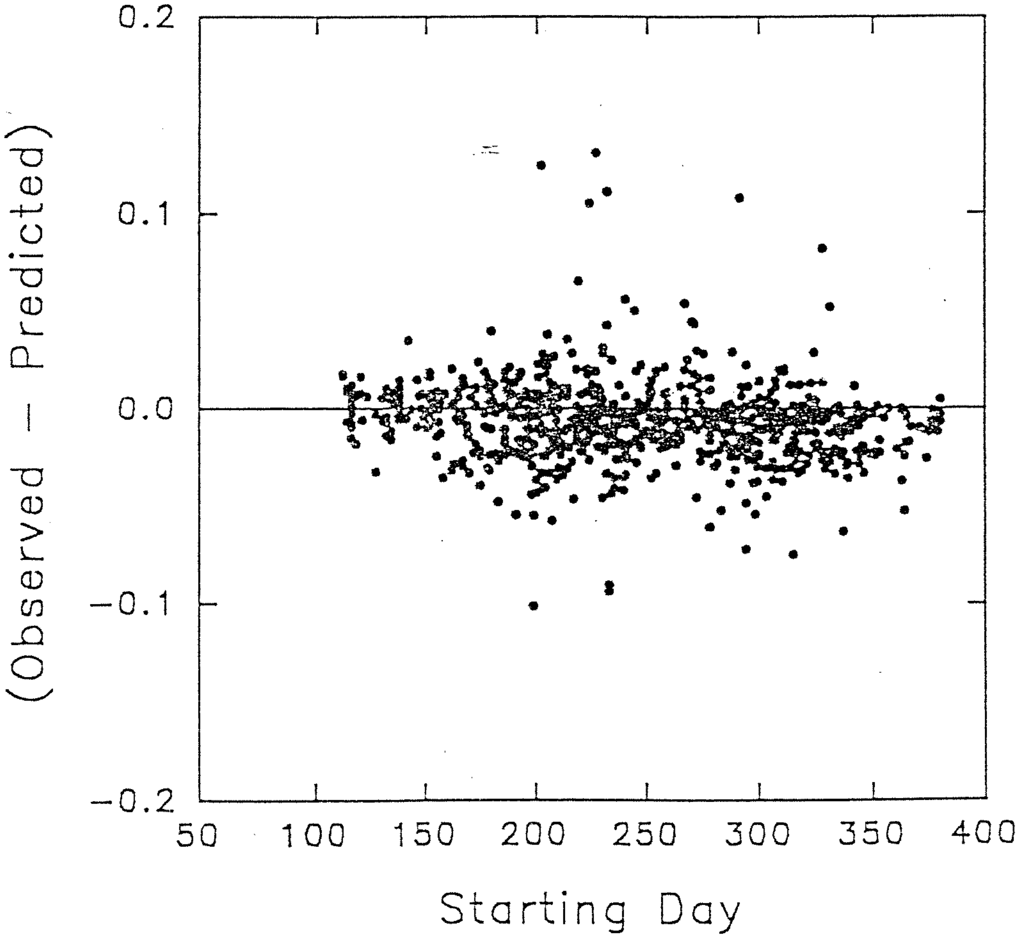
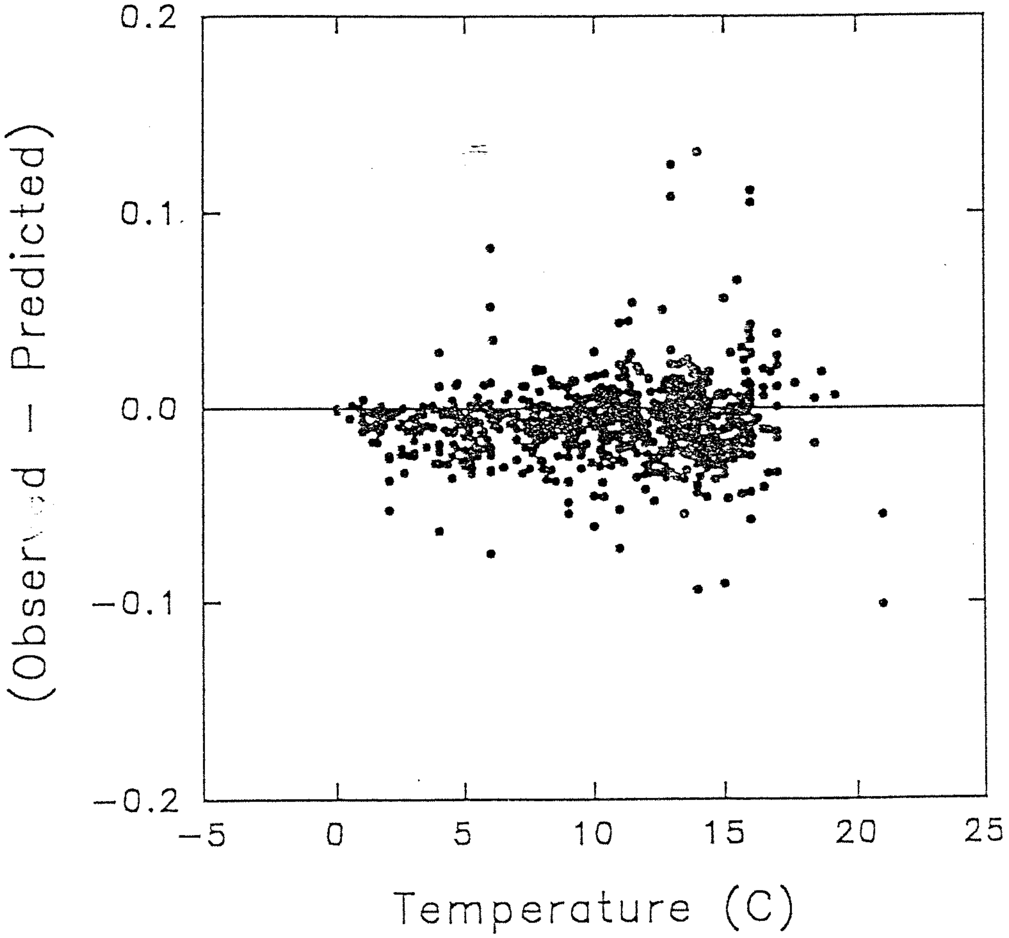
0.2
Observed G (per day)

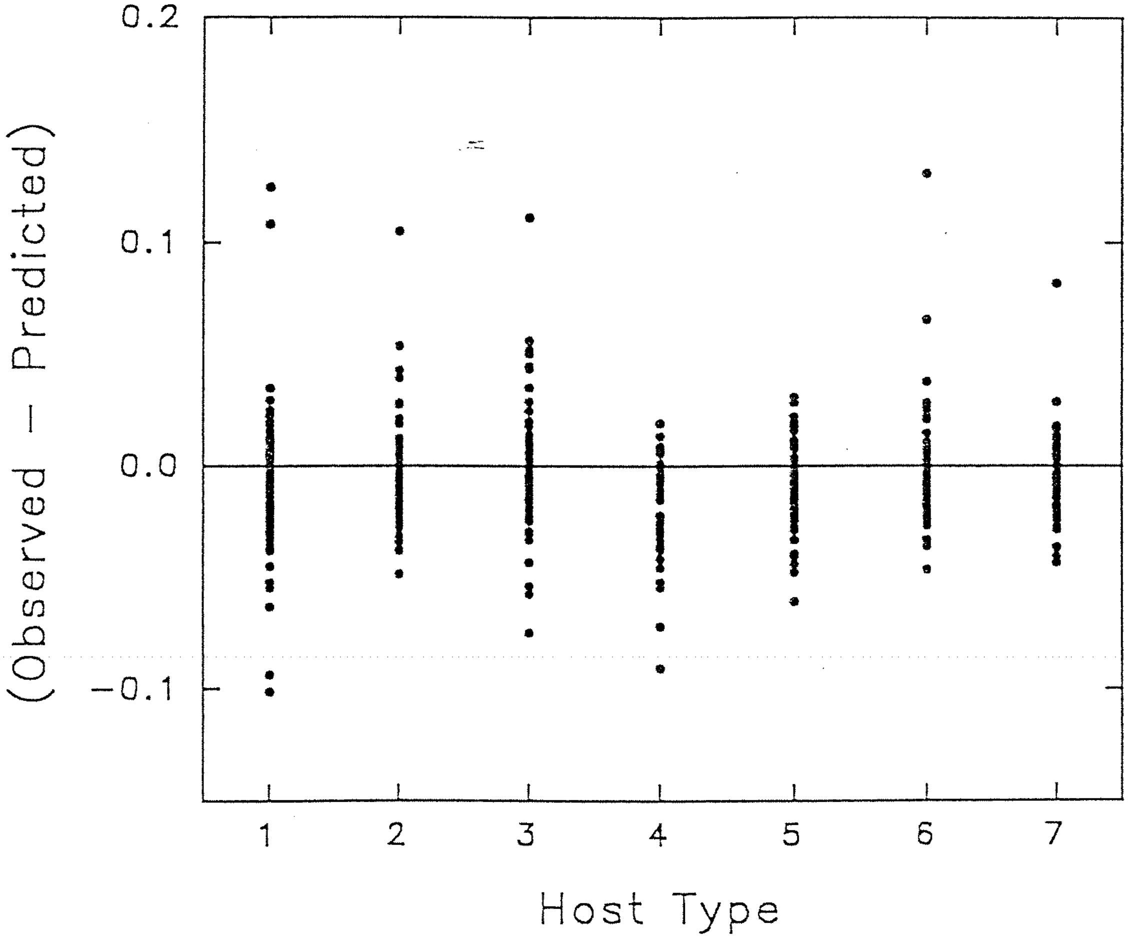

0.2
0.1
0.0
−0.1
−0.2
0
20
40
60
80
100
120
(Observed − Predicted)
Feeding Time (days)

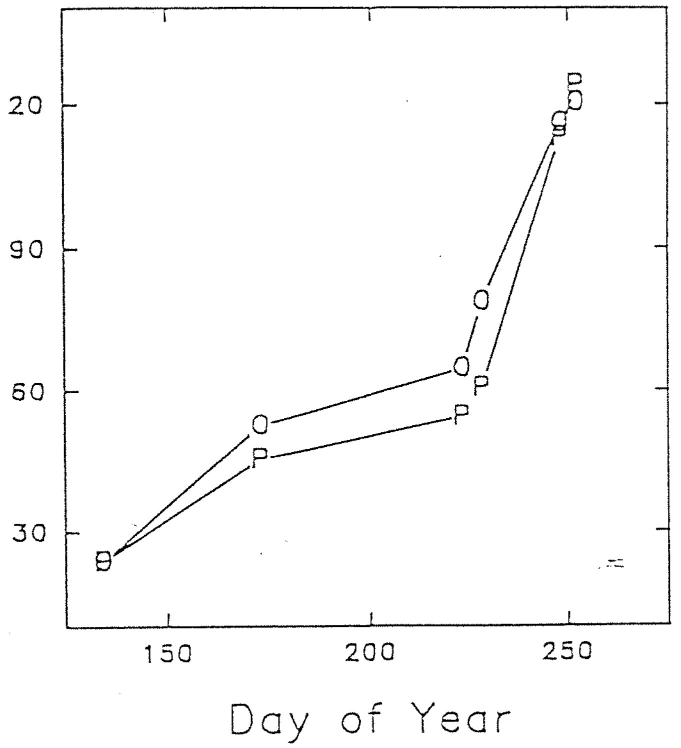


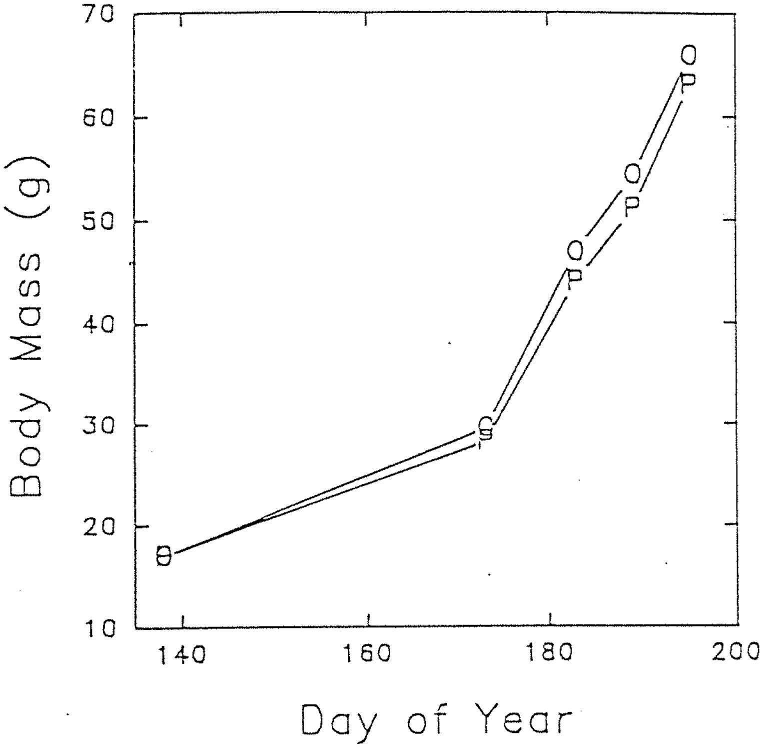
0.2
0.1
0.0
−0.1
−0.2
(Observed − Predicted)
0
100
200
300
400
500
Initial Lamprey Mass (g)

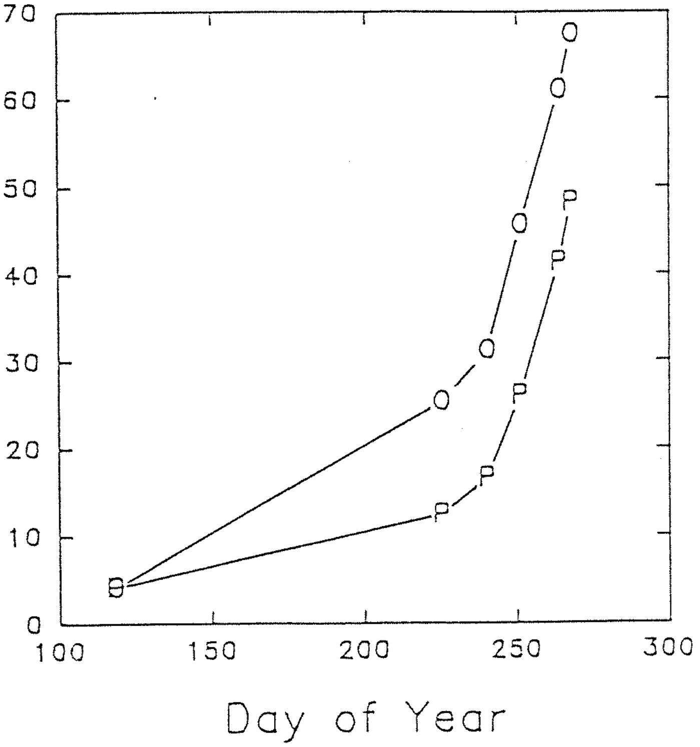

0.2
0.1
0.0
−0.1
−0.2
50
100
150
200
250
300
350
400
(Observed − Predicted)
Starting Day

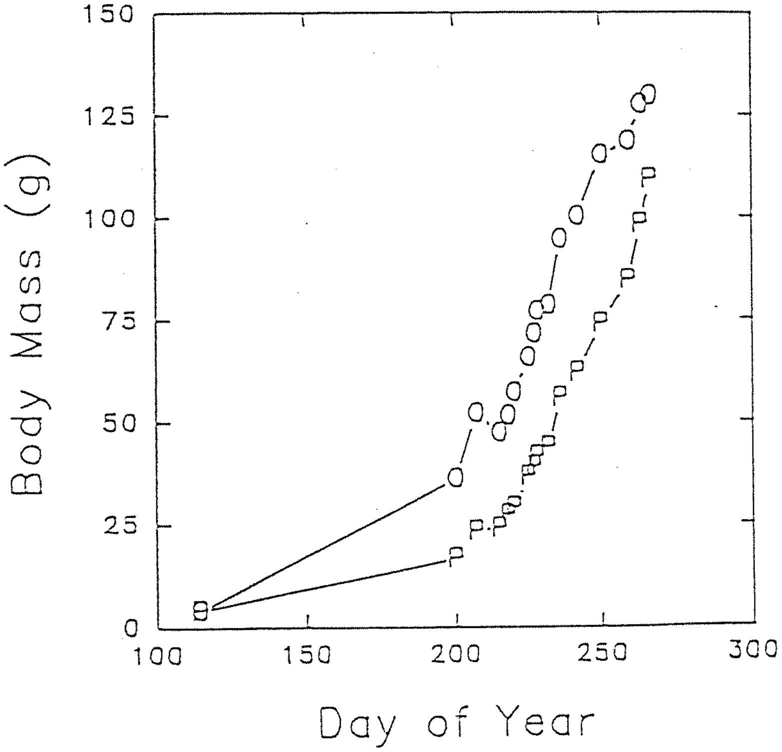

0.2
0.1
0.0
−0.1
−0.2
(Observed − Predicted)
−5
0
5
10
15
20
25
Temperature (C)

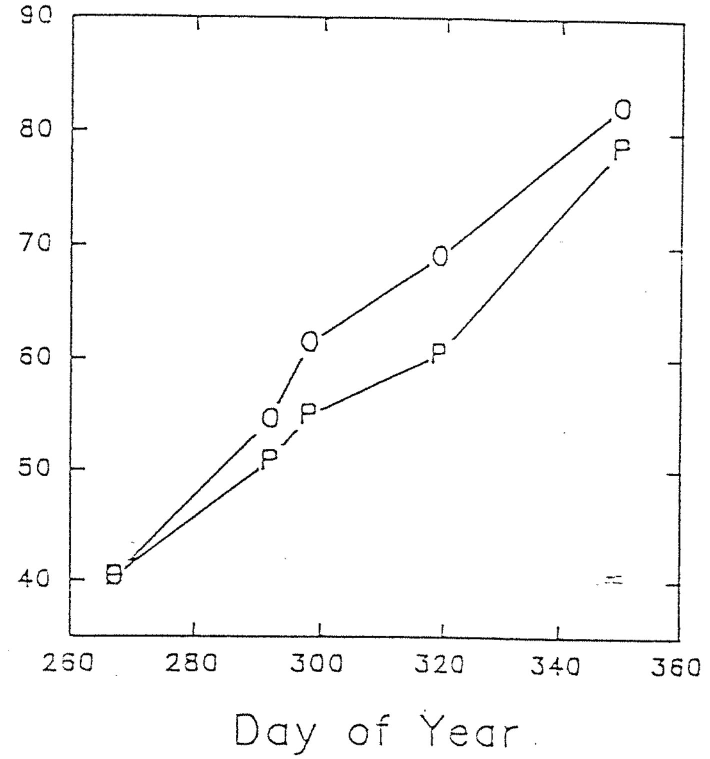

0.2
0.1
0.0
-0.1
(Observed - Predicted)
1
2
3
4
5
6
7
Host Type


20
90
60
30
150
200
250
Day of Year

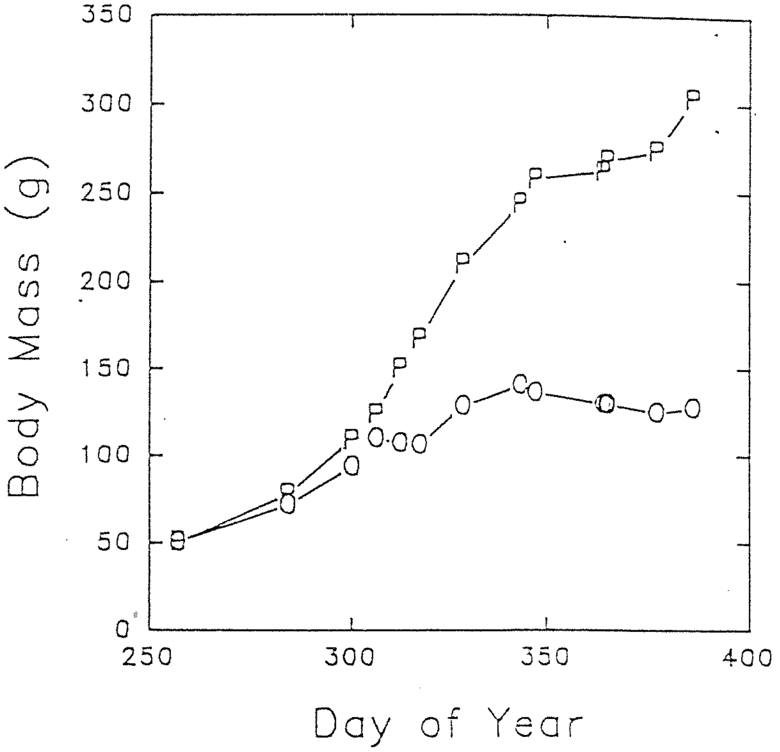

70
60
50
40
30
20
10
Body Mass (g)
140
160
180
200
Day of Year


70
60
50
40
30
20
10
0
100
150
200
250
300
Day of Year

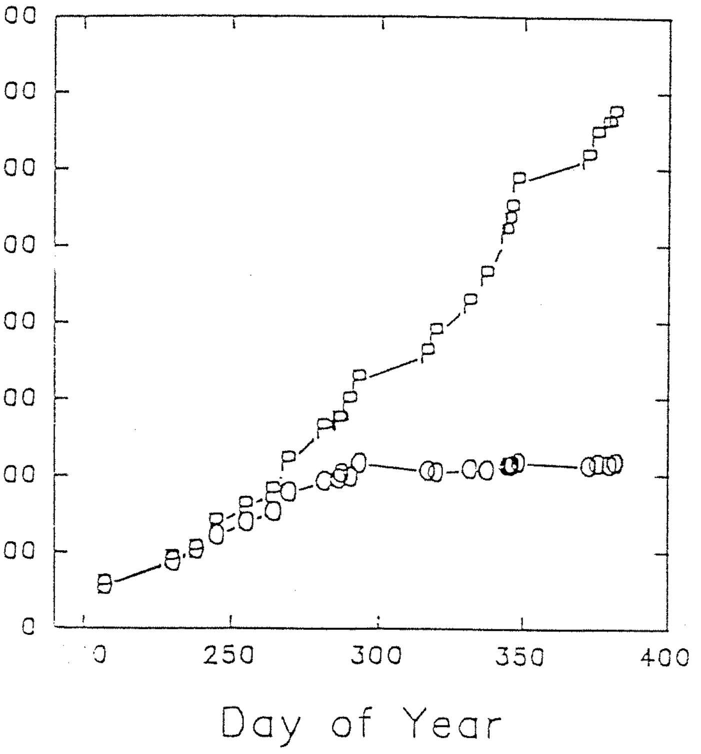

150
125
100
75
50
25
0
Body Mass (g)
100
150
200
250
300
Day of Year



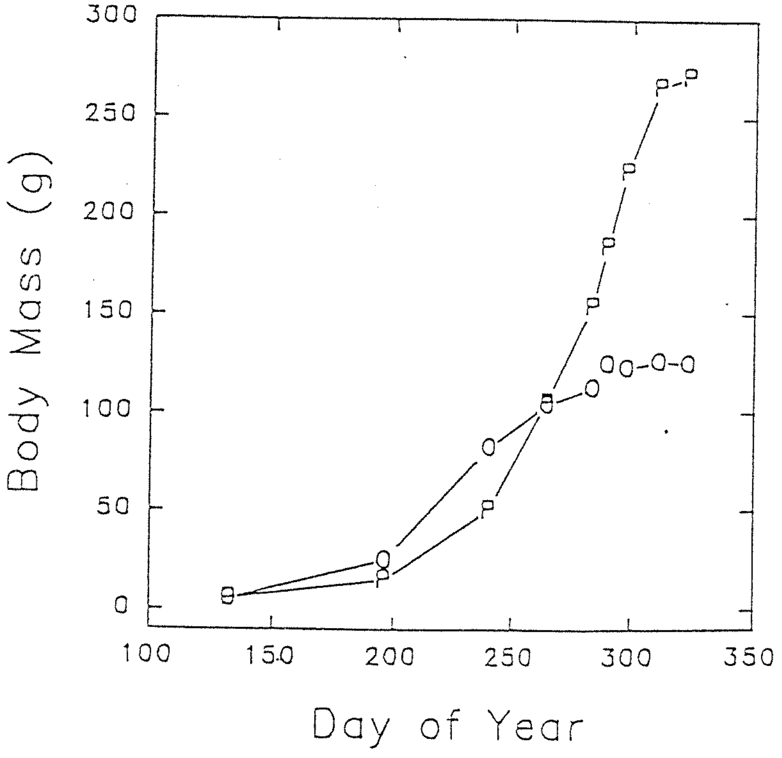
90
80
70
60
50
40
260
280
300
320
340
360
Day of Year
O
P



350
300
250
200
150
100
50
0
250
300
350
400
Body Mass (g)
Day of Year
O
P



700
300
200
100
0
250
300
350
400
Day of Year
O
P



300
250
200
150
100
50
0
100
150
200
250
300
350
Body Mass (g)
Day of Year
O
P

Appendix

TABLE 1. - Individual yearly correlations corresponding to those discussed in the text for the entire pooled data set. "Deviation" refers to the difference between observed and model-predicted instantaneous growth rates of sea lampreys (observed minus predicted). The columns 1989a and 1989b correspond to the high and low temperature experiments of Swink (1993). Statistical significance at the 0.05, 0.01, and 0.001 levels is indicated by one, two, or three asterisks, respectively.

	1983	1984	1985	1986	1987	1989a	1989b
Correlates	(N=63)	(N=172)	(N=155)	(N=159)	(N=107)	(N=45)	(N=32)
predicted vs. observed final lamprey mass	0.994***	0.979***	0.957***	0.964***	0.953***	0.984***	0.960***
predicted vs observed instantaneous growth rate	0.642***	0.384***	0.401***	0.259***	0.472***	0.608***	0.246
deviation vs. initial lamprey mass	-0.121	-0.276***	-0.193*	-0.231**	-0.209*	-0.233	-0.418*
deviation vs. initial date of feeding bout	-0.138	-0.157*	-0.171*	-0.176*	-0.113	0.006	-0.337
deviation vs. mean daily water temperature	-0.152	0.215**	0.096	0.077	0.014	-0.099	0.290

Appendix I

Using the Lamprey Feeding Model

The sea lamprey model originally used by Cochran and Kitchell (1989) was programmed in BASIC and designed for use on the Commodore Pet. A listing of the BASIC programming code of this model was used to create an updated version of the model. The new model was programmed in Pascal for use on IBM-compatible machines. Major changes to the sea lamprey model of Cochran and Kitchell (1989) include an ability of the new model to handle a large amount of data, a capability to operate at temperatures other than 10°C, and a more user-friendly interface. The core of the new lamprey model functions are displayed on a main menu, which allows the user to 1) use the lamprey model, 2) edit model parameters, 3) print data files, or 4) quit to DOS (Fig. 1) (see Appendix II for help in installing the lamprey model onto your computer).

The first option on the main menu, "lamprey model," executes the lamprey feeding and bioenergetics model. Before the model begins, the user is allowed to choose between entering lamprey feeding bout information manually or by using a file (Fig. 2). (When many lamprey feeding bouts are to be modelled, entering lamprey feeding bout information by using a file is more efficient than entering data manually.) If the user chooses to enter data by using a file and presses "Y," the user is asked to input the lamprey model information file name (Fig. 3) and the lamprey information in the file is inserted automatically into the model run information screen (Fig. 4) (see Appendix III for help in creating lamprey data files). If "N" is entered, information must be input manually in the model run information screen (Fig. 4). After the information is entered, daily calculations from the starving lamprey model are displayed to the screen (Fig. 5). When the lamprey attaches to the host and begins feeding, the user is notified of a switch to the feeding model (Fig. 6). At this time the user has the option to edit parameters (Fig. 7), a process described below. Next, the daily calculations from the lamprey feeding model are displayed to the screen (Fig. 5). Lastly, the results of the entire lamprey feeding bout are displayed (Fig. 8). In the case of manual entry of lamprey information, the main menu (Fig. 1) appears. Conversely, in the case of file entry of multiple lamprey feeding bouts, data on the next lamprey in the lamprey information file appears on the lamprey model run information screen (Fig. 4) (see Appendix IV for a brief outline of the above process).

The "edit parameters" choice on the main menu gives the user the ability to modify consumption, respiration, egestion, and excretion constants and the percent blood volume removed and temperature variables (Fig. 7). These modifications may be made either at the main menu or in between non-feeding and feeding intervals of a lamprey model run.

The third option, "print results," permits the user to print lamprey model results to a file. The print options menu displays three different methods for printing a file, as illustrated in Fig. 9. After a print option is selected, the user is prompted for the name of the print file (Fig. 10). Next, the user is notified of the print choice and the print options menu reappears (Fig. 9). Entering choice (4) returns the user to the main menu. The subsequent lamprey model run is printed to a file in the designated method. An exception to the above involves print option (1), which operates only if information is entered using a file.

To guarantee that the conversion of the model was accurate, it was validated with results previously obtained by Cochran and Kitchell (1989). The results of the conversion are summarized in Table 1. The correlation between model-predicted lamprey biomass in 1989 and 1996 was 1.0 and the correlation between modeled instantaneous growth rates in 1989 and 1996 was 0.998. The regression equation of instantaneous growth rates for 1989 and 1996 was : G_{96}=-0.000192+1.03 G_{89} (Fig. 11). There is a small discrepancy in the results between the two model versions because Cochran and Kitchell (1989) used partial days to calculate the percent blood volume removed whereas the 1996 model uses whole days only.

Appendix II

Getting Started

Requirements: An IBM compatible machine with the DOS operating system.

Procedure:

1) Go to the DOS prompt (C:\>).

2) At the C:\> prompt make a directory called lamprey and enter the lamprey directory. The following commands will perform this task:

```
mkdir  lamprey <enter>
cd lamprey <enter>
```

The result of these commands should put the cursor at the c:\lamprey\ prompt.

3) Copy all files from the lamprey model disk to the lamprey directory. The following commands will perform this task:

insert the lamprey model disk into drive a:

```
copy a:*.* c:\lamprey <enter>
```

The result of these commands should be the indication of the copying of all files. Note that some computers will use the b: drive instead of the a: drive. If you enter the above command and you get an error message, enter a b: in place of a: in the command above.

4) The sea lamprey model is now loaded onto your computer's c: drive. Anytime you wish to start the model type:

```
sealamp <enter>
```

at the c:\lamprey\ prompt.

5) When you have quit the model type:

```
cd..
```

at the c:\lamprey\ prompt and you will return to where you began (C:\>).

Appendix III

Creation of Temperature and Lamprey Model Information Files

1) Use spreadsheet applications and save the information as a text or ASCII file. Be sure there is at least one space between each column of data. To view and/or manipulate the data in the file type:

```
edit [filename] <enter>
```

where you replace [filename] with the name of your text file.

2) Format:

Temperature Files: Temperature files consist of a julian date and temperature (°C) (Fig. 12). These temperature files coincide with the year input in the lamprey model information screen. Unfortunately, the model will recognize only temperature files from the years 1983-1987, 1989 and a special file ten.prn, which has all temperatures set at 10°C. These files should be on your computer and have the name temp*.prn, where the * is replaced by the last two digits of the year. To use your own temperature data modify one of these using the edit command as described above and save the file. During the next lamprey model run enter the year that corresponds to the file you modified to use your modified temperature file. Also note that if a lamprey feeding bout extends beyond julian date 365, simply enter dates beyond 365 (e.g. 366, 367...).

Lamprey Model Information Files: Consist of a lamprey ID number, julian start day, julian attach day, julian detach day, number of days detached, number of days attached, lamprey initial biomass (g), lamprey final biomass (g), change in lamprey biomass (g), host biomass (g), year, host status (status of the host fish after the lamprey feeding bout, Y = host died and N = host alive), and fish type (Fig. 13). The fish type codes permit separate consideration of more than one host type. The model recognizes several codes used in past applications (lt - lake trout, ls - Seneca strain lake trout, lm - Marquette strain lake trout, ss - small lake trout, mm - medium lake trout, ll - large lake trout, rt - rainbow trout). In a typical application with one host type, use any one of these.

Appendix IV

Lamprey Model General Outline

1) Choose option 1 (Lamprey Model) at the main menu (Fig. 1).

2) Option of entering lamprey model run information using a file. If entering lamprey information manually skip to number 4.

3) Enter the name of the data file to be used as lamprey model run information (Fig. 2).

4) Lamprey model run information screen (Fig. 3). If inputting information manually, enter it now. If entering information by using a file, verify the lamprey feeding information.

5) The results of the starving lamprey model are displayed (Fig. 4).

6) Notification of a switch from the starving lamprey model to the feeding lamprey model (Fig. 5).

7) Option of adjusting parameters (Fig. 6).

8) The results of the feeding lamprey model are displayed (Fig. 4).

9) Summary of lamprey feeding bout (Fig. 7).

10) If entering information by file go to step 4. Otherwise the main menu will appear.

Table 1. Corresponding predictions of Cochran and Kitchell's (1989) model and the current model (1996). Listed are model predicted lamprey final biomass for 1989 and 1996, and lamprey instantaneous growth rate ([ln(final biomass/initial biomass)]/t) for 1989 and 1996, both based on the lamprey feeding histories in Cochran and Kitchell (1989).

Model Predicted Final Biomass 1989	Model Predicted Final Biomass 1996	Model Predicted Instantaneous Growth Rate 1989	Model Predicted Instantaneous Growth Rate 1996
11.75	11.78	0.0051140	0.0051393
13.23	13.25	0.0068578	0.0068814
10.96	10.99	0.0131215	0.0131916
9.51	9.53	0.0186239	0.0187079
8.66	8.67	0.0177941	0.0178422
14.27	14.29	0.0099024	0.0099233
11.78	11.80	0.0060719	0.0060926
12.94	12.97	0.0028105	0.0028273
11.38	11.36	0.0008832	0.0008506
14.13	14.39	0.0203984	0.0220560
17.57	17.59	0.0138513	0.0138838
10.90	10.93	0.0063761	0.0064088
8.83	8.85	0.0090019	0.0090726
11.18	11.21	0.0191848	0.0192518

Figure 1. Main menu screen. Listed are the three major options of the program. The 9 indicates where the user's choice is inserted.

```
    S E A   L A M P R E Y   B I O E N E R G E T I C S   M O D E L

                             M A I N   M E N U

                            1)  Lamprey Model
                            2)  Parameter Editing
                            3)  Data File Print Options
                            4)  Quit to DOS
                            CHOICE? 9

                                    _______
                     |\       ______\______\____
                     | \    /                   \
Sea Lamprey -->  ~~\ |    \_/   /~~~~~~~~~ /  *   \
                    ~|~~~~~~~~~~          |     ___\
                     |    /\_              \      /
                     | /    \_______       /___/
                     |/             /____ /
```

Figure 2. Screen prompting user to input entry method of lamprey feeding bout information. The X indicates where the user's choice is entered.

Input Lamprey Run Information
Using A File(Y or N)? X

Figure 3. Screen used to obtain the information file name which contains information on lampreys with multiple feeding bouts. This file must be saved in the C:\lamprey directory.

```
Please Enter the Name of the Data File to be Used : XXXXXXXXXXXXX
```

Figure 4. Lamprey information required for the model.

```
 L A M P R E Y   M O D E L   R U N   I N F O R M A T I O N

  BIOMASS INFORMATION
-----------------------
Observed Lamprey Final Biomass(g)  : 9999.99
Observed Lamprey Inital Biomass(g) : 9999.99
Host Biomass(g)                    : 9999.99

Host killed(Y or N) : X
Fish Type(Abbr.)    : XX
                                              ________
                               |\       _______\______\_____
TIMING INFORMATION(Julian)     |   \    /                   \
------------------------       |     \_/             /   *    \
Attachment Date     : 999      |                    |        ___\
Start of feeding    : 999      |     /\_             \         /
Detachment Date     : 999      |   /    \_______       /____ /
Year of Attack      : 99       |/              /____ /


            <Press F10 To Accept Data Set>
```

Figure 5. Results from daily calculations of both the starving model (top) and feeding model (bottom). Listed are the number of days of the lamprey bout, the julian date, lamprey biomass, temperature, net energy, and percent blood volume removed as adjusted to temperature.

```
      Julian Date     Biomass      Temperature      Net Energy      BloodVolume

 1        120          59.97            3             -0.17            0.00
 2        121          59.90            5             -0.49            0.00
 3        122          59.84            5             -0.80            0.00
 4        123          59.78            5             -1.12            0.00
 5        124          59.72            5             -1.43            0.00
 6        125          59.66            5             -1.75            0.00
 7        126          59.60            5             -2.06            0.00
 8        127          59.54            5             -2.37            0.00
 9        128          59.48            5             -2.69            0.00
10        129          59.41            5             -3.00            0.00
11        130          59.34            6             -3.39            0.00
12        131          59.28            5             -3.70            0.00
13        132          59.22            5             -4.02            0.00
14        133          59.16            5             -4.33            0.00
15        134          59.11            4             -4.57            0.00
16        135          59.03            6             -4.95            0.00
17        136          58.96            6             -5.34            0.00
18        137          58.90            5             -5.65            0.00
19        138          58.82            6             -6.04            0.00
20        139          58.76            5             -6.35            0.00
ress Any Key To Continue...

      Julian Date     Biomass      Temperature      Net Energy      BloodVolume

31        150          59.83            5             -0.85            9.41
32        151          61.87            6              9.57           10.36
33        152          64.09            7             20.95           11.37
34        153          66.30            7             32.31           11.37
35        154          68.33            6             42.69           10.36
36        155          70.35            6             53.06           10.36
37        156          72.76            8             65.38           12.44
38        157          75.16            8             77.69           12.44
39        158          77.56            8             89.97           12.44
40        159          79.90            8            101.97           12.44
41        160          82.04            7            112.98           11.37
42        161          84.17            8            123.85           12.44
43        162          86.20            9            134.29           13.57
44        163          88.13            9            144.14           13.57
45        164          89.94            9            153.42           13.57
46        165          91.68            8            162.33           12.44
47        166          93.33            8            170.81           12.44
48        167          94.84            9            178.57           13.57
49        168          96.04           11            184.71           15.92
50        169          96.99           12            189.57           17.11
Press Any Key To Continue...
```

Figure 6. Screen indicating a switch from the starving to the feeding lamprey model.

```
    T H E   S E A   L A M P R E Y   W I L L   N O W   B E G I N

                         F E E D I N G

                                    _______
                     |\       ______\______\____
                     |  \    /                   \
Sea Lamprey -->  ~~\ |    \_/   /~~~~~~~~~ /  *   \
                    ~|~~~~~~~~~~          |     ___\
                     |    /\_              \      /
                     |  /    \_______       /___/
                     |/             /____ /


Press Any Key To Continue...
```

Figure 7. Screen that allows the user to change parameters in lamprey model.

```
                        P A R A M E T E R S

    CONSUMPTION CONSTANTS
-------------------------------               <Press F10 To Accept>
Temperature optimum consumption 99                 <Data Set>
Temperature maximum consumption 99
Q............................. 9.9            BLOOD VOLUME CONSTANT
                                            -------------------------
     RESPIRATION CONSTANTS                    Percent Blood Volume 999.99
-------------------------------
Activity(9.99) ................ 9.99
a2(9.9999) .................... 9.9999
b2(99.99) ..................... 99.99
Qr(9.9) ....................... 9.9
Specific Dynamic Action(9.99)   9.99
Temperature Optimum Respiration 99
Temperature Maximum Respiration 99              TEMPERATURE CONSTANTS
                                            ----------------------------
  EGESTION/EXCRETION CONSTANTS              Thermoregulation Temperature 99
-------------------------------
alphaEgestion (9.99) .......... 9.99
alphaExcretion (9.99) ......... 9.99
```

Figure 8. Final results of a lamprey feeding bout, listing total number of days of lamprey observation, percent of host blood volume removed daily (not adjusted to temperature), observed instantaneous growth rate, modeled instantaneous growth rate, observed final biomass and modeled final biomass.

```
   C A L C U L A T E D   O U T P U T

Total Number Of Days Of Lamprey Observation : 60 day(s)

Modeled Instantaneous Growth Rate : 0.0088
Observed Instantaneous Growth Rate : 0.0085



Original Percent Of Host Blood Volume Removed Daily : 14.73%

Modeled Lamprey Biomass :  101.97
Observed Lamprey Biomass :  100.00
Press Any Key To Continue...
```

Figure 9. Print options main menu allowing the user to choose the information printed to a file. These choices are summarized below.

```
   P R I N T   O P T I O N S

 1)   Print Model Run Output to a File
 2)   Print Input Data and Parameters to a File
 3)   Print Model Parameters and Model run
            Input and Output Data to a File
 4)   Exit Print Options
 CHOICE? 9

                                    _______
                     |\       ______\______\____ \
                     |  \    /                    \
Sea Lamprey -->  ~~\ |    \_/   /~~~~~~~~~ /  *    \
                    ~|~~~~~~~~~~          |         \
                     |                          ___
                     |    /\_              \      /
                     |  /    \_______       /___/
                     |/             /____ /
```

Figure 10. Screen used to obtain name of print file.

```
Please Enter the Name of the Print File : XXXXXXXXXXXXXX
```

Figure 11. Instantaneous growth rate predicted by the 1995 conversion of the model versus Cochran and Kitchell 's (1989) original predictions. Both sets of predictions are based on the lamprey feeding histories listed in Cochran and Kitchell (1989).

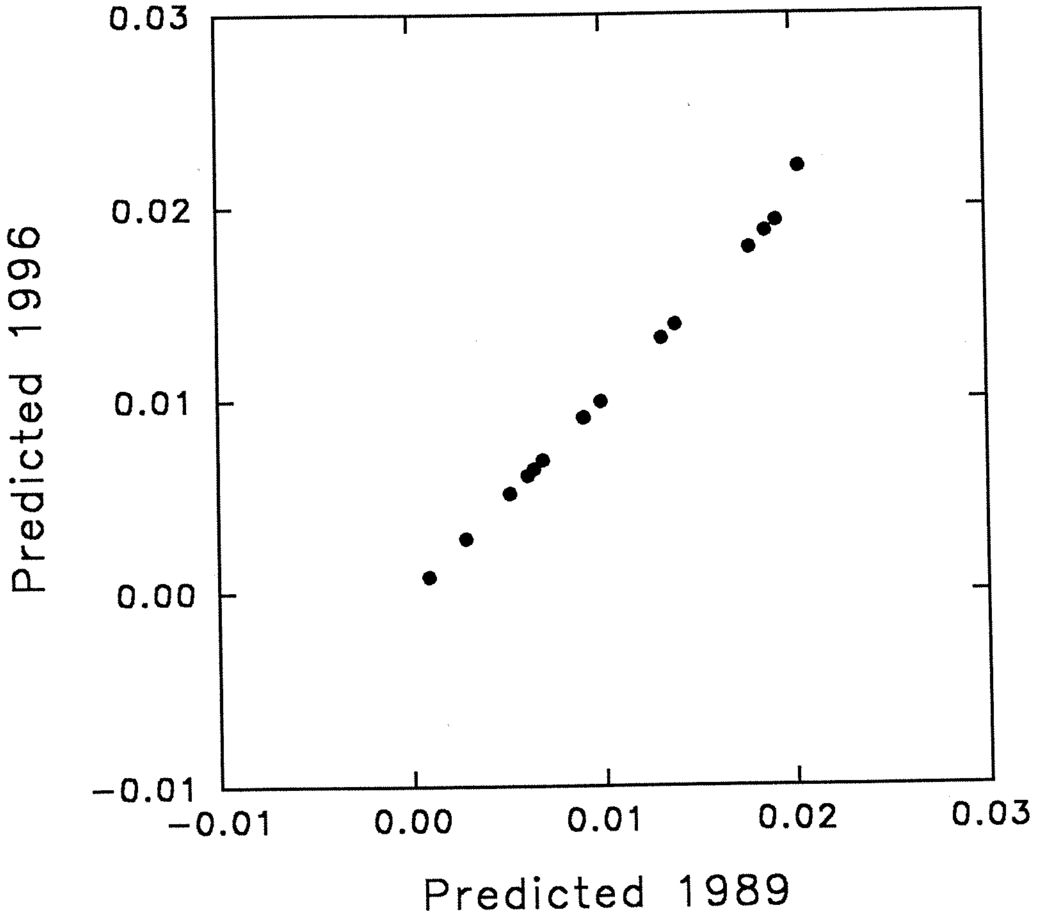

0.03
0.02
0.01
0.00
−0.01
Predicted 1996
−0.01
0.00
0.01
0.02
0.03
Predicted 1989

Figure 12. Sample temperature file consisting of julian dates and corresponding water temperatures (°C).

115	0
116	4
117	5
118	4
119	3
120	3
121	5
122	5
123	5
124	5
125	5
126	5
127	5
128	5
129	5
130	6
131	5
132	5
133	5
134	4
135	6
136	6
137	5
138	6
139	5
140	6
141	6
142	5
143	6
144	6
145	7
146	7
147	7
148	6
149	6
150	5
151	6
152	7
153	7
154	6
155	6
156	8
157	8
158	8
159	8
160	7
161	8
162	9
163	9
164	9
165	8
166	8
167	9
168	11
169	12
170	13
171	12
172	11
173	9
174	12
175	14

Figure 13. Sample lamprey model input file consisting of a lamprey ID number, julian start day, julian attach day, julian detach day, number of days detached, number of days attached, lamprey initial biomass (g), lamprey final biomass (g), change in lamprey biomass (g), host biomass (g), year, host status ("Y" or "N"), and fish type (lt - lake trout, ls - seneca strain lake trout, lm - marquette strain lake trout, ss - small lake trout, mm - medium lake trout, ll - large lake trout, rt - rainbow trout).

1	114	136	202	22	66	5.4	57.1	51.7	893	84	n	ls
1	202	210	212	8	2	57.1	58.2	1.1	371	84	y	lm
1	212	212	213	0	1	58.2	60.0	1.8	344	84	y	ls
1	214	217	219	3	2	60.0	63.7	3.7	505	84	y	lm
1	224	225	226	1	1	63.7	83.8	20.1	980	84	y	ls
1	226	229	230	3	1	83.8	84.0	0.2	470	84	y	lm
1	232	232	234	0	2	84.0	104.2	20.2	1290	84	y	ls
1	234	236	237	2	1	104.2	105.8	1.6	962	84	y	lm
1	237	238	239	1	1	105.8	115.3	9.5	1140	84	y	ls
1	239	244	245	5	1	115.3	115.3	0	870	84	y	lm
1	245	246	252	1	7	115.3	122.0	6.7	1083	84	y	ls
73	259	266	275	7	9	31.5	45.3	13.8	832	84	y	lm
91	278	283	289	5	6	79.2	101.5	22.3	1096	84	y	ls
100	302	306	311	4	5	51.8	62.1	10.3	526	84	y	lm
100	311	312	315	1	3	62.1	75.7	13.6	762	84	n	ls
100	315	315	316	0	1	75.7	72.7	-3.0	480	84	n	lm
100	316	317	336	1	19	72.7	84.3	11.6	1621	84	n	ls
2	116	139	170	23	31	3.9	4.0	0.01	651	84	n	lm
48	180	197	198	17	1	4.3	8.5	4.2	1134	84	n	ls
48	199	200	203	1	3	8.5	10.5	2.0	217	84	y	lm
48	203	204	207	1	3	10.5	14.1	3.6	765	84	y	ls
48	207	208	210	1	2	14.1	16.5	2.4	360	84	y	lm
48	210	211	213	1	2	16.5	18.6	2.1	525	84	y	ls
54	214	216	217	2	1	14.8	17.3	2.5	734	84	n	lm
54	218	234	239	16	5	17.3	21.8	4.5	1121	84	y	ls
54	240	242	246	2	4	21.8	25.9	4.1	582	84	y	lm
64	247	248	248	1	0	25.9	26.1	0.2	798	84	y	ls
64	250	250	252	0	2	26.1	28.8	2.7	608	84	n	lm
77	267	270	271	3	1	62.9	71.4	8.5	1007	84	n	ls
77	271	272	273	1	1	71.4	81.8	10.4	692	84	y	lm
3	114	118	211	4	93	4.7	60.5	55.8	550	84	y	ls
3	211	217	218	6	1	60.5	53	-7.5	332	84	y	lm
3	218	219	234	1	15	53	79.3	26.3	1321	84	y	ls
60	233	237	238	4	1	14.7	15.2	0.5	886	84	y	ls
63	245	246	251	1	5	7.9	9.4	1.5	767	84	y	ls
70	255	262	266	7	4	30.1	34.1	4	606	84	n	lm
86	275	283	284	8	1	43.2	57.4	14.2	674	84	n	ls
86	284	288	294	4	6	57.4	68.9	11.5	532	84	y	lm
86	294	297	298	3	1	68.9	58.9	-10	729	84	n	ls
86	298	302	302	4	0	58.9	56.1	-2.8	706	84	n	lm
86	302	305	313	3	8	56.1	65.2	9.1	542	84	y	ls