

A Model of Feeding by Parasitic Lampreys

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We derived a quantitative feeding model to estimate energy intake by parasitic sea lampreys (*Petromyzon marinus*) as a function of lamprey mass, host mass, and attachment time. Comparison of model predictions with observed growth by lampreys with known feeding histories suggests that the feeding model, used in conjunction with a previous model of lamprey energetics, generates unbiased predictions of energy intake and subsequent growth. On the basis of the relationship between energy intake and attachment time, and in accordance with previous theory on partial prey consumption, we hypothesized that duration of attachment by lampreys to individual hosts should vary inversely with host density. No significant difference in attachment time or latency to attack at two host densities could be detected, although the first attachment by a lamprey tended to be longer than its second, regardless of host density.

Les auteurs ont élaboré un modèle d'alimentation quantitative visant à calculer l'apport énergétique des lamproies de mer parasites (*Petromyzon marinus*) en fonction de la masse des lamproies, de la masse de l'hôte et de la durée de fixation. La comparaison des prédictions obtenues et de la croissance observée chez les lamproies dont l'alimentation est connue semble indiquer que ce modèle, utilisé avec un modèle de l'énergétique des lamproies élaboré précédemment, permet d'obtenir des prédictions non biaisées de l'apport énergétique et de la croissance qui en résulte. Conformément à une théorie précédente portant sur la consommation partielle des proies, et parce qu'il existe un lien entre l'apport énergétique et la durée de fixation, les auteurs ont émis l'hypothèse suivante : la durée de la fixation des lamproies à leur hôte est inversement proportionnelle à la densité des hôtes. Peu importe la densité des hôtes, aucune différence significative dans la durée de fixation ni dans le temps écoulé avant la fixation n'a pu être observée, bien que la première fixation d'une lamproie ait tendance à être plus longue que la deuxième.

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One puzzling aspect of interactions between populations of parasitic lampreys and their hosts has been the remarkable differences in host mortality that have been observed among localities. The evidence for such differences among freshwater populations of the sea lamprey (*Petromyzon marinus*) has been summarized by Kitchell and Breck (1980); lamprey-induced mortality is significant over nearly two orders of magnitude of variation in scarring frequency [the use of injuries to make inferences about the impact of predation has been addressed in other contexts by Schoener (1979), Murtaugh (1981), and Morin (1985)]. Although some host populations persist even when almost all fish carry multiple scars (Pearce et al. 1980), experimental work summarized by Farmer (1980) suggests that an adult lamprey can kill even large salmonids in a relatively short time, and lamprey-induced mortality rates may be high even though observed rates of wounding and scarring are low (Smith et al. 1974). The devastating contribution of sea lampreys to the collapse of lake trout (*Salvelinus namaycush*) and other fish stocks in the Upper Great Lakes is well known (Smith 1971), yet landlocked sea lamprey may have coexisted with lake trout and other fishes in lakes such as Lake Ontario, Lake Champlain, and the Finger Lakes for hundreds if not thousands of years (Brussard et al. 1981).

Kitchell and Breck (1980) proposed a hypothesis to explain the apparently conflicting relationships among lamprey-induced mortality and marking rates: lampreys may exercise choice between acting as predators, which kill their prey, and parasites, which do not, based on their perception of host density. They suggested that selection should favor parasitic feeding when host densities are high because (a) host blood quality declines as a lamprey remains attached to a single host (Farmer 1980), and (b) blood is a rapidly renewable resource, and its level will be restored after a lamprey detaches. It is perhaps more parsimonious to consider (b) a fortuitous consequence rather than a selective advantage, since the latter could only result from group selection.

A hypothesis closely related to that of Kitchell and Breck (1980), but based on duration of attachment, can be adapted from the theory of optimal foraging as applied to the partial consumption of prey (Cook and Cockrell 1978; Sih 1980). If quality of food ingested declines as a function of time spent feeding on an individual prey item, this theory predicts that feeding time should be positively related to expected costs (time and energy) of searching for another item. Thus, feeding time should decline when prey densities and encounter rates are high

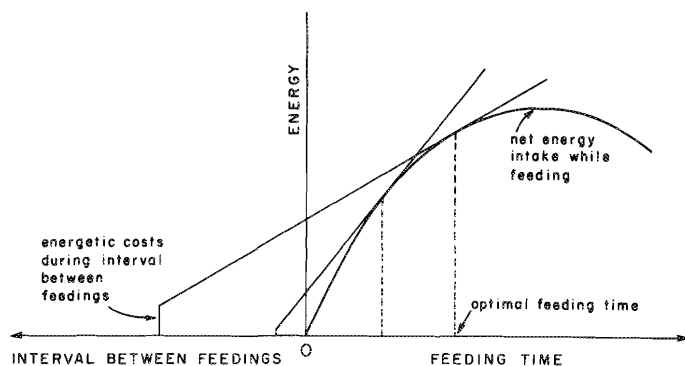


FIG. 1. Net energy intake by a predator from a single prey item as a function of time spent feeding on the item. The tangent drawn from an interval between feedings on the x axis locates the corresponding optimal feeding time in terms of overall rate of net energy intake. Optimal feeding time increases as either intercatch interval or non-feeding costs increase. Adapted from Sih (1980).

(Fig. 1). Food quality is most often measured in terms of energy (Pyke et al. 1977). Mean blood energy concentration (kJ/g wet weight) of trout has been shown to have declined by 84% just prior to death from lamprey attacks (Farmer 1980).

Implications of this hypothesis for lamprey-host dynamics are essentially the same as those outlined by Kitchell and Breck (1980). All else equal, a shorter mean attachment time generally should be associated with a lower host mortality rate. (However, if for some range of attachment times, stress, infection by pathogens, or some other agent causes delayed mortality subsequent to lamprey detachment, then a decrease in mean attachment time might result in a greater host mortality rate because more fish will be attacked). A lamprey-host system conceivably could be characterized by two stable states: a lower equilibrium with the host population held in check by high lamprey-induced mortality rates as a result of long attachment times, and a higher equilibrium with very short attachment times and low host mortality.

By far the greatest bulk of fisheries research on the trophic impact of parasitic phase sea lamprey has involved measurement and analysis of population attributes (marking rates, mortality rates, etc.). However, the impact of a lamprey population is the result of individual behaviors, and natural selection operates most strongly at the level of the individual. With this paper we address the need for informed observation and analysis of individual lamprey behavior. We develop and evaluate a quantitative model of energy intake by a lamprey from its host. We describe a laboratory experiment on the effect of host density on lamprey attachment times. Finally, we show how the lamprey feeding model can be used to examine such phenomena as host size selectivity.

Methods and Materials

The Feeding Model

Our model is applicable to those parasitic lampreys, such as *P. marinus*, that feed by removing blood through a hole rasped in the side of a fish (Potter and Hilliard 1987). Assume that the fraction of a host's blood volume removed during any instant by a feeding lamprey is proportional to the biomass of the lamprey (L) and inversely proportional to the biomass of the host (F), although a curvilinear relationship may prove to be more realistic over broader ranges of lamprey and host sizes

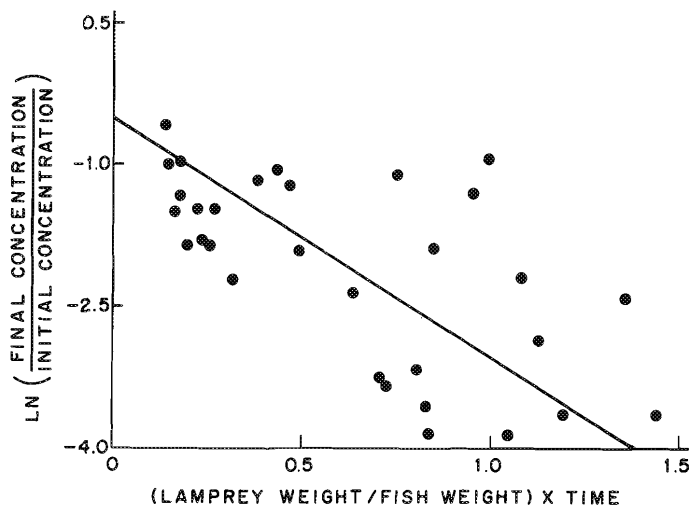


FIG. 2. Scatterplot of the ratio of the final to initial concentration of ^{51}Cr in blood of host trout (B/B_0) versus the product of the ratio of lamprey to host wet weight (L/F) and feeding time in days (t). The functional regression is $\ln(B/B_0) = -0.50 - 2.54 (L/F)t$, ($r^2 = 0.39$). Data from Farmer (1974).

than those considered here. Assume further that host blood volume remains constant due to osmotic influx of water (Farmer et al. 1975). It follows that

$$(1) \quad dB/dt = -K(L/F)B$$

$$(2) \quad B = B_0 \exp(-K(L/F)t)$$

and, by integration,

$$(3) \quad \ln(B/B_0) = -K(L/F)t$$

where K is a proportionality constant, B is the concentration of original blood remaining at time t after the onset of feeding, and B_0 is blood concentration at $t = 0$, the onset of feeding. We tested this hypothesis with data collected by Farmer (1974), who tagged the blood of trout with radioactive ^{51}Cr and measured its decline after feeding by lampreys of known size at 10°C (Fig. 2). The variables in Fig. 2 are strongly correlated ($r = -0.629$, $P < 0.01$) and a fit of equation (3) to the data produced a slope (K) of magnitude 2.54. [Probability levels and correlation coefficients presented here are those associated with normal least squares regression, but the GM functional regression advocated by Ricker (1973) was used to obtain model parameters.] The product of this slope and the ratio of lamprey to host biomass provides an estimate of the proportion of the host's blood volume removed daily.

Loss of blood to a feeding lamprey is offset to some extent by blood regeneration. G. Farmer (Dep. Fisheries and Oceans, Halifax, N.S., pers. comm.) observed that blood quality of attacked trout remained similar to that of control fish for some time after the initiation of an attack; his data (Fig. 3) can be used to estimate the minimum length of this interval as a function of the percentage of host blood volume removed daily (V):

$$(4) \quad \ln(Q) = 4.92 - 1.08(\ln(V))$$

where Q is the feeding time in days ($r^2 = 0.759$, $t = -4.69$, $P < 0.005$). The feeding time that results in host death (D) can also be related to the percentage of host blood volume removed daily (Fig. 3; see also Farmer et al. 1975):

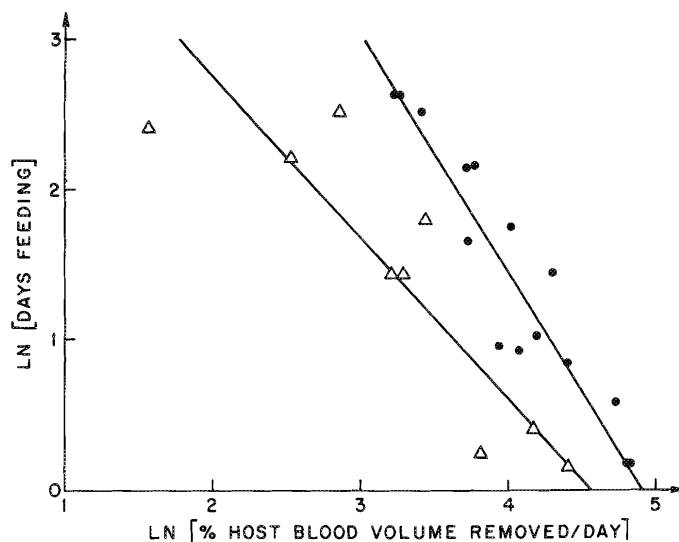


FIG. 3. Scatterplot of feeding time in days versus percentage of host blood volume removed per day for trout with normal blood quality (triangles) and moribund trout with reduced blood quality (dots), with corresponding functional regression lines [text equations (4) and (5), respectively]. Data from Farmer et al. (1975) and G. Farmer (Dep. Fisheries and Oceans, Halifax, N.S., per comm.).

$$(5) \ln(D) = 8.03 - 1.63(\ln(V))$$

$$(r^2 = 0.880, t = -9.77, P < 0.001).$$

One independent data set is consistent with equation (4). Kinnunen and Johnson (1985) allowed sea lampreys with a mean body mass of 13.5 g to feed on rainbow trout with a mean body mass of 309.1 g for 10 d at 12°C. At the end of this period, blood hematocrit and hemoglobin levels had not declined significantly from initial values. According to equation (3) above, the lampreys were removing 11.1% of their hosts' blood volume daily, and according to equation (4), the hosts should have been able to maintain blood quality for 10.2 d. Kinnunen and Johnson (1985) also allowed lampreys with a mean body mass of 25.3 g to feed on trout with a mean body mass of 328.4 g for 8 d, at which time blood hematocrit and hemoglobin had declined significantly. According to equation (3) the lampreys were removing 19.6% of their hosts' blood volume daily, and the hosts should have been able to maintain blood quality for 5.5 d.

The implications of equations (2), (4), and (5) taken together are that a lamprey of a given biomass (L) attached to a trout of a given biomass (F) receives a constant ration for Q days, during which time blood regeneration by the host is sufficient to offset losses to the lamprey (Fig. 4). Daily ration is the product of the proportion of host blood volume removed daily, the blood volume of the host (4.7% of wet body weight for *Oncorhynchus mykiss* (formally *Salmo gairdneri*) in freshwater — Smith 1966), and the energy concentration of the blood (3.29 kJ/g wet weight — Farmer 1980). Proportion of host blood volume removed daily can be estimated in two ways: (a) a posteriori from equation (5) if the host has been killed after a known period of time, or (b) a priori from equation (3) (i.e., $V/100 = 2.54(L/F)$). Equation (3) implies that daily ration in terms of wet weight is a constant proportion of lamprey biomass ($2.54 \times (L/F) \times 0.047F = 0.119L$). While this may be true on average, individual variability is great (Fig. 2), and the use of equation (5) for individual cases is preferable when applicable.

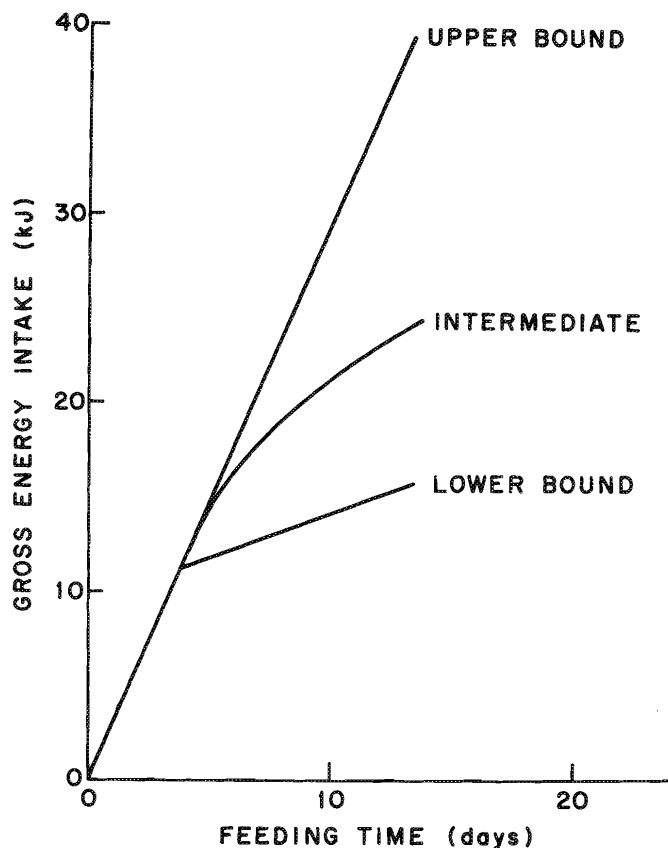


FIG. 4. Predicted gross energy intake by a 7.4 g lamprey from a 68.2 g trout as a function of feeding time. Host death occurs on the fourteenth day of feeding. Upper and lower bound: host blood energy concentration assumed constant at 3.29 and 0.54 kJ/g wet weight, respectively. Intermediate: host blood energy concentration assumed to decline exponentially from 3.29 to 0.54 kJ/g wet weight. Lamprey and host biomass correspond to mean values from first round of experiment.

During the period of feeding from time Q to time D , the predicted point of host death, daily ration declines as host blood energy concentration decreases from 3.29 to 0.53 kJ/g wet weight (Farmer 1980). Although we have no data on the dynamics of this decline, we suggest two extremes that bracket the range of possibilities. At one extreme, it can be assumed that the host's blood regenerative capability continues unabated up to the point of death, so that blood energy level remains constant. This should lead to an overestimate of energy intake. At the other extreme, it can be assumed that blood energy level on day Q declines instantly from 3.29 to 0.53 kJ/g and remains at that level until day D . This should provide a lower bound to energy intake during this interval. A simple and logical intermediate possibility is that blood energy declines exponentially during the period from Q to D (Fig. 4).

The lamprey feeding model thus requires the following information to estimate the energy taken up by a lamprey from its host: the biomass of the lamprey, the biomass of the host, and the duration of attachment. As a preliminary test of the model, we estimated energy consumption by 14 lampreys during the laboratory experiment described below, based on their known feeding histories during the experiment. We did not have direct measurements of the amount of energy actually consumed by each lamprey, but we did measure the weight change experienced by each individual. We therefore used our model estimates of energy uptake in conjunction with the sea lamprey

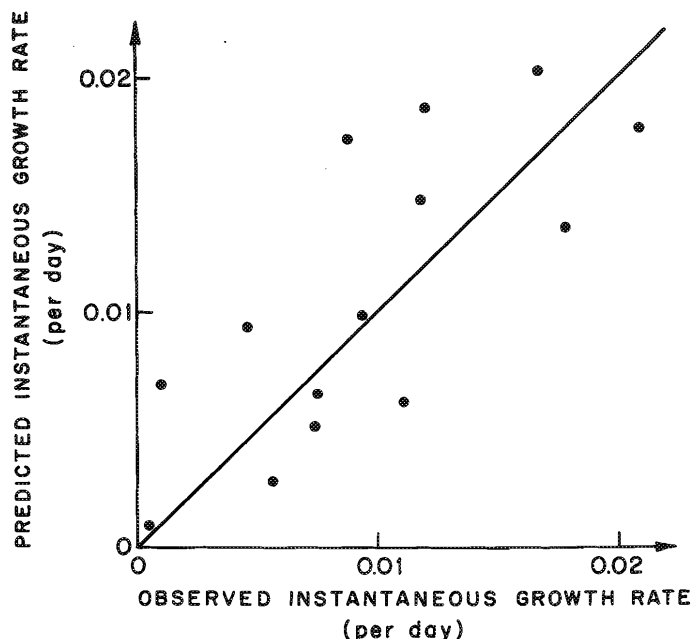


FIG. 5. Predicted instantaneous growth rates (per day) of individual experimental lampreys under intermediate assumption of exponential host blood energy decline versus observed rates ($r = 0.75$). The diagonal identity line ($y = x$) is provided for comparison.

bioenergetics model of Kitchell and Breck (1980) to predict growth by each lamprey during the experiment. An upper and lower estimate were provided for each lamprey by using the upper and lower estimates of energy uptake during the period of host blood decline, with the anticipation that these estimates would bracket observed growth. We also estimated growth based on the assumption that blood energy concentration declines exponentially.

Laboratory Experiment

Recently metamorphosed sea lampreys from the Lake Champlain drainage were acquired in December 1982, and maintained in a Living Stream (Frigid Units, Inc., Toledo, OH) filled with 520 L of filtered recirculated water. Photoperiod was held constant at 12:12 h light:dark, and water temperature was maintained at 10 ± 0.5 C. We used small lampreys (5.19–11.29 g wet biomass) so that the experiment could be scaled to a laboratory setting and to minimize individual variation in past feeding history. Small (47–95 g) captive-reared rainbow trout (*Oncorhynchus mykiss*) served as hosts. We chose small hosts so that host blood quality would be quickly affected by lamprey feeding. Lamprey to host biomass ratios ranged from 0.07 to 0.21.

Lampreys were tested individually in $50 \times 55 \times 38$ cm visually isolated compartments of Living Streams. Each compartment contained two bricks that were needed to prevent lampreys from escaping beneath the false bottom of the tank. These bricks also provided some cover for the trout and minimized agonistic interactions when more than one trout were present.

We compared attachment time and latency to attack for individual lampreys when confined with one and two rainbow trout. Thus, attachment time was measured for each lamprey in the presence and absence of an alternative host. Latency to attack, the interval between the beginning of a treatment and attachment by the lamprey to its host, may reflect both the availability

of hosts and the motivation of a lamprey to feed; we had no way of separating these factors, but expected that, on average, latency to attack would be greater when only one host was available. To control for the possible effect of treatment order, seven lampreys were initially confined with one trout and seven lampreys were initially confined with two trout. An attempt was made to minimize variation across treatments in the size of trout to which each lamprey was exposed; the mean ratio of the biomass of the larger to smaller host attacked by an individual lamprey during the experiment was 1.06 (range: 1.00–1.22). Observations were made at intervals of at most 12 h. Only attachments that resulted in a wound were included in the analysis. Lampreys were anesthetized with tricaine methanesulfonate and weighed prior to the experiment and subsequent to their final detachments. To allow for gut clearance, we let 36–48 h elapse between detachment and weighing.

Results

The Feeding Model

Because of uncertainty about the trajectory of the decline in host blood energy concentration prior to death, model predictions of lamprey growth were obtained under each of three assumptions (see model description). As expected, under the assumption that host blood energy concentration remained constant at a normal level until death, model predictions of instantaneous growth rates were significantly greater than observed rates (paired t -test, $t = 3.57$, $P = 0.0034$). Also as anticipated, observed growth rates were significantly greater than predicted under the assumption that host blood energy declined precipitously at time Q (equation 4) and remained at a constant low level until host death (paired t -test, $t = 2.43$, $P = 0.030$). Model predictions under the intermediate assumption that host blood energy concentration declined exponentially prior to death were not significantly different from observed values (paired t -test, $t = 0.88$, $P = 0.39$). Under all three assumptions, predicted growth rates were significantly correlated with observed growth rates, but most strongly so for the intermediate assumption ($r = 0.75$, $P < 0.01$; Fig. 5).

Attachment Time Experiment

Mean attachment times for lampreys confined with one and two trout were 15.4 and 10.1 d, respectively (Table 1). Although in the direction predicted by the optimal foraging hypothesis, differences between treatments were not significant (paired t -test, $t = 0.84$, $P = 0.42$). Attachment times were highly variable and ranged from less than a day to 70 d. Latency to attack was not significantly different between treatments (paired t -test, $t = 1.24$, $P = 0.24$), although the difference between means was in the direction expected (18.0 and 10.9 d with one and two hosts, respectively; Table 1).

The first attachment, regardless of host density, tended to be longer than the second attachment, with a mean difference of 4.3 d (sign test: $P = 0.022$; signed rank test: $P = 0.048$; paired t -test [omitting case 10 in Table 1]: $t = 3.04$, $P = 0.01$). The same was not true for latency to attack (paired t -test, $t = 0.24$, $P = 0.81$). At each host density, and with both densities combined, attachment time was significantly correlated with the preceding latency to attack ($P < 0.01$), but this was due in all cases to a few extreme data points.

Fifteen of 28 attacks resulted in death of the host (Table 1). In any consideration of lamprey attachment time, it must be

TABLE 1. Results of experiment to test the effect of host density on attachment time of sea lampreys (*Petromyzon marinus*). Individual lampreys (1–14) were exposed to either one trout followed by two trout (order 1–2) or two trout followed by one trout (order 2–1) at $10 \pm 0.5^\circ\text{C}$. Instantaneous growth rates over the duration of two feeding bouts were calculated as $[\ln(\text{final biomass}/\text{initial biomass})]/t$, where t is total duration in days of the two feeding bouts, including time spent unattached.

Order of densities	1 Host Present					2 Hosts Present					Instantaneous growth rate (per day)
	Initial biomass (g)	Host biomass (g)	Latency to attack (days)	Attachment time (days)	Host killed?	Host biomass (g)	Latency to attack (days)	Attachment time (days)	Host killed?	Final biomass (g)	
1 1–2	8.53	68.86	12.6	18.3	+	71.63	24.2	9.0	+	9.10	0.0010
2 1–2	6.57	67.00	0.5	24.0	+	54.79	11.0	3.0	+	12.90	0.0178
3 1–2	5.65	60.02	11.1	5.8	–	61.30	2.2	4.5	–	9.32	0.0209
4 1–2	7.35	74.73	13.0	9.1	–	83.89	6.1	7.9	–	13.90 ^a	0.0094
5 1–2	7.16	74.45	40.1	37.0	+	80.03	3.0	2.0	+	17.80	0.0111
6 1–2	11.29	58.10	6.0	1.3	+	53.23	0.2	3.5	–	12.66	0.0088
7 1–2	6.62	68.92	23.0	5.0	–	69.23	0.5	3.0	–	7.63	0.0046
8 2–1	7.01	64.20	18.0	9.5	–	66.08	33.1	40.0	+	14.94	0.0074
9 2–1	5.97	49.93	4.5	4.5	–	53.58	5.5	10.5	+	8.05	0.0120
10 2–1	8.78	82.45	62.0	70.0	–	82.35	5.1	1.0	–	19.27	0.0057
11 2–1	10.85	54.93	36.0	1.0	+	54.46	16.2	1.0	–	11.00	0.0003
12 2–1	10.82	94.50	9.5	5.5	–	91.62	2.4	17.0	+	15.96	0.0118
13 2–1	6.38	59.38	14.6	12.9	+	64.88	33.0	22.5	+	11.93	0.0075
14 2–1	5.19	76.00	0.5	11.5	+	69.45	10.5	16.0	+	9.80	0.0167

^aNot weighed until after an additional feeding.

kept in mind that death of the host may interrupt what might have been a longer attachment. This was probably not important in our comparison of attachment times between the two host densities, as host deaths were about equally split between host densities, and in five cases lampreys killed their hosts at both densities. Nine deaths occurred as a result of first attachments, regardless of host density, while six occurred as a result of second attachments. Lampreys that killed one host were not more likely to kill their second host (G test of independence, $P > 0.25$). Similarly, correlations between attachment times for individual lampreys at the two host densities ($r = -0.26$) and between latencies to attack at the two host densities ($r = -0.067$) were not significant. Thus, variation in feeding behavior was not attributable to consistent differences among individuals.

Growth by lampreys during the experiment was highly variable, at least in part because of great variability in individual feeding histories (Table 1). Increase in wet body weight after two feedings, as a percentage of initial weight, ranged from 1 to 149%.

Discussion

Attachment Time

There are several possible reasons for the lack of significant differences between attachment times for lampreys confined with one and two hosts. Not the least of these is the great variability that seems characteristic of the lamprey feeding process. Nevertheless, this variability was not great enough to prevent the detection of a significant difference between first and second attachments by individual lampreys.

If the previous interval between feedings is used by the lamprey as an approximate measure of current host abundance, then the lack of a significant difference between attachment times at the two host densities may be related to the lack of a significant difference in latency to attack. Thus, the difference in host density did not appear to affect how long it took a

lamprey to find and attack a host. We were surprised by the magnitude of the average latency and suspect that it may have been due at least in part to a reluctance to attack hosts as small as those used in this study. Although recently transformed *Petromyzon marinus* have been reported on relatively small fish (e.g., Davis 1967, Mansueti 1962), and we have observed attachments to trout as small as 30 g in our laboratory, most evidence suggests that parasitic lampreys are actively size-selective (Cochran 1985), and we have observed consistently shorter latencies to attack (usually much less than 1 d) for lampreys confined with larger trout. Alternatively, small trout may be more responsive to the physical presence of an approaching lamprey and thus more likely to avoid an attack.

If the energy uptake curve for a feeding lamprey is relatively flat in the neighborhood of the tangent line from the non-feeding time axis, then deviations from the optimal attachment time will not result in greatly reduced rates of energy uptake (Cochran and Kitchell 1986). Thus, according to our feeding model, a 7.4-g lamprey feeding on a 68.2-g trout with a mean latency to attack of 15.62 d (mean values from the first round of our experiment, both host densities combined) could achieve an optimal rate of net energy uptake of 0.34 kJ/d by remaining attached for 11 d (Fig. 6). It could achieve 97% of this rate by remaining attached for 14 d, the predicted host survival time. In light of inevitable variability in such factors as the interval between feedings, lamprey to host biomass ratio, and realized energy intake, differences of this magnitude are not likely to be statistically or biologically significant, and wide variability in attachment times should be expected. Moreover, a general tendency for lampreys to feed beyond the predicted optimal attachment time and kill their hosts (e.g., in the first round of our experiment, mean attachment time was 15 d and 9 hosts were killed) might be expected for two reasons: (1) attachment times greater than the optimum incur smaller penalties in terms of the rate of net energy uptake than attachment times less than the optimum and are less likely to be distinguishable from optimum (Cochran and Kitchell 1986), and (2) the available energy remaining in the host to which a lamprey is currently

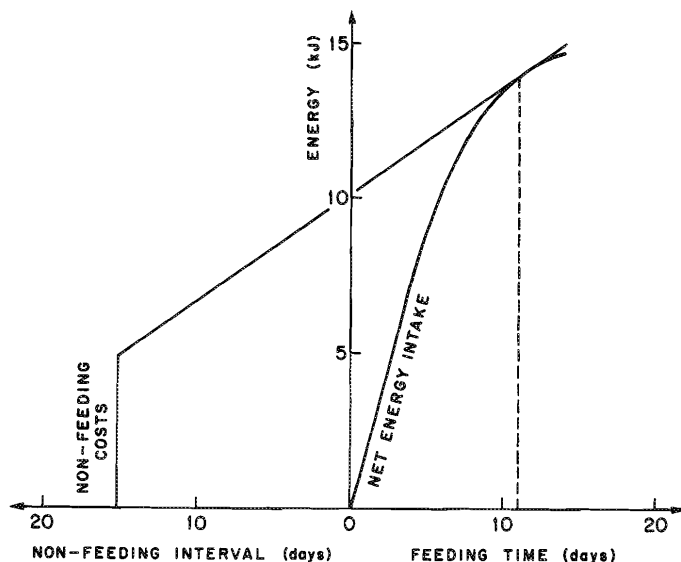


FIG. 6. Predicted net energy intake by a 7.4 g lamprey from a 68.2 g trout as a function of feeding time, with optimal feeding time located at 11 d for a non-feeding interval of 15.2 d. Non-feeding interval and biomass of lamprey and host correspond to mean values from first round of experiment. Energetic costs during the non-feeding interval were calculated with the bioenergetics model of Kitchell and Breck (1980).

attached is, all else equal, a more certain reward than that obtainable by detaching and seeking out a new host (see discussion of risk aversion by Real 1980).

We observed a significant decrease in the attachment time of individual lampreys from the first to the second attachment. Handling times for several sucking insect predators have been observed to decline during sequences of prey captures at constant prey densities (Bailey 1986; Kruse 1983; Giller 1980; and references therein). In one case (Giller 1980), this was associated with declines in the intercatch interval that may have resulted from an increase in search efficiency, but no such decrease in latency to attach was observed in the present study. Decreased attachment time on the second host may have resulted from growth by lampreys during the experiment. Use of the lamprey feeding and bioenergetics models as outlined above indicated that the experimental lampreys had increased in weight by a mean of 31% by the onset of the second attachment. Because host size was held relatively constant for each lamprey, host blood volume removed daily would increase by a similar percentage (equation 3), and blood quality would decline more quickly during the second attachment (equations 4 and 5). This is corroborated by the fact that in all five cases where lampreys killed both hosts, the second host was killed in a shorter period of time (Table 1).

Alternative Hypotheses

We here consider several possible alternative hypotheses that bear on our assumptions about lamprey foraging behavior. In some cases we are able to provide some insight into the applicability of these hypotheses.

We have assumed that energy is the most appropriate currency by which to evaluate host blood quality. Nutrient constraints may also be important to a consumer (Rapport 1980; Westoby 1978). Youngs and Morris (in Lawrie 1980) suggested that host blood may be a relatively more important source of

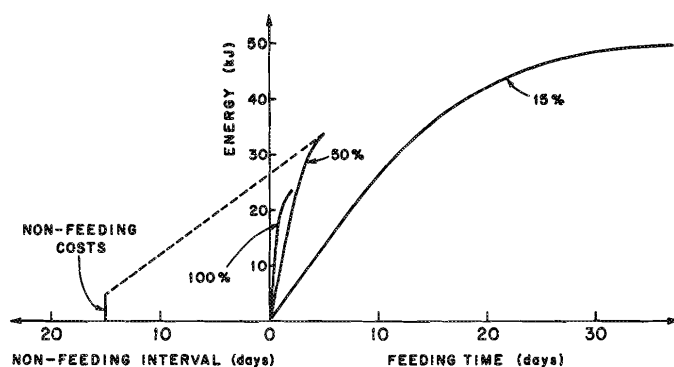


FIG. 7. Predicted net energy intake from a 200-g trout for lampreys removing 15, 50, and 100% of the host blood volume per day. For a mean non-feeding interval of 15 d, an intermediate removal rate is most profitable in terms of overall rate of net energy intake (slope of dotted tangent line is greater than the tangents to the other curves). See also Cochran and Kitchell (1986).

ions for lampreys in water of low ion concentration. They pointed out that chloride ion concentration is high in the Finger Lakes relative to that in Lake Superior, where lamprey-induced mortality per attack is generally much higher. They also suggested the possibility that ion levels may condition the survival of the host.

The first theoretical considerations of partial prey consumption (Cook and Cockrell 1978; Sih 1980) included the assumption that handling one prey and searching for the next are mutually exclusive activities. However, at least some predators violate this assumption (e.g. Bailey 1985), and predicted feeding times depend on whether or not it is applicable (Lucas and Grafen 1985). The ability to combine search and feeding would allow a lamprey to benefit from the movement of its host by increasing its rate of encounter with new hosts relative to that of a stationary unattached lamprey; several models of predator-prey encounter rates predict that encounter rates are positively related to the rate of predator movement (De Vita et al. 1982; Gerritsen and Strickler 1977; Gerritsen 1980). However, after several months of monitoring lampreys at 12-h intervals under a variety of conditions, we have no evidence that lampreys ever switch directly from one fish to another. With one exception, lampreys were found attached to tank walls or bottoms between consecutive attachments to hosts, and thus it is unlikely that search is combined with feeding.

Unlike the body fluids of prey in previously considered cases of partial prey consumption (Cook and Cockrell 1978; Sih 1980), the blood of a lamprey's host is, to at least some extent, a renewable resource, and Cochran and Kitchell (1986) showed that a lamprey in theory could adjust its rate of blood removal to extend the survival of its host and thereby achieve a greater cumulative uptake of blood. Indeed, one lamprey in our attachment time experiment followed a 62-d period without feeding with an attachment that lasted 70 d but did not kill its host (case 10 in Table 1). During this time it more than doubled in weight. Simulations with the lamprey feeding model suggest that such a strategy should be advantageous when the mean interval between feedings is great (Fig. 7). For the case depicted in Fig. 7, higher long-term rates of net energy intake can be achieved at intermediate rates of host blood removal. Optimization of the rate of net energy intake may necessitate simultaneous consideration of attachment time and rate of host blood removal. This may prove particularly useful in contrasting the feeding behav-

ior of lamprey species from habitats that differ in host abundance or availability.

In considering the problem of how long a lamprey should remain attached to its host, we have considered the individual lamprey as the potential optimizer of time investment. The strategy followed by an individual, however, may depend on the strategies adopted by conspecifics exploiting the same resources. Yamamura and Tsuji (1987) treated the problem of optimal patch residence time under exploitative competition and used a model of resource accrual closely similar to that in Fig. 1. Although some of their particular assumptions about the dynamics of resource supply and exploitation are not applicable to lamprey/host interactions, their approach, based on principles of game theory, may prove especially useful, particularly for lampreys in freshwater systems for which intraspecific competition may be significant.

The Utility of the Feeding Model

We are encouraged by the performance of the lamprey feeding model in tandem with the bioenergetics model of Kitchell and Breck (1980) in predicting growth by individual lampreys. Figure 5 suggests that these models should provide unbiased estimates of mean feeding and growth rates. Rice and Cochran (1984) enjoyed comparable success with a similar bioenergetics model for largemouth bass (*Micropterus salmoides*).

The feeding model provides a framework for examining a variety of behavioral phenomena. For example, one of the most consistent aspects of lamprey feeding is selective attachment to larger hosts (Cochran 1985; Henderson 1986; Noltie 1987). The feeding model can be used to assess the energetic costs and benefits of size-selective attack and to identify gaps in our understanding of these variables. The significance of host body size to lamprey feeding behavior can be predicted from its effect on the rate of net energy intake over an entire feeding bout, which in turn depends on the effects of host body size on (a) the initial slope of the energy intake curve (Fig. 1), (b) the peak value of the energy intake curve, and/or (c) the duration or energetic cost of the interval between feedings. All else equal, an increase in (a) or (b) or a decrease in (c) will result in an increase in the maximum possible overall rate of net energy intake; potential hosts should be ranked according to this rate.

It is unknown if initial blood quality (energy concentration) varies with host body size, but any such variation would be reflected in the initial slope of the energy intake curve (instantaneous rate of energy intake). In the absence of evidence to the contrary, we have assumed to this point that initial blood quality is a constant, but that assumption should be examined.

Preliminary results suggest that lampreys take longer to penetrate the scale and skin layer of larger hosts (Cochran, unpublished data); Webb and Skadsen (1979) reported that skin density (g/cm^2) increased with body size within several fish species, including rainbow trout. Greater handling times prior to feeding, by increasing factor (c) above, would represent an energetic liability of size-selective attack, but handling times are probably in many cases a small fraction of the total interval between feedings.

Two benefits for selecting larger hosts have been proposed (they are not mutually exclusive). First, it has been suggested that greater instantaneous rates of energy intake are achieved on larger hosts (Farmer 1974). Graphically, this means that the initial slope of the energy intake curve (factor *a* above) would be greater for a larger host. There is no evidence for this asser-

tion, and it is contrary to equation (1), which implies that the amount of blood removed does not vary with host size. However, it would be easy to test this hypothesis indirectly by comparing growth rates for lampreys of identical initial size allowed to feed for identical periods on hosts of different sizes. Second, the time of death of a host is inversely related to the proportion of its blood removed daily (Farmer et al. 1975; equation 5). Thus, a lamprey feeding at a given rate is assured of a longer period of feeding on a large host, and a greater cumulative energy intake (factor *b* above).

An obvious limitation of the current feeding model is its restriction to sea lampreys feeding on trout. It would be desirable to extend the model to other lampreys and host taxa, as well as to construct separate curves for attacks in various sites on the body surface of the host (Cochran 1986). Although the logistics of measuring blood consumption by lampreys are formidable (Farmer 1974), recent techniques for repeated sampling of blood from individual cannulated fish (Hoffmann and Lommel 1984; Nichols and Weisbart 1984) may prove applicable to the problem. Also, it may be useful to consider the possible feedback effect of a lamprey's growth on its ability to extract blood from its host, especially during long attachments. No such feedback is incorporated into the current model.

Our experiment on the effect of host density on lamprey attachment times was inconclusive, and the question of whether attachment time is the key to understanding the impact of lampreys in the field remains unresolved. Nevertheless, our lamprey feeding model proved useful in suggesting why it may be hard to demonstrate a significant difference in attachment times (see also Cochran and Kitchell 1986); more importantly, it should prove useful in the efficient design of future experiments. In addition, the model can be used to generate predictions about such feeding behaviors as size selectivity, from either within or outside the context of optimality theory.

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References

- BAILEY, P. C. E. 1985. 'A prey in the hand' — multi-prey capture behavior in a sit-and-wait predator, *Ranatra dispar* (Heteroptera: Nepidae), the water stick insect. *J. Ethol.* 3: 105–112.
- 1986. The feeding behavior of a sit-and-wait-predator, *Ranatra dispar* (Heteroptera: Nepidae): optimal foraging and feeding dynamics. *Oecologia* 68: 291–297.
- BRUSSARD, P. F., M. C. HALL, AND J. WRIGHT. 1981. Structure and affinities of freshwater sea lamprey (*Petromyzon marinus*) populations. *Can. J. Fish. Aquat. Sci.* 38: 1708–1714.
- COCHRAN, P. A. 1985. Size-selective attack by parasitic lampreys: consideration of alternate null hypotheses. *Oecologia* 67: 137–141.
- 1986. Attachment sites of parasitic lampreys: comparisons among species. *Environ. Biol. Fishes* 17: 71–79.
- COCHRAN, P. A., AND J. F. KITCHELL. 1986. Use of modelling to investigate potential feeding strategies of parasitic lampreys. *Environ. Biol. Fishes* 16: 219–223.

- COOK, R. M., AND B. J. COCKRELL. 1978. Predator ingestion rate and its bearing on the theory of optimal diets. *J. Anim. Ecol.* 47: 529-549.
- DAVIS, R. M. 1967. Parasitism by newly-transformed anadromous lampreys on landlocked salmon and other fishes in a coastal Maine lake. *Trans. Am. Fish. Soc.* 96: 11-16.
- DE VITA, J., D. KELLY, AND S. PAYNE. 1982. Arthropod encounter rate: a null model based on random motion. *Am. Nat.* 119: 499-510.
- FARMER, G. J. 1974. Food consumption, growth and host preferences of the sea lamprey, *Petromyzon marinus* L. Ph.D. thesis, Univ. Guelph, Guelph, Ont. 75 p.
1980. Biology and physiology of feeding in adult lampreys. *Can. J. Fish. Aquat. Sci.* 37: 1751-1761.
- FARMER, G. J., F. W. H. BEAMISH, AND G. A. ROBINSON. 1975. Food consumption of the adult landlocked sea lamprey, *Petromyzon marinus* L. *Comp. Biochem. Physiol.* 50A: 753-757.
- GERRITSEN, J. 1980. Adaptive responses to encounter problems, p. 52-62. *In* W. C. Kerfoot [ed.]. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, NH.
- GERRITSEN, J., AND J. R. STRICKLER. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Board Can.* 34: 73-82.
- GILLER, P. S. 1980. The control of handling time and its effects on the foraging strategy of a heteropteran predator, *Notonecta*. *J. Anim. Ecol.* 49: 699-712.
- HENDERSON, B. A. 1986. Effect of sea lamprey (*Petromyzon marinus*) parasitism on the abundance of white suckers (*Catostomus commersoni*) in South Bay, Lake Huron. *J. Appl. Ecol.* 23: 381-389.
- HOFFMAN, R., AND R. LOMMEL. 1984. Effects of repeated blood sampling on some blood parameters in freshwater fish. *J. Fish Biol.* 24: 245-251.
- KINNUNEN, R. E., AND H. E. JOHNSON. 1985. Impact of sea lamprey parasitism on the blood features and hemopoietic tissues of rainbow trout. *Great Lakes Fish. Comm. Tech. Rep.* 46: 17 p.
- KITCHELL, J. F., AND J. E. BRECK. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 37: 2159-2168.
- KRUSE, K. C. 1983. Optimal foraging by predaceous diving beetle larvae on toad tadpoles. *Oecologia* 58: 383-388.
- LAWRIE, A. H. (WITH APPENDICES BY W. D. YOUNGS, R. MORRIS, AND G. R. SPANGLER). 1980. Interactions between sea lamprey (*Petromyzon marinus*) and their forage base. A report from the SLIS Stock Effects Task Force. *Can. J. Fish. Aquat. Sci.* 37: 2193-2196.
- LUCAS, J. R., AND A. GRAFEN. 1985. Partial prey consumption by ambush predators. *J. Theor. Biol.* 113: 455-473.
- MANSUETI, R. J. 1962. Distribution of small, newly metamorphosed sea lampreys, *Petromyzon marinus*, and their parasitism on menhaden, *Brevoortia tyrannus*, in mid-Chesapeake Bay during winter months. *Chesapeake Sci.* 3: 137-139.
- MORIN, P. J. 1985. Predation intensity, prey survival and injury frequency in an amphibian predator-prey interaction. *Copeia* 1985: 638-644.
- MURTAUGH, P. A. 1981. Inferring properties of mysid predation from injuries to *Daphnia*. *Limn. Oceanogr.* 26: 811-821.
- NICHOLS, D. J., AND M. WEISBART. 1984. Dual cannulation of free-swimming Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* 41: 519-521.
- NOLTIE, D. B. 1987. Incidence and effects of sea lamprey (*Petromyzon marinus*) parasitism on breeding pink salmon (*Oncorhynchus gorbuscha*) from the Carp River, eastern Lake Superior. *Can. J. Fish. Aquat. Sci.* 44: 1562-1567.
- PEARCE, W. A., R. A. BRAEM, S. M. DUSTIN, AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in the Lower Great Lakes. *Can. J. Fish. Aquat. Sci.* 37: 1802-1810.
- POTTER, I. C., AND R. W. HILLIARD. 1987. A proposal for the functional and phylogenetic significance of differences in the dentition of lampreys (Agnatha: Petromyzontiformes). *J. Zool., Lond.* 212: 713-737.
- PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52: 137-154.
- RAPPORT, D. J. 1980. Optimal foraging for complementary resources. *Am. Nat.* 116: 324-346.
- REAL, L. A. 1980. On uncertainty and the law of diminishing returns in evolution and behavior, p. 37-64. *In* J. E. R. Staddon [ed.]. *Limits to action: the allocation of individual behavior*. Academic Press, New York, NY.
- RICE, J. A., AND P. A. COCHRAN. 1984. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65: 732-739.
- RICKER, W. E. 1973. Linear regressions in fishery research. *J. Fish. Res. Board Can.* 30: 409-434.
- RYAN, B. F., B. L. JOINER, AND T. A. RYAN, JR. 1985. *Minitab Handbook*. Second edition. Duxbury Press, Boston, MA. 379 p.
- SCHOENER, T. W. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* 60: 1110-1115.
- SIH, A. 1980. Optimal foraging: partial consumption of prey. *Am. Nat.* 116: 281-290.
- SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207-247. *In* M. W. Hardisty and I. C. Potter [ed.]. *The biology of lampreys*. Academic Press, New York, NY.
- SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953-1970. *Great Lakes Fish. Comm. Tech. Rep.* 26: 60 p.
- SMITH, L. S. 1966. Blood volumes of three salmonids. *J. Fish. Res. Board Can.* 23: 1439-1446.
- WEBB, P. W., AND J. M. SKADSEN. 1979. Reduced skin mass: an adaptation for acceleration in some teleost fishes. *Can. J. Zool.* 57: 1570-1575.
- WESTOBY, M. 1978. What are the biological bases of varied diets? *Am. Nat.* 112: 627-631.
- YAMAMURA, N., AND N. TSUJI. 1987. Optimal patch time under exploitative competition. *Am. Nat.* 129: 553-567.