

An experimental analysis of self-thinning in juvenile steelhead trout

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Mobile animal populations have been proposed to decline in density according to a slope based on the allometry of metabolic requirements or space requirements. In salmonid fishes, metabolic rate and food consumption scale to body mass by the exponent 0.87 and 0.73, respectively; whereas the territory size of steelhead trout scales to body mass by the exponent 0.86. Experimental cohorts of juvenile steelhead trout (*Oncorhynchus mykiss*) were used to test the hypothesis that mobile animal populations composed of individuals with indeterminate growth decline in density as a result of self-thinning. After controlling for experimentally manipulated levels of food abundance and stocking density, cohorts of steelhead trout declined in density with increasing body size according to a slope closest to the allometry of food consumption. Densities of steelhead trout were inversely related to average mass by the exponent -0.74 . Despite the similarity to the food consumption slope, a relatively wide confidence interval also precluded distinguishing the slope either the metabolic rate or territory size slopes. Data from the literature were also examined to determine if there was general support for the idea of self-thinning in natural populations of stream-dwelling salmonid fish. Although not all data suggest that populations of salmonids in streams decline as a result of density-dependent intraspecific competition, at least some appear to fit the idea of self-thinning; especially when density is above a minimum level of habitat saturation.

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For resource limited populations composed of individuals with indeterminate growth, density is predicted to decline with increasing body size as a result of intraspecific competition. This phenomenon, often called 'self-thinning', has been widely studied in plant populations (White 1980, Westoby 1984, Watkinson 1997). As individual plants within a stand increase in size, they shade out competitors that eventually die. Although self-thinning has received comparably little attention in animal populations, populations of animals may also decline in density as mean body size increases. For instance, sessile marine invertebrates self-thin as they compete for space and particulate organic matter, in a manner similar to the way plants compete for space and light (Hughes and Griffiths 1988, Fréchet and LeFaivre 1990, Fréchet et al. 1996).

In mobile animal populations, Begon et al. (1986) suggested that density should scale to body mass by the exponent -0.75 . If metabolism scales to body mass by the exponent 0.75 (Kleiber 1947, Zeuthen 1953, Peters 1983) and if the amount of food consumed per individual is proportional to metabolic rate, then the total amount of food consumed (f) per population (d) will be directly proportional to average individual mass raised to 0.75 ($f/d \propto M^{0.75}$). Therefore when food remains constant, density \propto mass $^{-0.75}$, predicting a self-thinning slope of -0.75 . However, because the scaling of metabolism to body size varies among taxa, a self-thinning slope should be established for the taxa under study (Latto 1994). In salmonid fishes, metabolic requirements have been measured on the basis of the allometry of metabolism or on the allometry of food

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consumption. In this taxonomic group, metabolic rate scales to body mass by the exponent 0.87, whereas food consumption scales to body mass by the exponent 0.73 (Steingrímsson and Grant 1999). Hence, in salmonids the metabolic hypothesis predicts two different self-thinning slopes depending on how metabolic demands are estimated.

Self-thinning in plants is thought to occur because in addition to having increased space requirements as individuals grow, plants compete for light, a resource with several unique properties: it constantly renews, it does not accumulate, and its input is unaffected by the population competing for it (Begon et al. 1986). An analogous mechanism may allow self-thinning to occur in stream-dwelling salmonid fish populations (Grant and Kramer 1990). Salmonids often defend feeding territories in streams that increase in size as individuals grow (Grant et al. 1989, Elliott 1990, Keeley and Grant 1995, Keeley and McPhail 1998). In addition, they feed primarily on drifting aquatic invertebrates (Wilzbach et al. 1986, Keeley and Grant 1997), a resource that shares similar properties to light: it is constantly renewing, it does not accumulate, and its production may be independent of the density of drift-feeding fish (Allan 1982, Culp 1986, Andersen et al. 1993, Friberg et al. 1994). Therefore, both the crown of a plant and a salmonid territory may function in the same manner; both capture energy and increase in size as an individual grows, shading or crowding out competitors (Grant 1993). In addition to the potential self-thinning slopes predicted by metabolic requirements, the space hypothesis predicts that the allometry of territory size will dictate the maximum density and therefore a third potential self-thinning slope for salmonids. For salmonids in general, territory size scales to body mass by the exponent 0.86 (Grant and Kramer 1990), which is similar to the exponent of 0.87 specifically for steelhead trout (Keeley 2000).

Studies of salmonids in streams provide indirect evidence for the idea of self-thinning in mobile animals; salmonid abundance declines with increasing fish size (Elliott 1993, Grant 1993, Bohlin et al. 1994, Dunham and Vinyard 1997, Steingrímsson and Grant 1999, Rincón and Lobón-Cerviá 2002). However, while observational declines in density with increasing mean fish size are consistent with the idea of self-thinning, no study has experimentally tested the self-thinning hypothesis in salmonid populations. Only populations declining in abundance that are experiencing density-dependent mortality and growth, as mean body size increases, can truly distinguish self-thinning from density-independent declines in population size (Armstrong 1997). Populations of experimental cohorts offer the ability to manipulate density and control for potential confounding influences of density-independent mortality.

In this paper, I extend the results from an earlier study (Keeley 2001) examining experimental populations of steelhead trout (*Oncorhynchus mykiss*) experiencing different levels of competition to provide a test of the self-thinning hypothesis in a mobile animal population. This study adds to the existing literature on self-thinning by providing the first experimental test for a stream-dwelling salmonid fish. A crucial assumption for testing the predicted self-thinning slopes, based on metabolic requirements, is the availability of constant amount of energy flowing through a population. Because of seasonal declines in food abundance in natural populations (Keeley and Grant 1997, Steingrímsson and Grant 1999), observational studies may often violate this assumption. Experimental studies offer the benefit of providing a constant amount of food to a population and hence a more rigorous test of the self-thinning hypothesis. By comparing cohorts of juvenile trout as individuals increase in size I tested the prediction that populations decrease in density as body increases within a cohort and that the rate of decline depends on the level of per capita competition experienced within a cohort. Secondly, by comparing the functional relationship between body size and density I attempt to distinguish between potential self-thinning slopes based on the allometry of metabolic or space requirements. Finally, by comparing populations open and closed to emigration I assessed whether declines in density due to mortality or emigration influence a self-thinning relationship.

Methods and material

Data collected from two experiments designed to test the effects of food and space competition on the demography of juvenile steelhead trout were re-analyzed to test aspects of the self-thinning hypothesis. The two experiments (hereafter experiment 1 and 2) were conducted over an eight-week period during the summers of 1995 and 1996, respectively. An abbreviated description of the methods is provided in this paper, while a more detailed description of the experimental design and set up can be found in Keeley (2001).

Adult steelhead trout were collected in the spring of 1995 and 1996 to use as broodstock for the two experiments. Sperm and eggs were collected from adult fish and used to produce embryos that were incubated in a hatchery and raised to the point of complete yolk sac absorption and exogenous feeding. Cohorts of juvenile trout were then stocked into 18 stream channels at the Cultus Lake Laboratory, Cultus Lake, British Columbia, Canada. Water was supplied to the stream channels from nearby Cultus Lake with a flow that averaged 7 cm/s and 10 cm deep in each channel. To control water temperature within a narrow range, water that

was pumped from the lake was drawn from above and below the thermocline, then mixed in a 1700 l tank to maintain it at $13 \pm 1.1^\circ\text{C}$ (mean ± 1 SD) before entering the stream channels. To prevent any invertebrates in the lake water from entering the stream channels, a 250 μm mesh filtered the water entering the mixing tank. A burlap canopy, 132 cm high, covered each stream channel to equalize shade and prevent predators from entering the experiment and a single layer of stream gravel, 5–10 cm in diameter, covered the bottom of each channel.

To compare demographic changes at different levels of competition, a stream channel received one of three densities of fish and one of three levels of food abundance. Each stream channel was stocked with a density of fish, representing either 100%, 200%, or 400% habitat saturation if occupied by territories of a size based on Grant and Kramer's (1990) allometric territory size regression. Percent habitat saturation (PHS) is calculated by the formula:

$$\text{PHS} = 100 \times \sum_{i=1}^n D_i \times T_i$$

where D_i is the density (number/ m^2) of size class i and T_i is the territory size (m^2) for size-class i , predicted from Grant and Kramer's (1990) territory size equation (see also Grant et al. 1998 for a review of habitat saturation). Food abundance was manipulated in the experiments by introducing food at one of three levels of abundance, representing either 72%, 143%, or 287% of the maximum ration predicted by Marschall and Crowder's (1995) model for salmonids. A channel thus received 146, 291, or 582 fish and a daily ration 1.44, 2.88, or 5.76 g/d of extruded pelleted food (15% size grade 1, Biodiet; 85% size grade 2, Biodry; Bioproduct, Warrenton, Oregon, USA), producing nine different treatment combinations. The daily ration of food was introduced over a 12 h period (beginning at 07:00) to simulate a natural encounter rate (Keeley and Grant 1997), using automated belt feeders attached to the top of each channel. All 18 channels were used in experiments 1 and 2. With nine treatment combinations, each treatment was replicated twice in both experiments.

Although both experiments monitored the demography of cohorts, experiment 2 differed from experiment 1 because fish were able to emigrate from the stream channels into a trap, in the second experiment. To allow fish to emigrate, the channels were modified during experiment 2 by attaching a 1 m long tube to the downstream end, which drained into a 4 l bucket with a screened drain hole. If a fish was captured in a trap it was marked with an adipose fin clip and returned to the channel. Any marked fish that were caught a second time were considered to be emigrants and they were removed from the experiment. Hence, while individual fish could be lost from either experiment through mor-

tality, individuals could also be lost by emigration in experiment 2.

To estimate the size of fish over the course of the experiment, an S-VHS video camera was used to record images of fish once every two weeks. Body sizes of 10–15 fish from the central area of each stream channel were measured from the video images. To convert a length on the video screen into an actual length in cm, a correction factor was created from a system of grid lines, spaced 10 cm apart, that were drawn on the walls of the channels and on a thin rope placed down the bottom center of each channel. Densities of fish were calculated by monitoring the number of mortalities or emigrants from each stream channel on a daily basis and subtracting the number removed from the initial number stocked. At the end of the experiment, all surviving individuals were collected by removing the gravel and dip-netting fish from the channels. Sub-samples of these fish were then measured for length and mass to provide a final estimate of body size.

Statistical analyses

To test the prediction that rates of decline in density are related to the intensity of competition in a population, I compared the slope from the body length versus density relationship for each channel according to treatment level. To calculate the slope, I used the size measurements collected at two-week intervals as an estimate of body size and I then regressed these values against their corresponding density to calculate the slope of the line. I assessed whether a significant proportion of the variance in slopes was accounted by treatment effects using analysis of variance (ANOVA). I then contrasted individual means using the contrast transformation available in SAS (SAS Institute 1989), to determine which means were different from each other.

To estimate a potential self-thinning relationship, I used the final density of fish from each channel versus its average final body mass. For both experiments, each cohort of fish that was held in a stream channel was considered to represent a single observation. An ordinary least-squares regression technique was used to examine the relationship between \log_{10} fish density versus \log_{10} average fish body mass (g). However, rather than a simple regression, a multiple-regression analysis was used to control for the influences of food abundance and stocking density. To control for differences between the two experiments, an analysis of covariance (ANCOVA) was used for comparisons. If no difference were detected between experiments, all samples were pooled into a single analysis. All tests of significance were based on type III sum-of-squares (SAS Institute 1989).

Results

As expected for cohorts that were experiencing different levels of intraspecific competition, densities of fish decreased in all channels as fish increased in size; however, the slopes of the equations predicting decreasing densities with increasing fish varied according to treatment level (Fig. 1, ANOVA, $F_{8, 27} = 8.02$, $P < 0.0001$). Cohorts that were stocked at high initial densities declined more rapidly than medium (Fig. 1, ANOVA, $F_{1, 27} = 4.22$, $P = 0.0026$) or low densities (Fig. 1, ANOVA, $F_{1, 27} = 28.32$, $P < 0.0001$). Conversely, cohorts of fish that received high levels of food abundance declined at slower rates with increasing fish size than cohorts receiving medium (Fig. 1, ANOVA, $F_{1, 27} = 4.87$, $P = 0.036$) or low levels of food abundance (Fig. 1, ANOVA, $F_{1, 27} = 26.69$, $P < 0.0001$). Although, the magnitude of the slope tended to increase with increasing stocking density and decreasing food abundance, the two treatment factors did not interact significantly (Fig. 1, ANOVA, $F_{4, 27} = 2.09$, $P = 0.11$). Despite the ability to emigrate from the stream channels in experiment 2, I could not account for any significant proportion of the variance in slopes by adding year as a covariate into the model (ANCOVA, $F_{1, 30} = 0.57$, $P = 0.46$).

Overall, the final density of steelhead trout that survived to the end of the experiments was inversely related to the mean body size of individuals within a cohort (Fig. 2; $r = -0.37$, $n = 36$, $P = 0.029$). When divided into observations from the first experiment, where fish could not emigrate, versus those from the second experiment allowing emigration, there was no inter-experiment effect after controlling for the effects of body size (ANCOVA, $F_{1, 33} = 0.22$, $P = 0.64$). In addition to the overall decline in fish density with

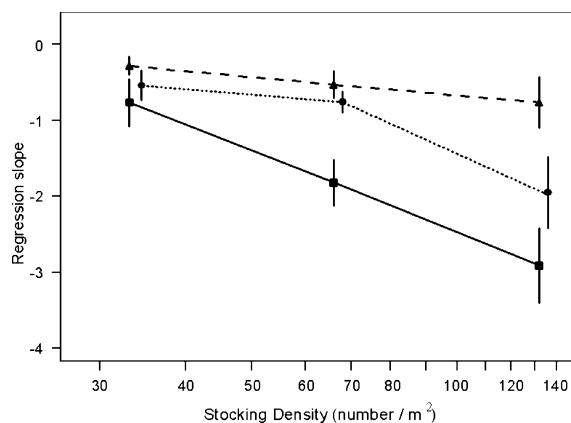


Fig. 1. Regression slopes (± 1 SE) calculated from body length-density relationships for steelhead trout held in experimental stream channels versus initial stocking density. Squares and solid lines represent low food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent high food levels.

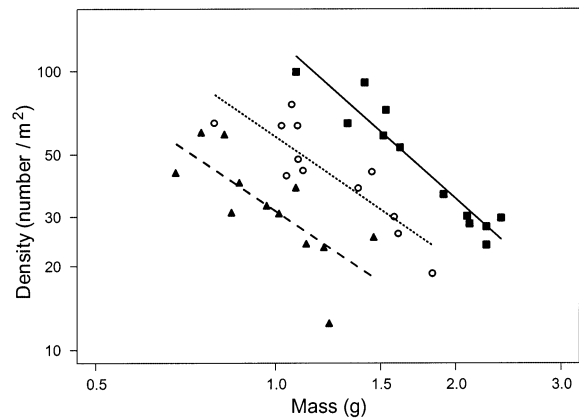


Fig. 2. The relationship between density of steelhead trout that survived through an eight week period in experimental stream channels and the average mass of an individual within a cohort. Line types and symbols represent cohorts of fish that experienced different levels of food abundance in the stream channels; they are defined as follows: high (solid line and squares), medium (dotted line and circles), or low food abundance (dashed line and triangles).

increasing body size, there were significant effects of both treatment factors on the relationship between density and body size (Fig. 2). Although the cohorts of fish in the stream channels were fed at one of three levels of food abundance, because each ration was constant over the entire experiment, these data can be used to compare the regression coefficient to distinguish among the potential self-thinning slopes. Interestingly, after controlling for the effects of food abundance and stocking density, the density of fish that survived or remained in the channels to the end of the experiments was related to mean body size by the exponent -0.74 (Table 1); very close and not significantly different from the exponent of -0.73 based on the allometry of food consumption ($t = 0.036$, $P > 0.50$). Although, the slope was most similar to the slope predicted by the allometry of food consumption, a relatively wide 95% confidence interval (-0.91 to -0.57) also precluded distinguishing the slope of -0.74 from the slopes predicted by metabolic rate or territory size.

Table 1. Multiple regression statistics predicting \log_{10} fish density based on experimental treatment levels and \log_{10} fish body mass.

Variable	Coefficient	sum-of-squares ^a	P-value ^a
Stocking density (number/m ²)	0.13	0.094	0.001
Food abundance (g/day)	0.17	0.13	0.0002
Body mass (g)	-0.74	0.05	0.013

^a Sum-of-squares and probability for each variable when entered into the model after all other variables (type III, SAS Institute 1989).

Discussion

Experimental populations of juvenile steelhead trout that were undergoing density-dependent mortality, growth and emigration exhibited declines in density with increasing mean body size. Densities of fish declined with increasing fish size, even after controlling for the effects of food abundance and stocking density. As predicted for populations that are undergoing self-thinning, the rate of decline was related to the intensity of competition. To my knowledge, these are the first experimental data that have met the assumptions of constant food abundance and density-dependent declines in population size needed to test the self-thinning hypothesis for a stream salmonid (see Dunham et al. 2000 for an experimental study of minnow cohorts).

Under controlled experimental conditions, fish density scaled to mean fish size by the exponent -0.74 ; very close to the predicted exponent of -0.73 based on the allometry of food consumption (Jobling 1993, Steingrímsson and Grant 1999). Because of the potential importance in predicting the population dynamics of stream salmonids, several studies have attempted to determine if population density scales to body size according to a general self-thinning slope. In natural populations, past studies have either found support for a self-thinning slope based on the allometry of metabolic requirements (Elliott 1993, Grant 1993, Bohlin et al. 1994) or the allometry of territory size (Steingrímsson and Grant 1999). These contradictory findings emphasize that under natural conditions a general self-thinning slope may not be easily applicable because factors such as food abundance and population density often vary across temporal and spatial scales (Folt et al. 1998, Grant et al. 1998). My study experimentally confirms that self-thinning can occur as mean body size within a cohort increases, but understanding how changing levels of resource abundance and competition influence self-thinning trajectories in natural populations will probably determine the general applicability of the self-thinning concept.

Although emigration can be an important mechanism affecting the demographic characteristics of a population (Łomnicki 1988), my study indicated little effect on a self-thinning relationship. Despite this result, emigration from a population can significantly influence population characteristics by increasing mean body size when small, weak competitors leave an area (Titus and Mosegaard 1991, Elliott 1994, Keeley 2001). Hence, after controlling for differences in body size among treatment levels, the lack of any effect on the self-thinning relationship may simply have been due to size differences among cohorts.

One potential predictor of declines in density in natural salmonid populations may come from territory size relationships. Self-thinning in salmonids has been linked to space requirements because of the occurrence

of feeding territories that increase in size with body size (Grant et al. 1989, Elliott 1990, Keeley and Grant 1995, Keeley and McPhail 1998). Given the seasonal declines in food abundance as well as the increasing prey size selectivity of salmonids with increasing body size, natural populations are unlikely to experience constant food availability (Grant et al. 1998). Because constant food availability is a prerequisite for applying the allometry of metabolism or food consumption as a predictor of self-thinning, these relationships may not be a reliable predictor of natural population dynamics. An alternative predictor may come from territory-body size relationships. Stream-dwelling salmonids defend areas to capture food and they scale territory size to maintain a maximum ration over their territories (Keeley and Grant 1995, Keeley and McPhail 1998). As a result, the allometry of territory size may integrate seasonal changes in food abundance as well as prey size constraints. If territory size is the proximate mechanism for self-thinning in natural populations of stream-salmonids, then the allometry of territory size will predict a steeper self-thinning slope when food abundance declines seasonally. Steingrímsson and Grant (1999) demonstrated this principle by following a cohort of juvenile Atlantic salmon (*Salmo salar*) and carefully monitoring declines in fish density and food abundance. Their results rejected the slope of the energetic equivalence hypothesis, but supported the slope predicted by the allometry of territory size. This does not mean that the self-thinning slope is unrelated to metabolic demands. It simply means that when food abundance declines seasonally, territory size is likely to be a more accurate predictor of self-thinning than either metabolic rate or food consumption because territory size may accurately integrate seasonal declines in food abundance. My experimental data indicate that changes in food abundance or population density will have a strong effect on how quickly populations self-thin. Hence, understanding how food abundance or population density varies seasonally or from year to year may help explain differences in self-thinning slopes across studies (Elliott 1993, Grant 1993, Steingrímsson and Grant 1999).

Self-thinning and the maximum density of salmonids in streams

To conclude that declines in natural populations are a result of self-thinning, it is necessary to distinguish density-independent from density-dependent mortality and growth (Armstrong 1997). However, if self-thinning is to be considered an important component of the factors that influence the abundance of salmonids in streams, there should be at least qualitative support for this idea at a broad level of comparison.

Chapman (1966) argued convincingly that the aggressive behaviour of stream dwelling salmonids might act to limit the density of salmonids in streams. Although there was little published data available at the time, Allen (1969) tested Chapman's (1966) idea by using density and body size estimates for several salmonid species. He found that the density of fish per area of stream declined in relation to average fish size, qualitatively consistent with the self-thinning hypothesis. Grant and Kramer (1990) extended this analysis by using data compiled from the literature to calculate space requirements based on territory size. They then used the inverse of the territory size-body size regression to determine whether space requirements predict the maximum densities of salmonids and found that in most instances, densities were bounded by territory size.

Since 1990, several studies have estimated densities of salmonids in natural streams, over a wide range of body sizes. I compiled these and earlier data sets to test the prediction that density is inversely related to body size. In these data, for five species of salmonids, there was a significant decline in fish density with body size (Fig. 3). Furthermore, the density of fish from these studies reached a maximum at an elevation predicted by the inverse of the territory size regression (Fig. 3), suggesting that space requirements limit the densities of wild stream-dwelling salmonids. However, some points fell well below the inverse of the territory size regression

(Fig. 3) and the scaling of salmonid density to body mass ($b = -0.68$) was significantly different from the inverse of the territory size slope ($b = -0.86$; $t = 49.68$, $P < 0.001$). These observations suggest that some populations of salmonids are limited by other factors, such as density-independent temperature or flow events (Elliott 1994), rather than by space competition.

As Grant et al. (1998) point out, the difficulty in applying the concept of self-thinning to natural populations is knowing whether a population is experiencing food or space-related competition at all. Grant and Kramer (1990) developed an index of habitat saturation using their territory-body size regression that may be useful in determining the level of population density where density-dependent competition begins. When percent habitat saturation (PHS) is 100%, habitats are predicted to be at maximum capacity. However, because not all habitats in a stream are usable, populations below 100 PHS are also likely to experience density-dependent mortality and be subjected to self-thinning. Grant and Kramer (1990) assessed the probability of observing a density-dependent response in a population from a compilation of studies using a logistic regression. They found that an inflection probability of 0.5 occurred when a PHS of 27% was reached, indicating a sharp increase in density-dependent responses even when only a fraction of the habitat was occupied. This rule of thumb may be useful in deter-

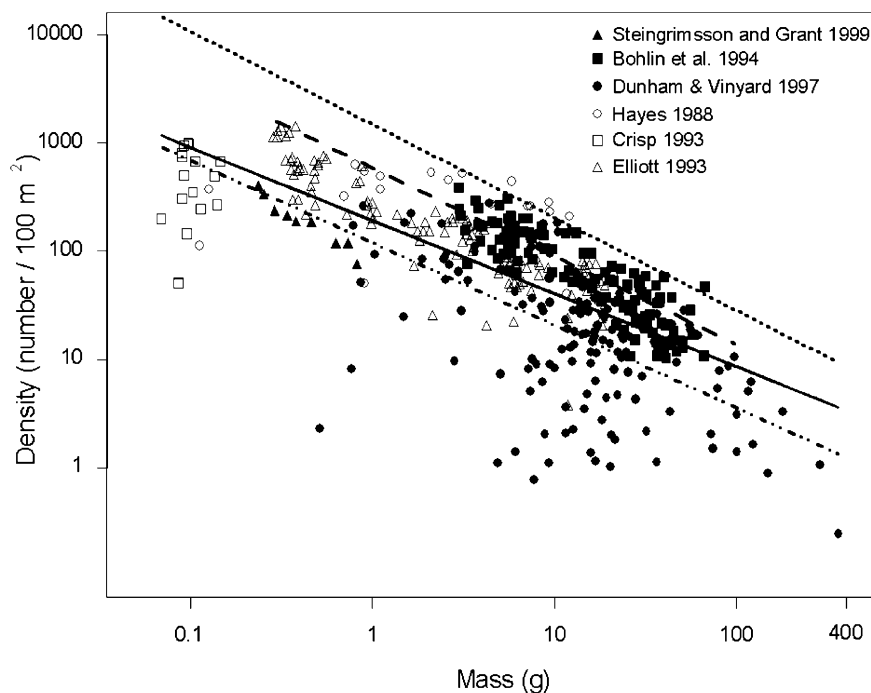


Fig. 3. The relationship between density of salmonid fishes in streams versus average body mass. The solid line represents the ordinary least-squares fit to all of the symbols ($\log_{10} \text{ density (number/100 m}^2) = -0.68 \log_{10} \text{ mass (g)} + 2.28$, $r^2 = 0.52$, $n = 433$, $P < 0.0001$). The dotted line represents the predicted maximum density of fish based on the inverse of Grant and Kramer's (1990) territory-body size regression for several salmonid species ($\log_{10} \text{ density (number/100 m}^2) = -0.86 \log_{10} \text{ mass (g)} + 3.17$). The dashed line represents the regression for points that fall equal to or above 27 percent habitat saturation ($\log_{10} \text{ density (number/100 m}^2) = -0.82 \log_{10} \text{ mass (g)} + 2.78$, $r^2 = 0.87$, $n = 185$, $P < 0.0001$). The dashed-dotted line represents the regression for points that fall below 27 percent habitat saturation ($\log_{10} \text{ density (number/100 m}^2) = -0.76 \log_{10} \text{ mass (g)} + 2.077$, $r^2 = 0.67$, $n = 248$, $P < 0.0001$). The data are compiled from the literature, see legend for sources.

mining which populations are likely to undergo self-thinning. From the data set I collected from the literature (Fig. 3), when I excluded those observations below a PHS of 27% the scaling of density to body mass was much closer ($b = -0.82$) and not significantly different from the inverse of the territory size slope ($t = 1.68$, $P > 0.05$).

Conclusions

This study indicates that experimental populations of steelhead trout decline as predicted by the self-thinning hypothesis, but the intensity of intraspecific competition strongly influences how quickly populations decline. This is the first study I know of that has provided experimental evidence for this idea in stream-dwelling salmonids. In addition, observational studies of stream-dwelling salmonids also provide qualitative support for this idea; however, the general applicability of the self-thinning relationship to salmonids may depend on whether most or all populations are limited by space competition at least during some point in a cohort's life cycle. In order to extend our current understanding of population dynamics in stream salmonids, future studies will need to determine if natural populations undergoing density-dependent mortality, growth and emigration also decline as mean body size increases within a population.

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