

Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids

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Abstract: In food and (or) space-limited populations, increases in average body size may be accompanied by increases in per capita space and (or) energy requirements. Thus, as body size increases in time or space, the equilibrium number of individuals that can be supported in a given environment should decrease. This relationship, referred to as self-thinning, produces a negative linear relationship between log body size (mass) and log population density. We studied body mass – population density relationships in stream-living populations of several trout species from the intermountain western United States. Our analyses of relationships between body mass and population density demonstrated that self-thinning can be manifested through both temporal and spatial variability in fish population characteristics. Several populations did not show self-thinning, possibly due to species-specific traits, temporal and spatial environmental variation, or both. Thinning lines may not reveal specific causal mechanisms, but they appear to be real, density-dependent responses and thus offer a potentially useful method for studying fish populations. Experimental studies of self-thinning under more controlled conditions are needed, however, to identify causal mechanisms and eliminate alternative explanations for body size – abundance relationships.

Résumé : Dans les populations limitées par la nourriture et (ou) l'espace, les augmentations de la taille corporelle moyenne peuvent s'accompagner d'une augmentation des besoins en espace et (ou) en énergie par individu. Ainsi, au fur et à mesure que la taille corporelle augmente dans le temps et dans l'espace, le nombre d'individus qu'un environnement donné peut soutenir en équilibre devrait diminuer. Cette relation d'autodécroissance produit une relation linéaire négative entre le log de la taille corporelle (masse) et le log de la densité de la population. Nous avons étudié les relations masse corporelle-densité de population chez des populations de plusieurs espèces de truites de ruisseau dans l'ouest des États-Unis (*intermountain western United States*). Nos analyses des relations entre la masse corporelle et la densité de population ont montré que l'autodécroissance peut se manifester aussi bien par suite de la variabilité temporelle que spatiale des caractéristiques de la population de poissons. Plusieurs populations n'ont pas fait preuve d'autodécroissance, peut-être à cause de caractéristiques spécifiques de l'espèce, d'une variation environnementale spatiale et temporelle, ou des deux. Les lignes d'autodécroissance peuvent ne pas révéler les mécanismes causaux spécifiques, mais elles semblent être réelles et, de ce fait, constituent une méthode potentiellement utile pour étudier les populations de poissons. Toutefois, des études expérimentales de l'autodécroissance dans des conditions mieux contrôlées sont nécessaires pour déterminer les mécanismes causaux et éliminer les autres explications pour les relations taille corporelle-abondance.

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Introduction

Individual variation in body size has important implications for population structure and dynamics (Peters 1983; Werner and Gilliam 1984; omnicki 1988). In fishes, body size is related to a variety of ecologically important characteristics, including competitive ability, survivorship, fecundity, diet breadth, and growth rate (Wootton 1990). Because larger individuals generally require more resources, the equilibrium number of individuals supported in a given environment (carrying capacity) should depend on average body size. The

expected relationship between equilibrium population density (N) and average body size (mass, W) is commonly expressed as

$$(1) \quad N = aW^{-b}$$

where a and b are constants referring to the intercept and slope, respectively, of the body mass – population density regression. When this pattern is observed within species, it is referred to as self-thinning, a result of intraspecific competition for limited resources. Self-thinning has been studied extensively in plants, but only recently has attention been directed at mobile animal populations (Begon et al. 1986; Fréchette and Lefavre 1995).

Some of the best evidence for self-thinning in fish populations comes from studies of stream-living salmonids in north-west England (Elliott 1993; Grant 1993), southern Sweden (Bohlin et al. 1994), and experimental stream channels (Grant 1993). The existence of a self-thinning relationship implies that some factor or combination of factors is acting to limit population density. Two factors, space and food, are thought to be of primary importance in limiting salmonid production

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in streams (Chapman 1966). Thinning lines (eq. 1) for stream-living salmonids limited by space (territoriality) are predicted to have a slope of approximately -0.93 (Grant and Kramer 1990; Grant 1993), while lines for food-limited populations are predicted to have a slope of approximately -0.88 (Bohlin et al. 1994). The territory size thinning line is an empirical estimate derived from the relationship between territory size and body mass (Grant and Kramer 1990; Grant 1993), while the food limitation line is based on the theoretical concept of "energetic equivalence" (Damuth 1981; Nee et al. 1991; Bohlin et al. 1994). Because (as we show in this study) slopes of thinning lines predicted from food and space limitation are very similar, they may be difficult to distinguish in practice.

Energetic equivalence is based on the fact that per capita energetic requirements increase as body mass increases. This increase is not 1:1, however, because metabolic rate slows down as body mass increases. The relationship between body mass and metabolic rate is

$$(2) \quad M = aW^b$$

where M is metabolic rate (milligrams O_2 per hour) and a and b are regression parameter estimates (Glass 1969). According to the energetic equivalence hypothesis, slopes of relationships between population density and average body mass should be the inverse of slopes relating metabolic rate and body mass ($-b$, see Bohlin et al. 1994 for further discussion). If this holds, the sum of individual energy requirements remains constant during self-thinning (=energetic equivalence). In other words, total energy flow through a population is independent of population density. This is expected if fish populations are limited by constant energy (food) inputs.

Slopes of thinning lines in stream-living salmonid populations studied to date generally are consistent with the energetic equivalence prediction (Elliott 1993; Grant 1993; Bohlin et al. 1994); thus, it appears that food, rather than space limitation, is more common (but see Keeley and Grant 1995). In this paper, we further investigate evidence for energetic equivalence in stream-living salmonids and attempt to identify important factors that may explain empirical deviations from its predictions.

Data used in this study come from intensive surveys of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) populations in Great Basin (United States) streams and from long-term population surveys of resident trout throughout the intermountain region of the western United States (Platts and Nelson 1988). We studied relationships between body mass and population density to (i) look for the existence of thinning lines in these data sets, (ii) examine the evidence for food and (or) space limitation, and (iii) examine spatial and temporal variation in self-thinning. To explicitly test for independence of energy flow through a population and population density, we compared a regression model of population energy flow based on average body mass with an individual-based method.

Materials and methods

Study sites

Study areas for long-term population surveys are described in Platts and Nelson (1988). Field surveys of Lahontan cutthroat trout were conducted during the summers of 1993–1994 in tributaries of the

upper Humboldt River, Humboldt and Elko counties, Nevada. Streams ranged in elevation from 1700 to 2300 m. Average water depths in the study areas were generally 15 cm or less, while wetted stream channel widths averaged 1–4 m. Stream conditions in this region are highly variable in space and time (Platts and Nelson 1988; Nelson et al. 1992). Winter conditions are often severe, with cold temperatures, anchor ice, and avalanches at higher elevations. In some years, heavy spring runoff leads to severe flooding, which may directly kill or displace fishes (Seegrist and Gard 1972; Erman et al. 1988; Strange et al. 1992). Summer air temperatures often exceed 30°C , with daily water temperature fluctuations of up to 20°C . Drought conditions in 1994 led to extensive stream drying and fish mortality in areas just downstream of several study sites (J.B. Dunham and G.L. Vinyard, personal observation). Other fish species, including Tahoe sucker (*Catostomus tahoensis*), speckled dace (*Rhinichthys osculus*), and Piute sculpin (*Cottus beldingi*), occurred in the study streams, but Lahontan cutthroat trout were generally the numerically dominant fish species present.

Sampling methods

In both data sets (long-term and Lahontan cutthroat trout), fish populations were sampled by electrofishing and population estimates obtained from multiple-pass depletions (van Deventer and Platts 1989). Details of sampling methods for long-term surveys are given in Platts and Nelson (1988). We used survey data from Platts and Nelson (1988) that spanned at least 5 yr with areal biomass estimates consistently greater than $0.1 \text{ g}\cdot\text{m}^{-2}$.

Lahontan cutthroat trout data came from surveys of abundance at 42 sites in six streams in 1993 and at 49 sites in seven streams in 1994 ($n = 7$ sites per stream). Sites without fish were dropped from the analysis. When possible, the same sites were sampled in each year. Each site consisted of an approximately 25-m stream reach blocked at up- and downstream ends with fine-mesh (3- to 4-mm-diameter) seines to prevent fish escape during sampling. As with the long-term data (Platts and Nelson 1988), fish population density was expressed as number per unit area. Population estimates were obtained separately for young-of-year (age 0) and older (age 1+) fish. All sampling was conducted during summer base-flow conditions (late July – September).

Statistical analyses

Body mass – abundance regressions

We analyzed body mass – abundance using ordinary least squares and reduced major axis (RMA, McArdle 1988) regression with population density (N) as the response and average body size (W) as a predictor variable with categorical stream effects in the model (Myers 1990). Abundance data from Platts and Nelson (1988) included several salmonid species (bull trout (*Salvelinus confluentus*), brook trout (*S. fontinalis*), Lahontan cutthroat trout (*Oncorhynchus clarki*), rainbow trout (*O. mykiss*), and brown trout (*Salmo trutta*)) in several streams. Stream and species effects could not be distinguished, so data were analyzed with a combined species–stream categorical variable to simultaneously account for species and stream effects. Data were analyzed with the SAS General Linear Models procedure (Littell et al. 1991). Data were \log_{10} transformed to linearize the relationship

$$\log(N) = \log(a) - b\log(W)$$

with terms as defined above.

The first step in the analysis was to ensure that model assumptions were satisfied. Residuals were obtained from the linearized statistical model and examined for normality with the SAS Univariate procedure (Littell et al. 1991). Output indicated that studentized residuals were normally distributed, but a Levene's test (Kuehl 1994) on the absolute residuals indicated significant variance heterogeneity in the Lahontan cutthroat trout data. Because the models tested here are based on log–log relationships between body size and abundance, we

Table 1. Analysis of variance table for multiple regression analysis of the long-term data set ($R^2 = 0.90$).

Source	df	MS	F	P
Species stream	8	0.167	4.69	0.0003
Average body mass	1	0.775	21.78	0.0001
Interaction	8	0.824	2.89	0.0109
Error	45	0.036		

did not attempt further transformations. Instead, a weighted analysis was conducted by using $1/\sigma_j^2$ for body size at the j th site in stream i , following recommendations in Myers (1990) and Littell et al. (1991). This was necessary for both body size – abundance analyses and analyses of energy flow in relation to population density for Lahontan cutthroat trout (see Population energy flow below).

A preliminary analysis indicated (species–stream)-body size interactions were significant ($P < 0.05$) in the long-term data set, so slopes and intercepts were determined separately for each population. Stream-body size interactions were not significant ($P > 0.20$) for the Lahontan cutthroat trout data, so the interaction term was dropped and the analysis was run again to estimate slopes.

Population energy flow

According to the hypothesis of energetic equivalence, population energy flow should be independent of population density. Thus far, theoretical arguments about relationships between body size and population density have been based on the relationship between average body mass and abundance. If the distribution of body sizes has a large variance or is substantially skewed, then average body size may poorly represent total energy flow in a population or community (Cyr and Pace 1993). If there is no size variation among individuals, overall energy flow through a population, F , is represented as

$$(3) \quad F = aW^b \cdot N,$$

the product of average mass-specific energy requirements (aW^b) and population density (fish per square metre). If, however, there is substantial variation in the distribution of body sizes, then overall energy flow through a population is more correctly specified as the sum of individual energy requirements. Taking w as individual body mass and summing for $i = 1$ to n , the number of individuals in a population, total energy flow may be calculated as follows:

$$(4) \quad F = \sum w^b \cdot m^{-2}.$$

This formulation is more realistic for populations with large variation or skewed distribution in body size, as is often the case for species with Type III survivorship (e.g., fishes). Note in this case that total energy flow (F) is expressed in units of milligrams O_2 per hour per square metre, which may be converted to energetic equivalents (Elliott and Davison 1975).

To compare the influence of underlying size frequency distributions on the relationship between body size and population density, we compared regressions of estimated total energy flow calculated from averages and from individuals versus population density. Total energy flow based on average and individual body mass was estimated as described above and analyzed in relation to population density using the log-transformed linear model. Total energy flow was estimated using constants for *O. nerka*, obtained by Brett (1965). Differences between actual numbers of fish captured and population estimates (van Deventer and Platts 1989) were generally very small (<10%). In cases where population estimates exceeded the number of fish captured, energy flow based on individuals was calculated by substituting average body size in place of the uncaptured individuals at each site. Average body size was calculated separately for young-of-year (age 0) and older (age 1+) fish and multiplied by the number

of uncaptured individuals in the corresponding size class to estimate total energy flow.

Results

Body size – abundance

For the long-term data set, multiple regression with body mass and the composite species–stream categorical variable explained approximately 90% of the variance in population density (Table 1). The moderately strong interaction between body mass and species–stream indicates that the slope of the relationship between body size and abundance depends on stream effects, species effects, or a combination of both. For the 1993 Lahontan cutthroat trout data, multiple regression indicated a weak, but significant stream-body size interaction effect ($F = 2.96$, $P < 0.03$, $df = 5$) and significant stream effects ($F = 7.17$, $P < 0.0003$, $df = 5$), but no significant effect of body size alone (overall model $R^2 = 0.87$). Body size was highly significant for the 1994 Lahontan cutthroat trout data ($F = 40.79$, $P < 0.0001$, $df = 1$), with significant stream effects as well ($F = 15.62$, $P < 0.0001$, $df = 5$), but no significant stream-body size interaction (i.e., among-stream differences in regression slopes could not be distinguished). Together, body size and stream effects explained 80% of the variance in population density in 1994 ($R^2 = 0.81$).

Of the nine species–stream ordinary least squares slope estimates (b_{OLS}) in the long-term data (Fig. 1), four were found to be statistically significant (Table 2). With the exception of the RMA slope estimate (b_{RMA}) for bull trout, 95% confidence intervals around b included values predicted by the energetic equivalence and territory limitation hypotheses. The ordinary least squares slope of the body size – abundance regression for Lahontan cutthroat trout surveyed in 1994 was -0.99 ± 0.26 (95% CI), while the RMA slope estimate was -1.10 , with the 95% CI ranging from -1.12 to -0.90 . The latter slope estimate is significantly steeper than slope predictions from food limitation (-0.88), but not different from the slope predicted by space limitation (-0.93).

Energy flow versus population density

Self-thinning generally did not apply for Lahontan cutthroat trout sampled in 1993 (Fig. 2). As a consequence, we only considered data from 1994. Multiple regression with stream effects included in the model as above indicated no significant relationships between population density and energy flow estimated from averages and individuals for Lahontan cutthroat trout sampled in 1994. Probability (P) values from partial F -tests of population density effects were 0.81 and 0.15 for energy flow estimated from averages and individuals, respectively.

Discussion

Results from this study are more equivocal than previous investigations of self-thinning in stream-living salmonids (Grant and Kramer 1990; Elliott 1993; Grant 1993; Bohlin et al. 1994). Below, we discuss possible reasons for differences between our results and those from previous studies and briefly discuss what we view as important and untested issues and assumptions that must be addressed before self-thinning is widely accepted as a real phenomenon.

Fig. 1. Scatterplots of body mass – population density relationships for five salmonid species studied in nine streams (data from Platts and Nelson 1988). Each point represents one annual population estimate. Thinning lines with significant slopes (Table 2) are shown in the left graph, while those with nonsignificant slopes are shown in the right graph.

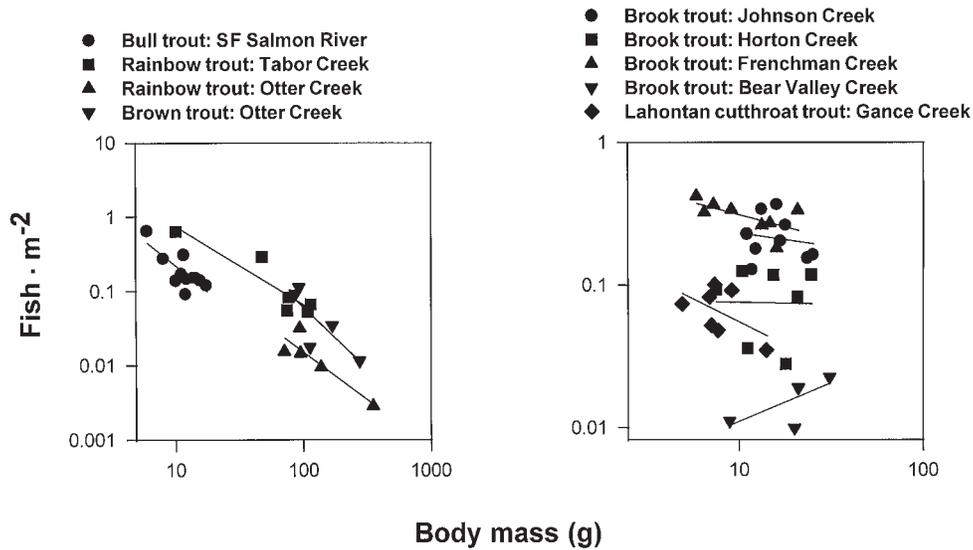


Table 2. Parameter estimates and 95% CI for slopes from regression analyses of body size versus abundance in the long-term data set (Platts and Nelson 1988).

Species (locality)	b_{RMA} (95% CI)	b_{OLS} ($\pm 95\%$ CI)	n	P
Bull trout	-1.79	-1.40	11	0.0033
(SF Salmon River)	(-2.81, -1.13)	(± 1.02)		
Rainbow trout	-1.14	-1.06	6	0.0001
(Tabor Creek)	(-1.91, -0.69)	(± 0.60)		
Rainbow trout	-1.43	-1.28	5	0.0006
(Otter Creek)	(-3.01, -0.68)	(± 1.17)		
Brown trout	-2.06	-1.65	5	0.0007
(Otter Creek)	(-5.37, -0.80)	(± 1.43)		
Brook trout	—	-0.19	9	NS
(Johnson Creek)	—	(± 1.23)		
Brook trout	—	-0.02	7	NS
(Horton Creek)	—	(± 1.09)		
Brook trout	—	-0.34	8	NS
(Frenchman Creek)	—	(± 0.86)		
Brook trout	—	0.54	5	NS
(Bear Valley Creek)	—	(± 1.51)		
Cutthroat trout	—	-0.65	8	NS
(Gance Creek)	—	(± 1.36)		

Note: Sample sizes (n) represent the number of annual surveys. P -values are for slopes (b_{OLS}). RMA slopes (b_{RMA}) were not estimated when least squares were not significant (McArdle 1988).

Evidence for self-thinning

Combined evidence from this study and others (Elliott 1993; Grant 1993; Bohlin et al. 1994) suggests that self-thinning may occur in stream-living salmonids, but exceptions here require further explanation. In the long-term data set, several species-stream combinations did not show a significant self-thinning pattern (Table 2). Regression slopes for streams with bull, rainbow, and brown trout all showed the pattern expected from self-thinning, while streams with Lahontan cutthroat trout and brook trout did not. The consistent lack of a self-thinning

pattern for brook trout is especially noticeable, with 5–9 yr of data from four different streams showing no relationship between average body mass and population density. If there are indeed species-specific differences in body size – abundance relationships, perhaps these can be attributed to different habitat preferences and competitive interactions (Gard 1961; Rodríguez 1995). Alternatively, stream habitats in this study may not have supported brook trout populations at equilibrium density.

Abundance and energy flow

Our finding of no significant relationship between population density and energy flow estimated from averages or individuals suggests that the use of averages in body size – abundance regressions did not bias our analyses supporting energetic equivalence for Lahontan cutthroat trout in 1994. In other words, food limitation appears to be operating to adjust population density in relation to per capita energy requirements such that energy flow remains constant. This assumes, of course, that food limitation is directly operating to limit populations (see Defining causal mechanisms below).

There are ecological as well as statistical reasons for considering the underlying distribution of body sizes in body size – abundance analyses. Bohlin et al. (1994) correctly pointed out that ontogenetic changes in diet, mortality, and growth may lead to b -values substantially different from those predicted by the hypothesis of energetic equivalence. Our data sets cover a relatively wide range of body sizes within and among streams, but overall homogeneity of slopes for streams with wide variation in body size in the 1994 Lahontan cutthroat trout data suggests that b -values are similar in this range.

Results from other studies of stream-living salmonids indicate that ontogenetic dietary differences may not be as large as one might suspect. A recent study of dietary overlap in stream-living Colorado cutthroat trout (*Oncorhynchus clarki pleuriticus*, Bozek et al. 1994) found considerable overlap in taxonomic composition and size of food items consumed by

individuals ranging from 24 to 188 mm (total length) and that food items too large to be accommodated by the gape size of age 0 fish were rarely encountered. Mortality patterns also may not vary substantially for different size classes because all populations in this study were surveyed during low summer flows. Summer mortality in stream-living salmonids is generally low in comparison with winter and spring (Seegrist and Gard 1972; Strange et al. 1992; Hutchings 1993). However, during our studies of Lahontan cutthroat trout, large adults occasionally were observed acting aggressively toward smaller individuals. Thus, smaller individuals may be displaced to areas of higher predation risk and reduced growth.

Temporal versus spatial variation

Confidence intervals for slopes and intercepts are much wider for the long-term data (Platts and Nelson 1988) than for the Lahontan cutthroat trout data set. Since the former data were from annual surveys and the latter were from surveys conducted in a single year, increased variability in the long-term data may reflect higher temporal variation in ecological factors affecting salmonid populations. The contrasting results for self-thinning in Lahontan cutthroat trout in 1993 and 1994 lead us to suspect that environmental variation has a large temporal component. This also may explain why body mass – abundance regressions for Lahontan cutthroat trout were not significant in the long-term data. For this reason, we suggest that parameter estimates for body mass – abundance regressions will be more precise when population data come from many sites sampled in a relatively narrow time period, as opposed to fewer sites sampled over longer (e.g., yearly) time periods.

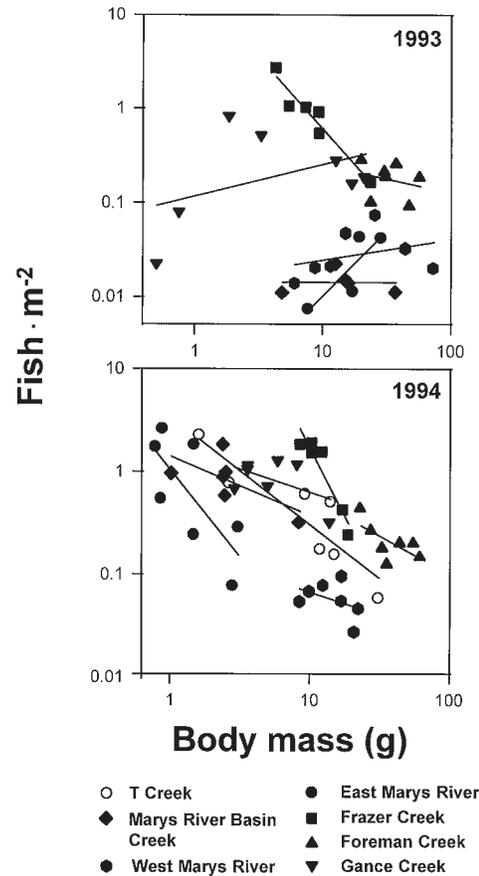
Strong temporal effects on body mass – abundance relationships are suggested by our data that show a strong self-thinning pattern for Lahontan cutthroat trout in 1994, but not in 1993. The significant stream-body size interaction observed in 1993 was probably due to the strong, negative relationship between body mass and population density in Frazer Creek (Fig. 2). Other streams sampled in 1993 give little indication of such a relationship (Fig. 2).

We suspect that differences between these two years are related to variation in stream discharge. Data collected by the U.S. Geological Survey in the upper Humboldt River basin, Nevada (which includes Gance Creek), show that stream discharges in 1994 were among the lowest recorded in the last 50 yr. Low water levels and reduced habitat volume may have caused an intraspecific competitive “crunch” (sensu Wiens 1977) during drought conditions of 1994.

Defining causal mechanisms

When populations in this study did show patterns expected with self-thinning, slopes of thinning lines were equally compatible with predictions from food (energetic equivalence) or space (territoriality) limitation. Two exceptions were bull trout in the long-term data, where the b_{RMA} slope was steeper than either slope predicted by space or food limitation, and the Lahontan cutthroat trout data for 1994, where the b_{RMA} slope was consistent with space limitation, but significantly steeper than predicted by food limitation. Analyses of energy flow in relation to population density for Lahontan cutthroat trout in 1994 are consistent with food limitation, however. Our inability to distinguish between space and food limitation may stem from several related complications in the analysis of thinning

Fig. 2. Scatterplots of body mass – population density relationships for Lahontan cutthroat trout studied in six streams in 1993 and seven streams in 1994 (T Creek added in 1994). Each point represents a population estimate for one site. Regression lines are the weighted least squares line for each population.



lines. First, predicted slopes from the food and space limitation hypotheses are very similar (approximately -0.88 versus -0.93 , respectively), so random error in estimates of body size and population density must be very small to effectively distinguish alternatives. Natural variability in environmental conditions also may increase variation around thinning lines, possibly affecting slopes and intercepts as well. It is well known that temperature and metabolic rate are closely coupled in fishes. For example, metabolic scaling exponents (b in eq. 2) for brown trout were found to range from 0.92 to 1.15, depending on temperature (Beamish 1964; Glass 1969). Predicted slopes of thinning lines for food-limited brown trout populations thus range similarly as ambient temperatures vary. Other factors such as spatial and (or) temporal variation in underwater visibility, habitat structure, or physicochemical conditions may also affect behavioral interactions and metabolic rates. Finally, a recent analysis of this problem by Marschall and Crowder (1995) suggests that food and space limitation may be theoretically indistinguishable.

In closing, we must mention our concerns with the use of observational data and correlational analyses to examine thinning lines. In this study, we considered only body mass as a correlate of population density. Significant correlations between these variables may not be a direct result of causal relationships.

This could be a problem for at least two important reasons. First, we have no direct, independent measure of food and (or) space limitation. Second, body mass may be affected by factors with little relation to intraspecific competition for food and (or) space, such as size-related predation risk or proximity to spawning areas (e.g., Beard and Carline 1991). Before self-thinning becomes a widely accepted phenomenon, we emphasize the need for experimental studies under more controlled conditions (e.g., Begon et al. 1986; Latto 1994; Fr chet and Lefaivre 1995) to more clearly define causal mechanisms.

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