GREAT LAKES FISHERY COMMISSION

Project Completion Report[1]

Change in the energy density of the sea lamprey (*Petromyzon marinus*) during its parasitic phase: implications for modelling food consumption and growth

by:

Philip A. Cochran[2], Jay Y. Hodgson[3], and Andrew P. Kinziger[4]

[2] Division of Natural Sciences
St. Norbert College
DePere, Wisconsin 54115

[3] Department of Natural Resources and Environmental Sciences
University of Illinois
Champaign, IL 61820

[4] Department of Biology
St. Louis University
3507 Laclede Avenue
St. Louis, MO 63103-2010

August 1999

---

[1] Project completion reports of Commission-sponsored research are made available to the Commission's Cooperators in the interest of rapid dissemination of information that may be useful in Great Lakes fishery management, research, or administration. The reader should be aware that project completion reports have not been through a peer review process and that sponsorship of the project by the Commission does not necessarily imply that the findings or conclusions are endorsed by the Commission.

Change in the energy density of the sea lamprey (*Petromyzon marinus*) during its parasitic phase: implications for modelling food consumption and growth

Philip A. Cochran, Jay Y. Hodgson[1], and Andrew P. Kinziger[2]
Division of Natural Sciences
St. Norbert College
DePere, Wisconsin 54115

[1]Department of Natural Resources and Environmental Sciences, University of Illinois, Champaign, IL 61820
[2]Department of Biology, St. Louis University, 3507 Laclede Avenue, St. Louis, MO 63103-2010

Introduction

This project represents part of a larger attempt to integrate modeling and field data to improve the estimation of damage done by sea lampreys to host populations. It is hoped that ultimately a sea lamprey individual-based model (IBM) will be developed for use in predicting the consequences of varying the abundances and size distributions of sea lampreys and host populations. Specific objectives of the larger project are to (1) refine a combined model of sea lamprey bioenergetics (Kitchell and Breck 1980) and feeding (Cochran and Kitchell 1989, Cochran et al. 1999), (2) develop an IBM for seasonal growth by parasitic-phase sea lampreys using the modified bioenergetics and feeding model and the data of Bergstedt and Swink (1995), (3) use the IBM to determine the seasonality of blood consumption by the sea lamprey population and the distribution of consumption among individuals, and (4) expand the capabilities of the IBM by including a consideration of sea lamprey feeding behavior and calibrating the model to lamprey wounding data. Personnel from three institutions are collaborating in this effort: P.A. Cochran at St. Norbert College, R. Bergstedt at the Lake Huron Biological Station, and C.P. Madenjian at the Great Lakes Science Center. The portion of this project contracted to St. Norbert College involved objective (1) above.

Cochran and Kitchell (1989) presented a model of sea lamprey feeding that quantified energy consumption by a sea lamprey as a function of lamprey size, host (trout) size, duration of the feeding attachment, and interval between feedings. Rates of energy consumption predicted by the feeding model were used as input to the bioenergetics model of Kitchell and Breck (1980) to generate predictions of lamprey growth. Unlike the original bioenergetics model, the feeding model accounted for changes in the host's blood quality (energy concentration) during the course of a feeding attachment, and it allowed for variation in feeding behavior among individual lampreys and among individual feeding bouts by the same lamprey. It proved useful for examining qualitatively such facets of feeding behavior as duration of attachment, size selectivity, and host species selectivity (Cochran and Kitchell 1986,1989; Cochran 1994). The feeding model was tested quantitatively in a preliminary way by Cochran and Kitchell (1989), who compared observed instantaneous growth by fourteen captive lampreys to predictions generated by the model on the basis of the lampreys' known feeding histories. More recently, Cochran et al. (1999) performed a much more extensive test of the feeding model by comparing model predictions to observed instantaneous growth by captive lampreys feeding on trout during six years of experiments at the Lake Huron Biological Station (733 feeding bouts).
Model predictions were highly correlated with observed growth rates, and a decomposition of the deviations between observed and predicted values (using the method of [Theil 1961] as applied to the evaluation of fish bioenergetics models by Rice and Cochran [1984] and Whitledge and Hayward [1997]) revealed that most of the variance (88.5%) was due to random variation rather than systematic biases. Nevertheless, predicted growth tended to exceed observed growth by large lampreys late in the year . Cochran et al. (1999) suggested several possible reasons for this pattern, including seasonal changes in host blood quality, a "slowing down" in blood removal rates by overwintering lampreys, a seasonal or size-related change in lamprey metabolic rate (Claridge and Potter 1975), or a seasonal or size-related change in energy concentration of lamprey tissue (Beamish et al. 1979). In the latter case, an increase in wet energy density of lamprey tissue (cal/g wet mass) with increasing lamprey size would be associated with an

overestimate of growth in wet mass by a model that assumed a constant wet energy density.

A recent application of the lamprey feeding model of Cochran et al. (1999) not only provided an example of the model's utility but also helped to narrow the focus of efforts to improve the model. Although the main goal of the analysis was to support a study of mortality in burbot (*Lota lota*) from sea lamprey attack (Swink and Fredricks, MS) by comparing the growth performance of captive sea lampreys feeding on burbot to that of lampreys feeding on trout, the exercise provided insights useful to the goals of the present study. Growth by lampreys feeding on burbot (55 feeding bouts) was compared with model predictions for lampreys feeding on trout of identical sizes for identical lengths of time. Also, deviations between observed and predicted growth rates for lampreys feeding on burbot were compared with those obtained by Cochran et al. (1999) for lampreys feeding on trout. Striking similarities in the patterns obtained for burbot and trout suggested that burbot and trout of equivalent sizes are virtually interchangeable with respect to their value to lampreys as food resources. Even though the feeding model was originally derived from data for lampreys feeding on trout, model predictions of growth by lampreys feeding on burbot were highly correlated with observed values ($r = 0.441$, $P < 0.01$), and almost all of the difference between them (99.8%) was due to random variation rather than systematic bias. Just as observed by Cochran et al. (1999) for lampreys feeding on trout, however, model predictions tended to overestimate growth by large lampreys feeding on burbot late in the year. That similar discrepancies were observed for two unrelated host taxa justifies the focus in the present study on potential refinements to the lamprey portion of the feeding model rather than to model parameters having to do with the host.

As outlined above, a potential source of bias in previous model predictions of lamprey growth may have resulted from the assumption that energy density of lamprey tissue is constant. Beamish et al. (1979) found that lipid content as a percentage of wet mass increased dramatically during the trophic phase of the anadromous sea lamprey. If such a shift occurs in the Great Lakes sea lamprey and is associated with an increase in energy density, then the current model may predict greater increases in wet mass than are actually observed. Hence, one goal of the present study was to measure through bomb calorimetry the energy density of parasitic-phase sea lampreys collected in Lake Huron throughout the growing season. In the event that significant shifts in wet energy density occurred with changes in wet mass, a second objective was to determine to what extent predictions of lamprey growth could be improved by making appropriate modifications in the model.

Materials and Methods

Collection and Initial Processing of Lampreys

Parasitic phase sea lampreys were obtained in 1996 and 1997 from commercial fishers operating in the vicinity of the Lake Huron Biological Station. They were measured for total length and wet mass prior to freezing at -80°C and longterm storage at -20°C. Measurements were repeated when lampreys were thawed prior to analyses of energy density and water content, and sex was determined from inspection of gonads (Applegate and Thomas 1965).

Energy density

We used bomb calorimetry (Vondracek et al. 1996, Kitchell et al. 1977) to assess the energy density of lamprey tissue. Lampreys designated for bomb calorimetry were homegenized with distilled water in a commercial blender, frozen at -20°C, and freeze-dried to constant mass. Dried tissue was ground with a mortar and pestle, and at least three subsamples (~1.0 g each) from most lampreys were combusted in a Parr Model 1108 Plain Oxygen Bomb Calorimeter some lampreys were too small to provide more than one or two subsamples).

Water content

We found it necessary to assess water content of lamprey tissue by freeze-drying a subsample of lampreys separately from those used for bomb calorimetry. The latter were homogenized before drying because it was difficult to homogenize their skin after drying, but it was also difficult to recover their entire wet mass from the blender.

Statistical analyses

Statistical procedures were conducted with Minitab 12 for Windows following the standard protocols of Snedecor and Cochran (1967). Double logarithmic transformations were applied prior to linear regression analyses to stabilize variances and straighten curvilinear relationships.

Modelling

After our analyses revealed a relationship between energy density of lamprey tissue and lamprey mass (see Results), this relationship was incorporated into the lamprey feeding model. To assess whether this change contributed to improved prediction of sea lamprey feeding and growth, we used the same Lake Huron Biological Station data set originally used by Cochran et al. (1999) to test the lamprey feeding model. This data set consists of feeding and growth histories for individual sea lampreys used in laboratory experiments during the period 1983-1989, and it includes requisite information (initial lamprey mass, host mass, feeding duration, water temperature, etc.) for comparing model predictions of lamprey growth with growth actually recorded during the experiments. We compared the original model predictions by Cochran et al. (1999) for the 1984 data subset to the performance of the revised lamprey feeding model by using the same procedures followed by Cochran et al. (1999), including Theil's (1961) decomposition of mean squared error (MSE). We also generated predicted trajectories of growth over multiple feeding bouts for the same eight individual lampreys used as examples by Cochran et al. (1999; their Figs. 5 and 6) and compared them to the actual and original predicted trajectories.

Results

Water Content

Dry mass as a percentage of wet mass increased with wet mass. This was evident as a curvilinear relationship between dry mass and wet mass (Fig. 1), and for subsequent regression analyses we we used the natural logarithms of both variables (Table 1). Multiple linear regression analyses for lampreys collected in 1996 and 1997 indicated that in neither year did season (day of year) contribute significantly to prediction of ln(dry mass) once ln(wet mass) was included in the regression. Comparison of regression lines for the two sexes within each year failed to reveal significant differences in residual variances (1996: $F_{12,18} = 1.05$, $P = 0.45$; 1997: $F_{17,7} = 1.64$, $P = 0.36$), slopes (1996: $F_{1,30} = 0.38$, $P = 0.54$; 1997: $F_{1,24} = 0.06$, $P = 0.80$), or y-intercepts (1996: $F_{1,31} = 0.01$; $P = 0.91$; 1997: $F_{1,25} = 0.38$, $P = 0.54$). Similarly, a comparison of regression lines for the two years, with data for males and females pooled within years, failed to reveal significant differences (residual variances: $F_{32,26} = 1.43$, $P = 0.18$; slopes: $F_{1,58} = 0.04$, $P = 0.84$; y-intercepts: $F_{1,59} = 0.22$, $P = 0.64$).

Energy Density

Dry energy density (cal/g dry mass) increased with wet body mass (Fig. 2). A multiple regression analysis indicated that season (day of year) failed to contribute significantly to the prediction of ln(dry energy density) once ln(wet mass) was included in the regression. Comparison of regression lines for the two sexes (Table 2) revealed no significant differences between residual variances ($F_{49,38} = 1.41$, $P = 0.14$), slopes ($F_{1,87} = 1.83$, $P = 0.18$), or y-intercepts ($F_{1,88} = 2.96$, $P = 0.09$).

We estimated wet energy density (cal/g wet mass) for each lamprey used in the calorimetric analyses by (1) using the ln(dry mass)-ln(wet mass) regression from the appropriate year (Table 1) to estimate its dry mass, (2) multiplying its dry energy density by its dry mass to estimate its total energy content, and (3) dividing its total energy content by its wet mass.

Wet energy density increased with wet mass in a curvilinear fashion (Fig. 3), and we used the natural logarithms of the two variables in subsequent regression analyses (Table 3). A multiple regression analysis indicated that season (day of year) failed to contribute significantly to the prediction of ln(wet energy density) once ln(wet mass) was included in the regression. Comparison of regressions for the two sexes in 1996 yielded results identical to those for dry energy density.

Results for lampreys collected in 1997 were consistent with those obtained in 1996. We measured energy density for only 10 lampreys from 1997 (range in wet mass = 31-248 g) and did not calculate a regression of ln(wet energy density) on ln(wet mass) for that year, although the two variables were highly correlated ($r = 0.92$, $P < 0.001$). When we used the 1997 lamprey wet masses in conjunction with the 1996 regression (Table 3) to predict wet energy densities, the predicted values were highly correlated with the measured values ($r = 0.86$, $P = 0.002$), and the mean deviation between predicted and measured wet energy density was only 1.9% of the measured value. This difference was not significantly different from zero (paired *t*-test, $t = 0.98$, $P = 0.35$).

Modelling

When we incorporated the relationship between wet energy density and sea lamprey wet body mass (Table 3) into the sea lamprey feeding model, the model's ability to predict growth by individual lampreys with known feeding histories was improved. For example, in comparison to predictions of instantaneous growth rates for the 1984 Lake Huron Biological Station data set with the unmodified model (Cochran et al. 1999), the modified model produced predictions that were more highly correlated with measured growth rates ($r = 0.43$ versus $r = 0.38$) (Fig. 4).

Moreover, the mean deviation between observed values and the predictions of the modified model (0.00178, $n = 172$) was not significantly different from zero (paired-*t* test, $t = 1.01$, $P = 0.32$), whereas the greater mean deviation for the unmodified model (0.00349) was of marginal significance ($T = 1.92$, $P = 0.056$). The magnitude (absolute value) of the deviation between observed and predicted instantaneous growth rates was greater for the unmodified model than it was for the revised version (paired-t test, t = 4.77, P < 0.0001). Decomposition of mean squared error (MSE), which was smaller in the modified model (0.00053 versus 0.00058), revealed that a greater proportion of that error was due to random variation rather than systematic error (97% for the modified model versus 93% for the unmodified).

Examples of the improvement in model prediction that resulted from accounting for changing wet energy density were provided by growth trajectories for eight individual lampreys over the course of multiple feeding bouts (Figs. 5,6). In comparison to the trajectories predicted by Cochran et al. (1999) for the same individuals, the trajectories predicted by the modified model tend to diverge less from the actual trajectories, especially for large lampreys late in the year (Fig. 6), and correlations between observed and predicted values are greater for the modified model (paired-*t* test, $T = 2.73$, $P = 0.029$).

Discussion

We hypothesized that wet energy density would increase with body size of parasitic-phase sea lampreys in the Great Lakes. This expectation was based not only on the results of previous modelling exercises (Cochran et al. 1999), but also on empirical measurements of proximal body composition in anadromous sea lampreys (Beamish et al. 1979), which showed that lipid content increased substantially during the parasitic phase. Our results are consistent with our initial expectation.

The increase in wet energy density with increasing wet mass that we observed reflected both a decline in water content as a percentage of wet mass and an increase in concentration of energy in dry matter. Beamish et al. (1979) reported a decrease in percentage water content with increasing body mass of parasitic-phase anadromous sea lampreys. To compare their results to ours, we used the wet masses listed in their Table 2 with our regression of ln(dry mass) on ln(wet mass), using the equation derived by pooling data for both sexes in both years (Table 1), to generate predictions of percentage water content. For parasitic-phase animals, our estimates are within 3% of the measured values (Table 4), but our regression becomes increasingly inadequate as percentage water content increases during migration, spawning, and the subsequent time before death. We caution that our results are applicable only during the parasitic phase.

Our confidence in the adequacy of our measurements and analyses of water content and energy density is bolstered by the consistency of our results between the years 1996 and 1997. Moreover, coefficients of variation (*CV*) among calorimetric subsamples from individual lampreys (mean $CV = 2.29\%$, range = 0.12-14.34%) were generally comparable to previously reported values (e.g., the mean *CV*s $\leq 4.26\%$ reported by Vondracek et al. 1996), with a single exception that resulted from the first lamprey combusted.

The mean of our wet energy density measurements (1199 cal/g) is only 2.0 % lower than the constant value (1224 cal/g) used in previous energetics-based models of sea lamprey feeding and growth (Kitchell and Breck 1980, Cochran and Kitchell 1989, Cochran et al. 1999). This value was derived from the empirical measurements of Farmer (1974), who reported mean values for percentage water content (79.7 %) and dry energy density (6029 cal/g) very similar to our overall means (76.9% and 6068 cal/g, respectively). Farmer (1974), however, provided no indication of whether water content or energy density varied with body size. Our results suggest that a lamprey of 73 g wet mass should have a wet energy density of 1224 cal/g, and that as wet mass varies above or below this value, wet energy density should increase or decrease, respectively (Fig. 3).

Adjusting the lamprey feeding model to account for the relationship between wet mass and wet energy density improved the model's ability to predict growth. Although predictions were improved for both small and large lampreys, the improvements were most noticeable for larger lampreys (Fig. 6), apparently because of their greater absolute increments of wet body mass. There is still a great deal of scatter in the plot of observed versus predicted instantaneous growth rates (Fig. 4), and the tendency of the model to overestimate growth by large lampreys late in the year was not completely eliminated (Fig. 6). As discussed by Cochran et al. (1999), much of the variability in deviations between observed and model-predicted growth rates may result from natural variability in lamprey feeding rates, and the feeding model may tend to overestimate lamprey energy consumption and growth if lampreys do not actively feed during the entire time that they remain attached to prey. Additional hypotheses that remain to be tested include the possibilities that (1) a late seasonal "slowing down" in blood removal rates by large lampreys results in energy consumption rates even less than predicted by the feeding model on the basis of reduced water temperatures, and (2) a seasonal or size-related increase in metabolic rate, of the sort observed by Claridge and Potter (1975) in the European river lamprey (*Lampetra fluviatilis)*, results in a reduced growth increment for a given amount of energy consumed (Cochran et al. 1999).

In the present study, our modelling efforts were made simpler by a lack of significant differences between sexes in the shifts in water content and energy density that occur with increasing wet mass and by the lack of significant seasonal effects once the effects of wet mass were accounted for. Indeed, it would have been problematic to test the model against data for captive lampreys if seasonal effects had been important. Nevertheless, sex-related or seasonal effects could in theory be included in an energetics-based model of feeding and growth. The need to make such modifications should not be dismissed as a shortcoming of the modelling approach. As discussed by Pielou (1981), and as exemplified by the evolution of the lamprey feeding model to its current form, models are valuable not only for their explanatory power or their ability to make successful predictions, but also for their ability to contribute to the generation of testable hypotheses. It is only when observations and model predictions do not agree that hypothesized relationships are reexamined in a self-corrective process that is characteristic of the general scientific enterprise.

Acknowledgements

We thank the personnel at the Lake Huron Biological Station for facilitating this effort, especially Roger A. Bergstedt, who provided sea lampreys, the bomb calorimetor, and useful discussion, and William D. Swink, who made available data from his laboratory experiments.

David Poister of St. Norbert College provided assistance with the freeze drier. This work was funded primarily by the Great Lakes Fishery Commission. In addition, JYH received support from an Anselm M. Keefe Summer Research Fellowship through St. Norbert College.

References

Applegate, V.C. and M.L.H. Thomas. 1965. Sex ratios and sexual dimorphism among recently transformed sea lampreys, *Petromyzon marinus* Linnaeus. Journal of the Fisheries Research Board of Canada 22:695-711.

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 landlocked sea lampreys (*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 (eds.). 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.

Cochran, P.A., W.D. Swink, and A.P. Kinziger. 1999. Testing and extension of a sea lamprey feeding model. Transactions of the American Fisheries Society 128:403-413.

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

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.

Kitchell, J.F., J.J. Magnuson, and W.H. Neill. 1977. Estimation of caloric content for fish. Environmental Biology of Fishes 2:185-188.

Pielou, E.C. 1981. The usefulness of ecological models: a stock-taking. The Quarterly Review of Biology 56:17-31.

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

Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods, 3rd edition. Iowa State University Press, Ames, IA.

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

Vondracek, B., B.D. Giese, and M.G. Henry. 1996. Energy density of three fishes from Minnesota waters of Lake Superior. Journal of Great Lakes Research 22:757-764.

Whitledge, G.W. and R.S. Hayward. 1997. Laboratory evaluation of a bioenergetics model for largemouth bass at two temperatures and feeding levels. Transactions of the American Fisheries Society 126:1030-1035.

Table 1. Simple linear least squares regressions of the natural logarithm of dry mass in grams on the natural logarithm of wet mass in grams for parasitic-phase sea lampreys collected in northern Lake Huron in 1996 and 1997. Also indicated for each regression are the sample size (*n*) and the coefficient of determination (r^2).

Year	Sex	Regression	*n*	r^2
1996:	males -	ln(dry mass) = -2.01 + 1.09*ln(wet mass)	20	0.951
	females -	ln(dry mass) = -2.27 + 1.16*ln(wet mass)	14	0.929
	pooled -	ln(dry mass) = -2.08 + 1.11*ln(wet mass)	34	0.944
1997	males -	ln(dry mass) = -2.22 + 1.17*ln(wet mass)	19	0.975
	females -	ln(dry mass) = -2.28 + 1.18*ln(wet mass)	9	0.971
	pooled -	ln(dry mass) = -2.24 + 1.17*ln(wet mass)	28	0.974
Both years pooled:		ln(dry mass) = -2.19 + 1.15*ln (wet mass)	62	0.959

Table 2. Simple linear least squares regressions of the natural logarithm of dry energy density (cal/g dry mass) on the natural logarithm of wet body mass in grams for sea lampreys collected in northern Lake Huron in 1996. Also indicated for each regression are the sample size (*n*) and the coefficient of determination (r^2).

Sex	Regression	*n*	r^2
Male	ln(dry energy density) = 8.58 + 0.0284*ln(wet mass)	51	0.135
Female	ln(dry energy density) = 8.51 + 0.0507*ln(wet mass)	40	0.318
Pooled	ln(dry energy density) = 8.55 + 0.0386*ln(wet mass)	91	0.216

Table 3. Simple linear least squares regressions of the natural logarithm of wet energy density (cal/g wet mass) on the natural logarithm of wet body mass in grams for sea lampreys collected in northern Lake Huron in 1996. Also indicated for each regression are the sample size (*n*) and the coefficient of determination (r^2).

Sex	Regression	n	r^2
Male	ln(wet energy density) = 6.50 + 0.138*ln(wet mass)	51	0.787
Female	ln(wet energy density) = 6.43 + 0.161*ln(wet mass)	40	0.824
Pooled	ln(wet energy density) = 6.47 + 0.149*ln(wet mass)	91	0.804

Table 4. Percentage water content of anadromous sea lampreys measured by Beamish et al. (1979) at various stages and predicted for lampreys of the same wet body masses using the regression from the present study for both sexes and years pooled (Table 1).

Stage	Sex	Wet Mass (g)	Observed % Water	Predicted % Water
small feeding				
	male	2.7	85.3	87.0
	female	3.5	85.6	86.5
large feeding				
	male	35.7	78.5	80.9
	female	34.2	80.4	81.0
early immature migrant				
	male	876.1	75.8	69.1
	female	896.1	71.6	69.0
nearly mature migrant				
	male	868.4	76.5	69.1
	female	885.2	72.9	69.0
spawning				
	female	777.0	78.6	69.6
spent				
	male	776.7	82.6	69.6
	female	645.1	82.3	70.5

Fig. 1. Dry mass (g) versus wet mass (g) for male (solid circles) and female (solid diamonds) parasitic-phase sea lampreys collected in northern Lake Huron in 1996 and 1997.

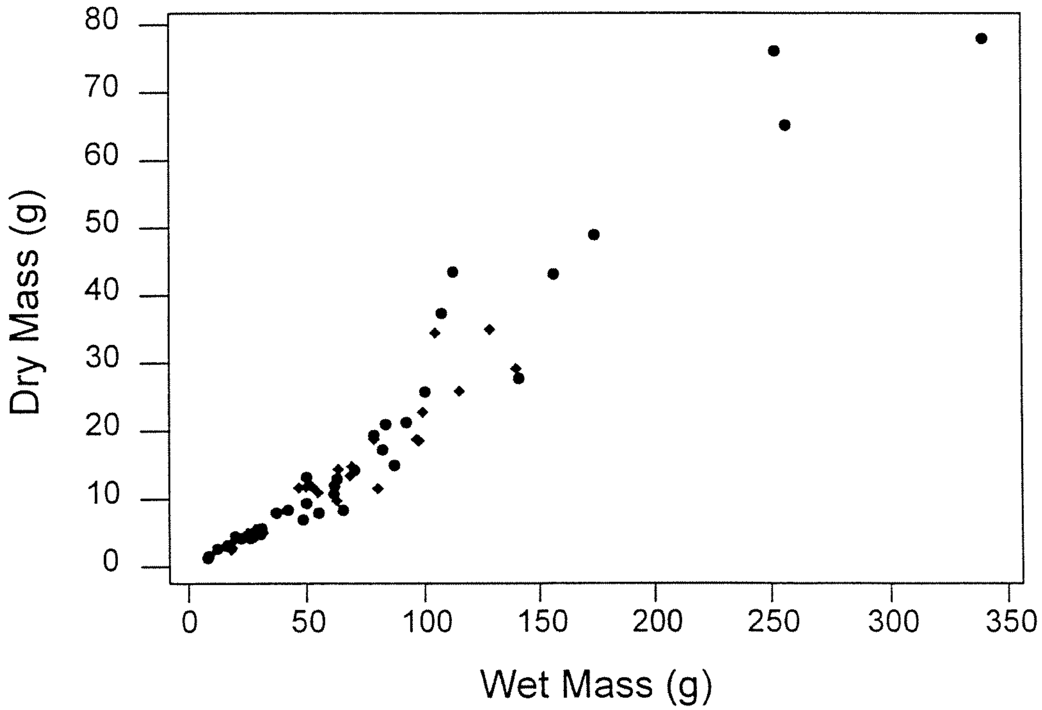
Fig. 2. Dry energy density (cal/g) for male (solid circles) and female (solid diamonds) parasitic-phase sea lampreys collected in northern Lake Huron in 1996.

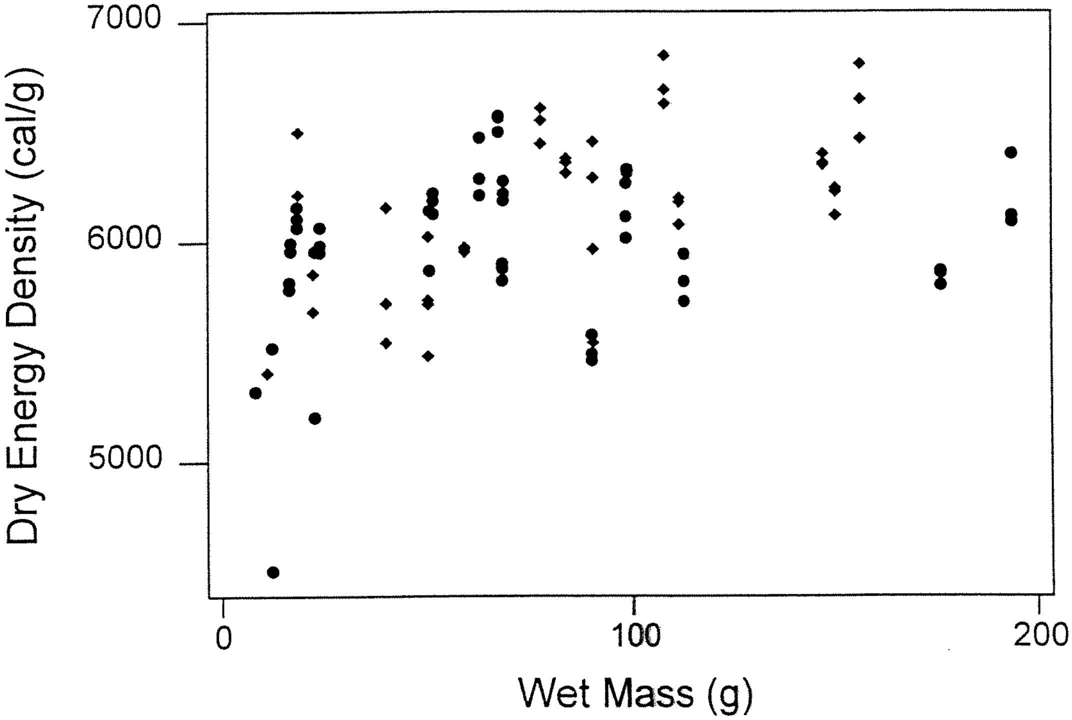
Fig. 3. Wet energy density (cal/g) for male (solid circles) and female (solid diamonds) parasitic-phase sea lampreys collected in northern Lake Huron in 1996. The dashed line indicates the constant value assumed in previous energetics and feeding models (Kitchell and Breck 1980, Cochran and Kitchell 1989, Cochran et al. 1999).

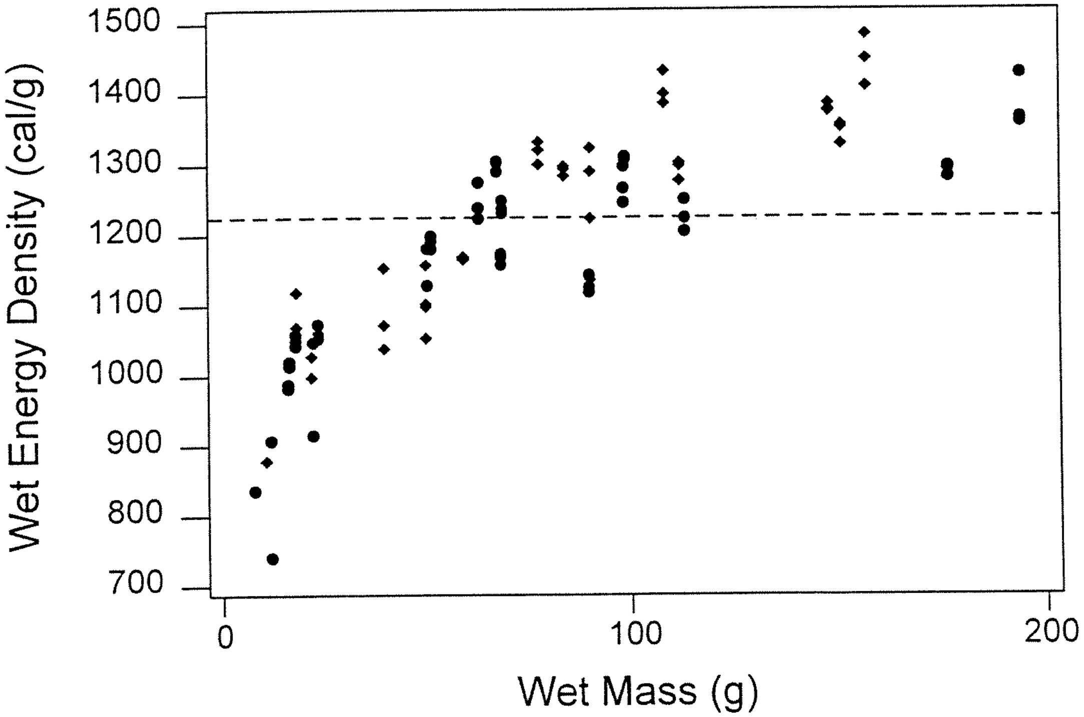
Fig. 4. Observed versus predicted instantaneous rates of growth (G) in wet mass by captive parasitic-phase sea lampreys in the Lake Huron Biological Station 1884 data set. Each dot represents a feeding bout by an individual sea lamprey. Growth for the top panel was predicted with the feeding model of Cochran et al (1999), which did not account for change in energy density with increasing body mass. Growth for the bottom panel was predicted with the feeding model as modified during the present study to account for changing energy density.

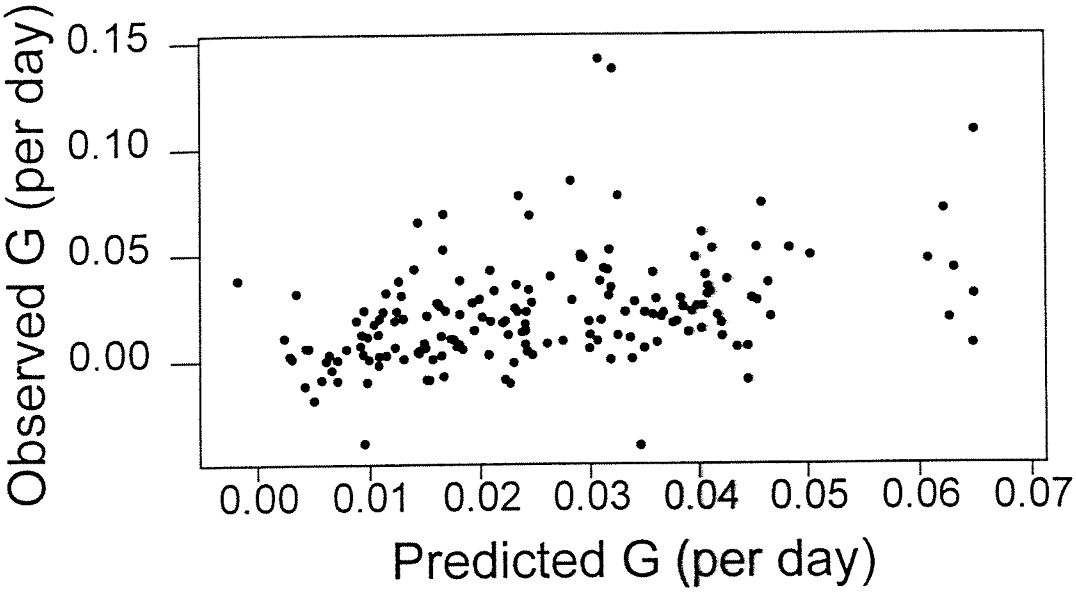
Fig. 5. Representative examples of observed (solid lines and circles) and model-predicted lamprey wet mass (g) versus time (day of year) for captive sea lampreys with feeding histories consisting of multiple feeding bouts early in the year. The examples used here are the same individuals used in Fig. 5 of Cochran et al. (1999). Each panel represents an individual lamprey. The dotted lines indicate the trajectories predicted by Cochran et al. (1999), whereas the dashed lines indicate the trajectories predicted with the feeding model as modified during the present study to account for changing energy density with increasing body mass.

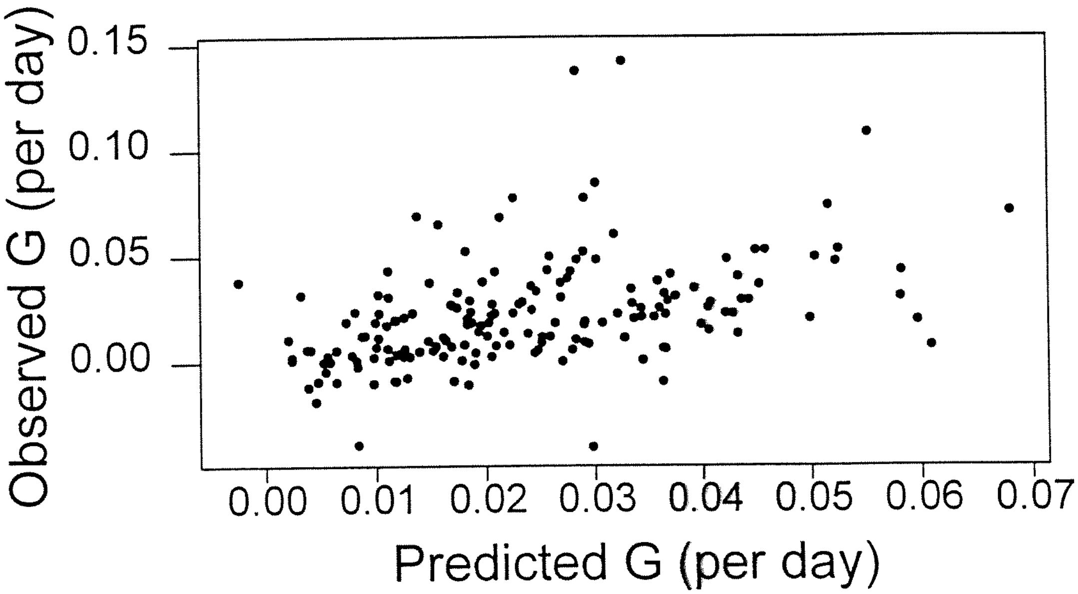
Fig. 6. Representative examples of observed (solid lines and circles) and model-predicted lamprey wet mass (g) versus time (day of year) for captive sea lampreys with feeding histories consisting of multiple feeding bouts late in the year. The examples used here are the same individuals used in Fig. 6 of Cochran et al. (1999). Each panel represents an individual lamprey. The dotted lines indicate the trajectories predicted by Cochran et al. (1999), whereas the dashed lines indicate the trajectories predicted with the feeding model as modified during the present study to account for changing energy density with increasing body mass.

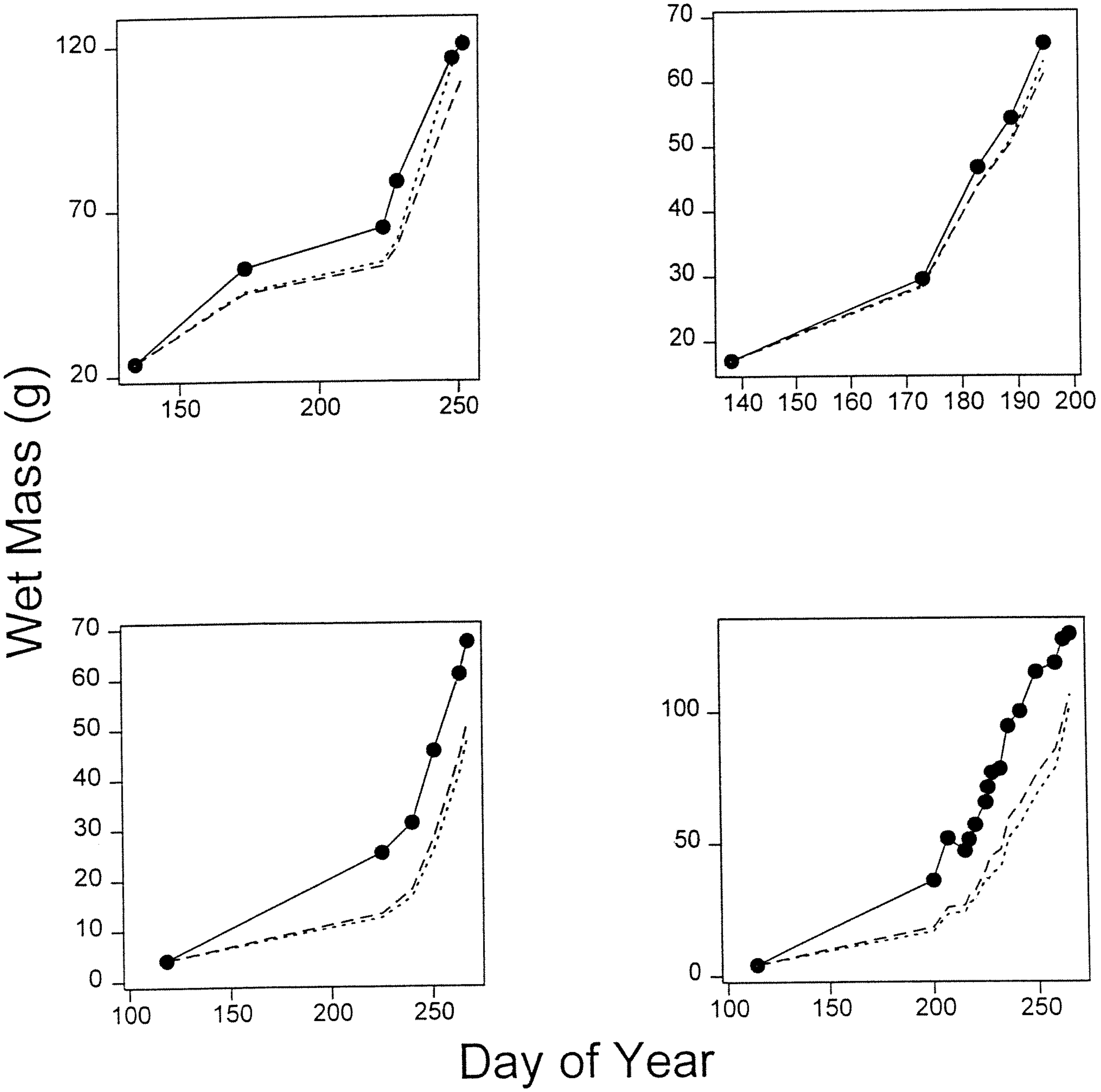

80
70
60
50
40
30
20
10
0
Dry Mass (g)
0
50
100
150
200
250
300
350
Wet Mass (g)

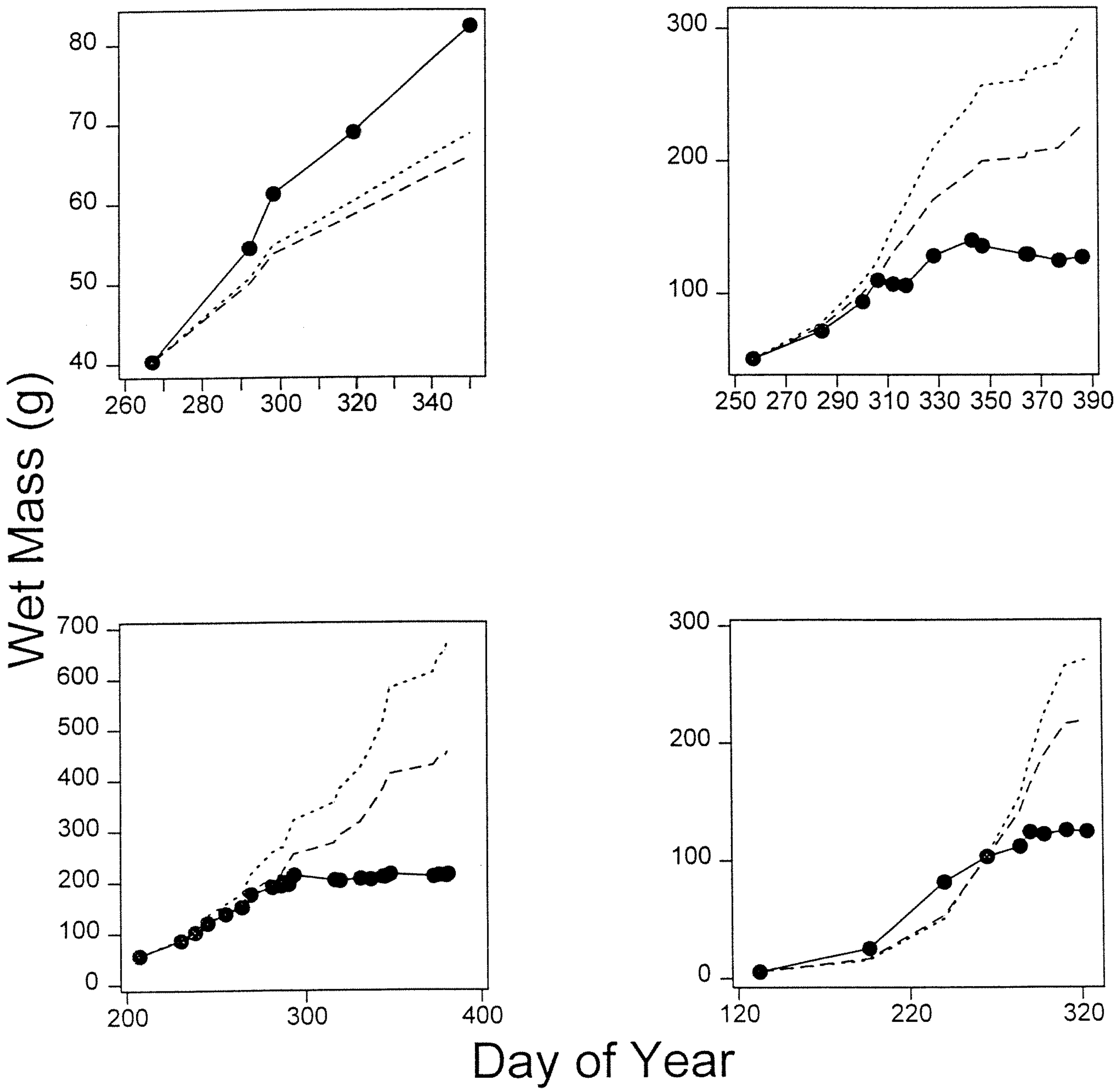

7000
6000
5000
Dry Energy Density (cal/g)
0
100
200
Wet Mass (g)


Wet Energy Density (cal/g)
1500
1400
1300
1200
1100
1000
900
800
700
0
100
200
Wet Mass (g)


Observed G (per day)
0.15
0.10
0.05
0.00
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
Predicted G (per day)


Observed G (per day)
0.15
0.10
0.05
0.00
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
Predicted G (per day)


Wet Mass (g)
Day of Year
120
70
20
150
200
250
70
60
50
40
30
20
140
150
160
170
180
190
200
70
60
50
40
30
20
10
0
100
150
200
250
100
50
0
100
150
200
250



Wet Mass (g)
Day of Year
80
70
60
50
40
260
280
300
320
340
300
200
100
250
270
290
310
330
350
370
390
700
600
500
400
300
200
100
0
200
300
400
300
200
100
0
120
220
320