

# Territory Size as a Predictor of the Upper Limit to Population Density of Juvenile Salmonids in Streams

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We examined the old, but untested hypothesis that territory size limits the maximum population density of salmonids in streams. We used published data to derive an interspecific regression of territory size ( $m^2$ ) on fork length (cm) ( $\log_{10}$  territory size =  $2.61 \log_{10}$  length —  $2.83$ ,  $r^2 = 0.87$ ,  $n = 23$ ). Growth and mortality trajectories of salmonid cohorts from eight experimental studies were compared to the maximum-density regression, the inverse of the territory–size regression. In shallow habitats, such as riffles and raceways, the cohort trajectories followed the maximum density regression quite closely and were consistent with the territory–size hypothesis. In addition, natural densities in eight other studies did not exceed the predicted maximum density and tended to fall within the 95% C.L. of the maximum-density regression. Data from shallow habitats, therefore, provide strong support for the territory–size hypothesis. A linear logistic response model showed that the probability of observing density-dependent growth, mortality, or emigration increased significantly with increasing values of an index of habitat saturation, developed from the territory–size regression. Our results suggest that the territory–size regression has practical value for predicting the maximum densities of stream-dwelling salmonids in shallow habitats and the occurrence of density-dependent population responses.

Nous avons étudié l'ancienne hypothèse non vérifiée selon laquelle la superficie du territoire limite la densité maximale de population des salmonidés dans les cours d'eau. Nous avons utilisé les données existantes afin de dériver une régression interspécifique de la superficie du territoire ( $m^2$ ) à la longueur à la fourche (cm) ( $\log_{10}$  superficie du territoire =  $2,61 \log_{10}$  longueur —  $2,83$ ,  $r^2 = 0,87$ ,  $n = 23$ ). Les trajectoires de croissance et de mortalité de cohortes de salmonidés provenant de huit études expérimentales ont été comparées à la régression de densité maximale, l'inverse de la régression de la superficie du territoire. Dans le cas d'habitats en eau peu profonde avec courant rapide, les trajectoires des cohortes suivaient la régression de la densité maximale assez étroitement et elles étaient conformes à l'hypothèse de la superficie du territoire. De plus, les densités naturelles dans huit autres études ne dépassaient pas la densité maximale prévue et avaient tendance à se trouver dans l'intervalle de la limite du seuil de confiance de 95% de la régression de la densité maximale. Les données concernant les habitats en eau peu profonde appuient donc fortement l'hypothèse de la superficie du territoire. Un modèle de réponse logistique linéaire a montré que la probabilité d'observer une croissance, une mortalité ou une émigration dépendante de la densité augmentait significativement avec les valeurs croissantes d'un indice de saturation de l'habitat, élaboré à partir de la régression de la superficie du territoire. Il semble, d'après nos résultats, que la régression de la superficie du territoire a une valeur pratique pour prévoir la densité maximale des salmonidés dans les habitats avec cours d'eau peu profonds et l'occurrence des réactions de la population dépendante de la densité.

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Juvenile salmonids in streams commonly defend feeding territories (Dill et al. 1981; McNicol et al. 1985; Puckett and Dill 1985). This territorial behaviour has been hypothesized to play a role in limiting population density (e.g. Chapman 1966; Allen 1969; Mortensen 1977; Elliott 1984a). If a minimum territory size exists, then territoriality will limit maximum population density because excess individuals that do not acquire a territory presumably die or emigrate. The best evidence that territoriality can limit the population density of animals comes from studies of breeding birds (for a review, see Patterson 1980; Gauthier and Smith 1987). Similar evidence for stream-dwelling salmonids is lacking, but flat-topped stock-recruitment curves (see Solomon 1985 for a review) are at least

consistent with the hypothesis that territoriality limits population density.

There is not necessarily a logical link between territoriality and the limitation of population density. If territory size is inversely proportional to population density and there is no minimum territory size, then territoriality would play no role in limiting density. Behavioural ecological studies of stream-dwelling salmonids are more consistent with the view that territory size is flexible rather than rigid. Not all individuals defend territories (McNicol et al. 1985; Puckett and Dill 1985; Grant and Noakes 1988), and when they do, territory size is influenced by the abundance of food and intruder pressure (Slaney and Northcote 1974; Dill et al. 1981; McNicol and Noakes 1984). In addition, territoriality in animals often ceases at high population densities (see Wilson 1975, p. 296–297) when the costs exceed the benefits of defence. Juvenile salmonids may

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conform to this generalization because they appear to switch from territorial to schooling behaviour when population densities are sufficiently high (Kalleberg 1958; Kawanabe 1969).

Despite scepticism (e.g. Noakes and Grant 1986) about the hypothesis that territory size limits population density (hereafter, the territory-size hypothesis), the resolution of this question has important management implications, because the territory-size hypothesis predicts maximum population densities which should not be exceeded by stocking or escapement quotas. In a stimulating paper, Allen (1969) suggested a unique way to test the territory-size hypothesis. The inverse of a regression of territory size on body size (the maximum-density regression) predicts the maximum density of a salmonid population that is composed of a single size-class. Allen (1969) could not test the territory-size hypothesis rigorously because he lacked sufficient territory-size data. However, his data suggested that space was not limiting because only 2–20% of the habitat appeared to be occupied by territories. But, instead of rejecting the territory-size hypothesis, Allen concluded that only 2–20% of the habitat has the right environmental features for the territories of any single size-class of fish.

Many studies have investigated the effects of population density on growth, mortality, or emigration rate (e.g. Le Cren 1973; Egglisshaw and Shackley 1977; Mortensen 1977; Elliott 1984a) or tested the general idea that space may limit salmonid population density (e.g. Chapman 1962; Mason 1969). However, no study has attempted to test quantitatively the hypothesis that territory size limits density. Therefore, our purpose was to re-examine this old question using a large database. We had three specific objectives: (1) to develop an interspecific regression of territory size vs. body size for juvenile stream-dwelling salmonids, (2) to test quantitatively the territory-size hypothesis by comparing population-density data from the literature with

the maximum-density regression, and (3) to determine whether the maximum-density regression can predict the occurrence of density-dependent changes in growth, mortality, or emigration. Our study included data for seven species: coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), rainbow trout (*O. mykiss*, formerly *Salmo gairdneri*), cutthroat trout (*O. clarki* formerly *Salmo clarki*), Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and brook trout (*Salvelinus fontinalis*).

## Allometry of Territory Size

### Methods

We searched the literature for data relating territory size to body size of stream-dwelling salmonids, starting with Dill (1978). We included only studies where territory size was measured directly and did not include those where territory size was inferred from the inverse of population density. Some authors did not explicitly say how territory size was measured, but most appeared to use a version of the minimum-convex-polygon method (Schoener 1981). When studies reported territory sizes for fish under different conditions, such as high or low intruder pressure or high or low food density, a datum was included for each environmental condition, rather than calculating an average territory size. Because errors in the estimate of body size are much less than in territory size, we used the least-squares method to regress territory size on body size.

The interspecific regression was compared to a regression for brook trout (Grant et al. 1989). The brook trout regression underestimated territory size because it was based on average territory radius rather than the convex-polygon method. As

TABLE 1. Territory sizes of stream-dwelling salmonids.

Number <sup>a</sup>	Species <sup>b</sup>	Conditions <sup>c</sup>	n <sup>d</sup>	Territory area (m <sup>2</sup> )	Fork length (cm)	Source
1.	<i>S.s.</i>	F	3	0.970	10.0	Stradmeyer and Thorpe 1987
2.	<i>S.s.</i>	F	3	1.633	13.0	Stradmeyer and Thorpe 1987
3.	<i>S.s.</i>	ST-high ration	8	1.136	11.4	Symons 1971
4.	<i>S.s.</i>	ST-low ration	9	1.120	11.8	Symons 1971
5.	<i>S.s.</i>	ST	—	0.011	2.5	Kalleberg 1958
6.	<i>S.s.</i>	ST	—	0.030	4.5	Kalleberg 1958
7.	<i>S.t.</i>	ST	1	4.0	23.0	Kalleberg 1958
8.	<i>O.m.</i>	A	2	0.043	4.3	Stringer and Hoar 1955
9.	<i>O.m.</i>	A	2	0.050	5.3	Stringer and Hoar 1955
10.	<i>O.m.</i>	A	2	0.118	6.3	Stringer and Hoar 1955
11.	<i>O.m.</i>	ST-low prey	4	0.037	2.5	Slaney and Northcote 1974
12.	<i>O.m.</i>	ST-intermediate prey	6	0.018	2.5	Slaney and Northcote 1974
13.	<i>O.m.</i>	ST-high prey	6	0.010	2.5	Slaney and Northcote 1974
14.	<i>O.m.</i>	A	7	0.258	7.6	Yamagishi 1962
15.	<i>O.k.</i>	A	2	0.066	4.3	Stringer and Hoar 1955
16.	<i>O.k.</i>	A	2	0.088	5.3	Stringer and Hoar 1955
17.	<i>O.k.</i>	A	2	0.113	6.3	Stringer and Hoar 1955
18.	<i>O.k.</i>	F-high intruder pressure	12	0.131	4.5	Dill et al. 1981
19.	<i>O.k.</i>	F-low intruder pressure	9	0.199	4.5	Dill et al. 1981
20.	<i>O.k.</i>	ST-riffles	—	0.195	6.5	Mason 1969
21.	<i>O.k.</i>	ST-pools	20	0.130	6.5	Mason 1969
22.	<i>S.f.</i>	ST	8	0.110	5.4	McNicol and Noakes 1981
23.	<i>S.f.</i>	F	6	0.340	4.6	McNicol et al. 1985

<sup>a</sup>Numbers refer to data in Fig. 1.

<sup>b</sup>*S.s.* = Atlantic salmon; *S.t.* = brown trout; *O.m.* = rainbow trout; *O.k.* = coho salmon; *S.f.* = brook trout.

<sup>c</sup>F = field, unconfined fish in a natural stream; ST = stream tank with directional water currents; A = aquarium with weak directional water currents.

<sup>d</sup>n = number of fish observed.

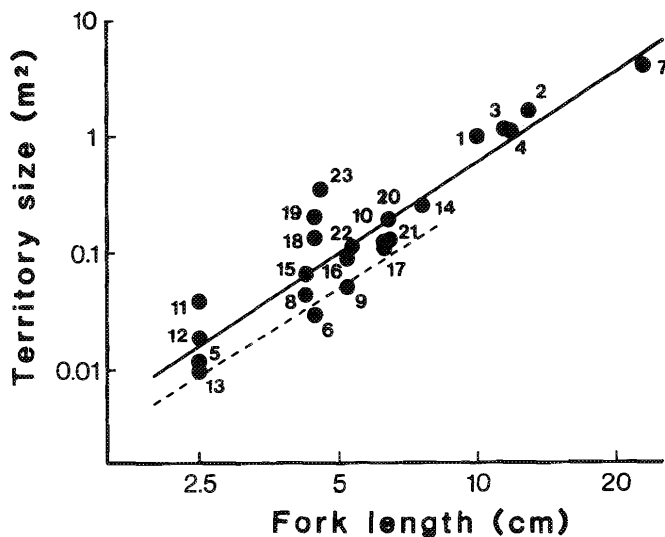


FIG. 1. Interspecific relationship between territory area ( $m^2$ ) and fork length (cm) for stream-dwelling salmonids; numbers refer to data in Table 1. The equation of the least-squares regression is  $\log_{10} \text{area} = 2.61 \log_{10} \text{length} - 2.83$ ,  $r^2 = 0.87$ ,  $n = 23$ ,  $P < 0.001$ ; 95% C.L. for the slope and intercept are 2.15–3.07 and  $-3.19$  to  $-2.46$ , respectively. The dashed line is the territory-size regression for brook trout ( $\log_{10} \text{area} = 2.48 \log_{10} \text{length} - 2.84$ ,  $r^2 = 0.70$ ,  $n = 23$ ,  $P < 0.001$ ; 95% C.L. for the slope is 1.74–3.22; data from Grant et al. 1989). The brook trout data were multiplied by 1.64 to make them comparable to the interspecific data. For the sake of graphical presentation, the uncorrected regression is shown ( $y$ -intercept =  $-3.05$ ).

Grant et al. (1989) discuss, the latter method gave a result that was 1.64 times larger than the former, so territory sizes of brook trout were multiplied by 1.64 to correct for this bias.

To calculate a general mass (g) vs. fork length (cm) regression for stream-dwelling salmonids, we used regressions in Carlander (1969) supplemented with those in Brett and Glass (1973), Gee et al. (1978b), Englert et al. (1982), and Elliott (1985). A mean slope and intercept were calculated for each of sockeye salmon, rainbow trout, cutthroat trout, Atlantic salmon, brown trout, and brook trout. The overall regression was calculated as the mean for the six species:  $\log_{10} \text{mass} = 3.03 \log_{10} \text{fork length} - 1.93$ .

## Results

We found territory-size data for five species in 10 different studies (Table 1). Territory size ( $m^2$ ) increased with increasing body length (cm) (Fig. 1):

$$\log_{10} \text{area} = 2.61 \log_{10} \text{length} - 2.83.$$

Given the diverse environmental conditions under which the studies were conducted, body size explained a surprisingly high percentage of the variation in territory size. There were no obvious differences among species in territory size, but there was an order-of-magnitude variation about the line that appeared related to environmental conditions. For example, points 11, 12, and 13 reflect an inverse relation between food density and territory size (see Slaney and Northcote 1974), whereas points 18 and 19 reflect the inverse relation between intruder pressure and territory size (see Dill et al. 1981).

Also shown in Fig. 1 is the territory size — body size regression for young-of-the-year brook trout (Grant et al. 1989). No significant differences occurred between the slopes of the regressions (ANCOVA,  $P = 0.80$ ), and the intercept of the cor-

rected brook trout regression was almost identical to the intercept of the interspecific regression, and was well within its 95% C.L. ( $-3.17$  to  $-2.46$ ). The similarity of the two regressions gave us more confidence in the validity of the interspecific regression. We used the interspecific regression to test the territory-size hypothesis because it includes data for five of the seven species in our study.

## Discussion

Territory size increased as a power function of body length raised to exponents between 2.48 and 2.61 (Fig. 1). Because body mass ( $M$ ) increases in proportion to fork length raised to the power of 3.03, territory size increased in proportion to  $M^{0.82-0.86}$  ( $2.48/3.03 - 2.61/3.03$ ). In salmonids, metabolic rate is proportional to  $M$  raised to exponents between 0.75 and 1.10 (Brett 1965; Brett and Glass 1973; Schmidt-Nielsen 1984) rather than the ubiquitous exponent of 0.75 (Peters 1983). Therefore, Fig. 1 was consistent with the hypothesis that juvenile salmonids increase their territory size as they grow in proportion to their increasing energetic requirements.

Unlike salmonids, the home range/territory size — body mass relationships for birds, mammals, and lizards have greater exponents than their corresponding metabolic rate — body size relationships (Harestad and Bunnell 1979; Calder 1984; Lindstedt et al. 1986). Damuth (1981) suggests that the greater than expected slopes occur because the number of conspecifics that share a home range increases with increasing body size, at least for herbivorous mammals. Salmonids are unique in a number of ways that may account for the apparent difference in the allometry of their territories. They defend relatively two-dimensional territories near the stream bottom, and yet feed throughout the water column on drifting aquatic invertebrates. Hence, the productivity of a salmonid territory will be directly proportional to the cross-sectional area of the territory or the square root of territory area. However, larger salmonids tend to occupy faster and deeper water (Chapman and Bjornn 1969), both of which will increase the food production of a territory. In addition, range overlap will be independent of body size because salmonids defend relatively exclusive territories. Thus, even if salmonid territory size increases in direct proportion to metabolic requirements, it is not clear how they should scale to body size.

Juvenile salmonids defend territories of about seven body lengths in diameter (Grant et al. 1989). Compared to data for birds (Schoener 1968), salmonid territories [ $\log_{10} \text{area} (m^2) = 0.86 \log_{10} M (g) - 1.17$ ] are five orders of magnitude smaller than bird territories [ $\log_{10} \text{area} (m^2) = 1.14 \log_{10} M (g) + 4.00$ ]. The only other data available for poikilotherms, suggest that the home range size of lizards ( $\log_{10} \text{area} (m^2) = 0.95 \log_{10} M (g) + 3.12$ ) are four orders of magnitude larger than salmonid territories (Turner et al. 1969). Thus, the territory-size hypothesis predicts that the maximum densities of stream-dwelling salmonids will be much higher than those of most animals of comparable size (see Peters 1983, chapter 10).

Some of the variation about the interspecific regression may reflect species differences, different methods of measuring territory size, and stochastic variation related to small sample sizes. The mean square error about the interspecific regression was 0.066 compared to 0.089 for the brook trout regression in Fig. 1 and 0.253 for a brook trout regression for 110 less frequently aggressive fish (Grant et al. 1989). Hence, there was considerable variation about the brook trout regressions, even

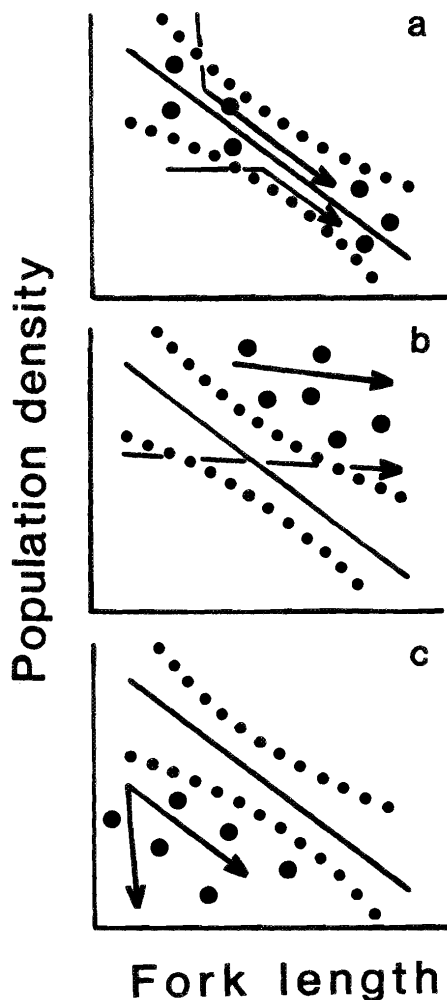


FIG. 2. Hypothetical population density data from single samples (dots) or from following cohorts through time (arrows) in relation to the maximum-density regression (solid line) and its 95% C.L. (dotted lines), predicted by the inverse of the territory-size regression. The data in (a) strongly support the hypothesis that territoriality limits density, whereas those in (b) falsify the hypothesis, and those in (c) suggest the hypothesis is irrelevant.

when the effects of species and methodology were removed. We suspect this variation is real and is related to factors such as food density, intruder pressure, current velocity, and water depth. Including these factors in a multiple regression would potentially decrease the variation about the allometric regressions, but the data are not currently available to do this.

### Territory Size and the Limitation of Population Density

#### Predictions of the Territory-Size Hypothesis

When a single size-class of fish occupies a habitat, the territory-size hypothesis predicts that their maximum density will be the inverse of their territory size predicted from the territory-size regression. To test this prediction, we compared population density data from the literature to the maximum-density regression (i.e. the inverse of the territory-size regression):

$$\log_{10} \text{ density} = -2.61 \log_{10} \text{ fork length} + 2.83.$$

In Fig. 2 we show how we would use three hypothetical data sets to test this prediction. The arrows represent cohorts of fish that are sampled repeatedly through time. An arrow moving horizontally to the right indicates growth of fish with no mortality whereas an arrow moving vertically down indicates mortality or emigration with no growth. Dots represent single population samples.

The territory-size hypothesis predicts that a cohort beginning above the regression will move steeply down and then follow a trajectory along the maximum-density regression (Fig. 2a), that a cohort beginning below the regression will initially move horizontally and then follow a trajectory along the maximum-density regression, and that individual data points will cluster about the maximum-density regression within the 95% C.L. The territory-size hypothesis would be falsified by a cohort that begins and remains above the maximum-density regression, by a cohort that begins below and crosses above the regression, or by individual data points consistently above the upper 95% C.L. (Fig. 2b). Cohorts that begin below and do not approach the maximum-density regression (Fig. 2c) do not falsify the hypothesis but suggest that it is irrelevant. Other factors such as food, predation, or the quality of habitat must be limiting density. We would draw a similar conclusion if individual data points were consistently below the lower 95% C.L. of the maximum-density regression.

The simple graphical test of the hypothesis (Fig. 2) cannot be used when more than one size-class of fish is present in the habitat unit that is sampled for population density. Instead, we used the territory-size regression to calculate an index of habitat saturation. For fish of size  $i$ , maximum density ( $D_i \text{ max}$ ) was calculated from the maximum-density regression; this maximum density was defined as 100% saturated. For populations with  $n$  cohorts or size-classes present at one time, percent habitat saturation (PHS) was calculated as:

$$\begin{aligned} \text{PHS} &= 100 \cdot \sum_{i=1}^n D_i / D_i \text{ max}, \\ &= 100 \cdot \sum_{i=1}^n D_i \cdot T_i \cdot 1.19, \end{aligned}$$

where  $D_i$  is the actual density (per  $\text{m}^2$ ) of size-class  $i$ ,  $T_i$  is the territory size ( $\text{m}^2$ ) for size-class  $i$  predicted from the territory size — body size regression, and 1.19 is a correction factor that is needed to remove bias introduced when the data were  $\log_{10}$  transformed (Sprugel 1983). If different size-classes do not have overlapping territories, due either to habitat segregation by size or to defence against all size-classes, then the territory-size hypothesis predicts that the maximum PHS will be 100. However, if territories of different size-classes overlap, i.e. no defence between size-classes, then PHS could be greater than 100.

The abundance of salmonids in streams is often reported as biomass ( $\text{g} \cdot \text{m}^{-2}$ ) or production ( $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ), neither of which can be used to test the predictions in Fig. 2. However, if  $\log_{10}$  maximum density ( $\text{no.} \cdot \text{m}^{-2}$ ) =  $2.83 - 2.61 \log_{10}$  fork length (cm) (i.e. the inverse of the territory-size regression in Fig. 1), and  $\log_{10}$  mass =  $3.03 \log_{10}$  fork length - 1.93 (see Methods) then  $\log_{10}$  biomass ( $\text{g} \cdot \text{m}^{-2}$ ) =  $0.42 \log_{10}$  fork length + 0.90. This implies that the biomass of salmonids in cultures of uniform size will increase with body length. For salmonids of 23 cm, the largest fish in our interspecific regression (Table 1), the predicted biomass is  $30 \text{ g} \cdot \text{m}^{-2}$ . We can use this as a rough

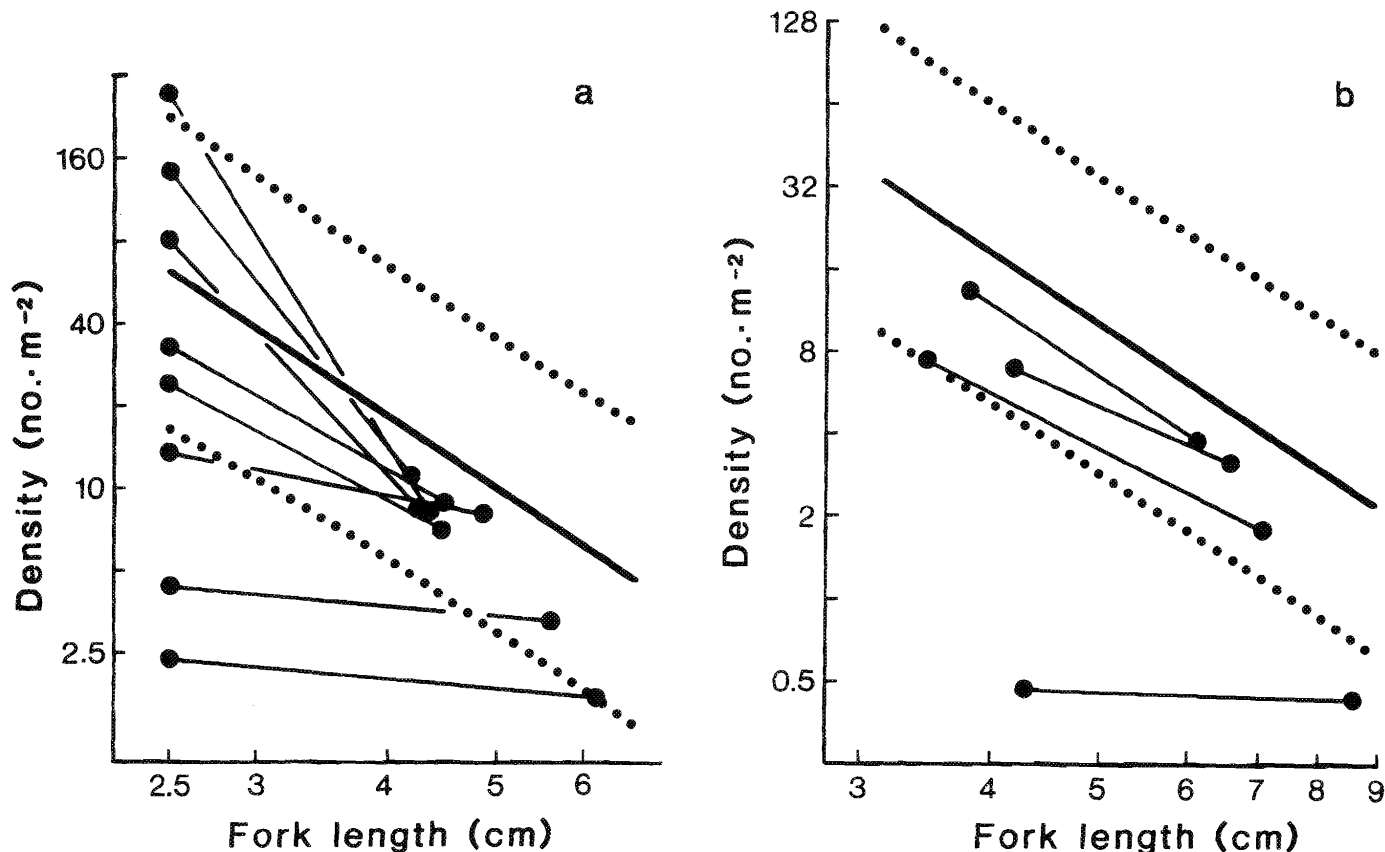


FIG. 3. (a) Population density and mean size of 0+ brown trout stocked in cages or screened sections of streams and recovered 133 d later (Le Cren 1965, 1973). Lines join the initial population to the recovered population. The heavy line is the maximum-density regression with 95% C.L. for individual predicted values. (b) Total population density and mean size of juvenile coho salmon and steelhead trout stocked and recovered in artificial stream channels (Fraser 1969). Lines join the initial and final populations after a 163 d experiment.

estimate of the predicted maximum biomass of salmonids in streams.

#### Methods

The clearest data for testing the hypothesis come from experimental studies that follow a single cohort of fish through time. These studies typically provide relatively uniform habitats and accurate estimates of fish size and density. Experimental studies are presented in detail in the results if a single size-class of fish was stocked at a variety of densities and followed for at least 1 mo. Studies are presented in less detail if more than one size-class of fish was used, the fish were stocked at a single or small range of densities, or the fish were followed for less than 1 mo.

Non-experimental data are also important because they reflect densities of fish under natural conditions. These observational data are of three types: local-habitat densities, average-stream densities, and average-stream biomass. Local-habitat densities are the most relevant of the three types for testing the hypothesis. Because of habitat patchiness, some areas of the stream bed will be unsuitable for stream-dwelling salmonids in general or for a particular size-class of fish. By focussing on smaller sampling units, local-habitat densities restrict the size range of fish per sample, which facilitates graphical testing of the hypothesis (i.e. Fig. 2). In addition, smaller sampling units increase the range and hence maximum densities encountered (Krebs 1989, chapter 3); the latter are important for testing the hypothesis.

Most local-habitat densities in the literature are from focal-animal observations (Altmann 1974). By definition, these data exclude unused and low-density habitats, thereby providing the maximum densities in suitable habitats. As part of a study of the social behaviour of young-of-the-year brook trout (see Grant and Noakes 1988), the number of conspecifics was counted within a 1 m<sup>2</sup> area around the focal fish. We searched the literature for similar data for other species.

Because average stream-density data are less satisfactory for testing the predictions of Fig. 2, we included only those originally presented by Allen (1969) and the exceptional 17-yr data set for Black Brows Beck (Elliott 1984a, 1984b, 1985, 1987, 1988).

Because they ignore the distribution of mass among individuals, average-stream biomass were the least relevant of the three types of observational data for testing the predictions of Fig. 2. Hence, we rely primarily on data in a recent review by Mann and Penczak (1986).

#### Results

##### *Experimental studies*

Le Cren (1965, 1973) — Le Cren stocked brown trout alevins into small screened sections of a natural stream and counted the survivors 133 d later. The trout fed on natural food that drifted into the sections. Le Cren's original data provided strong evidence of a flat-topped stock-recruitment curve, which led him to conclude that territorial behaviour was responsible for

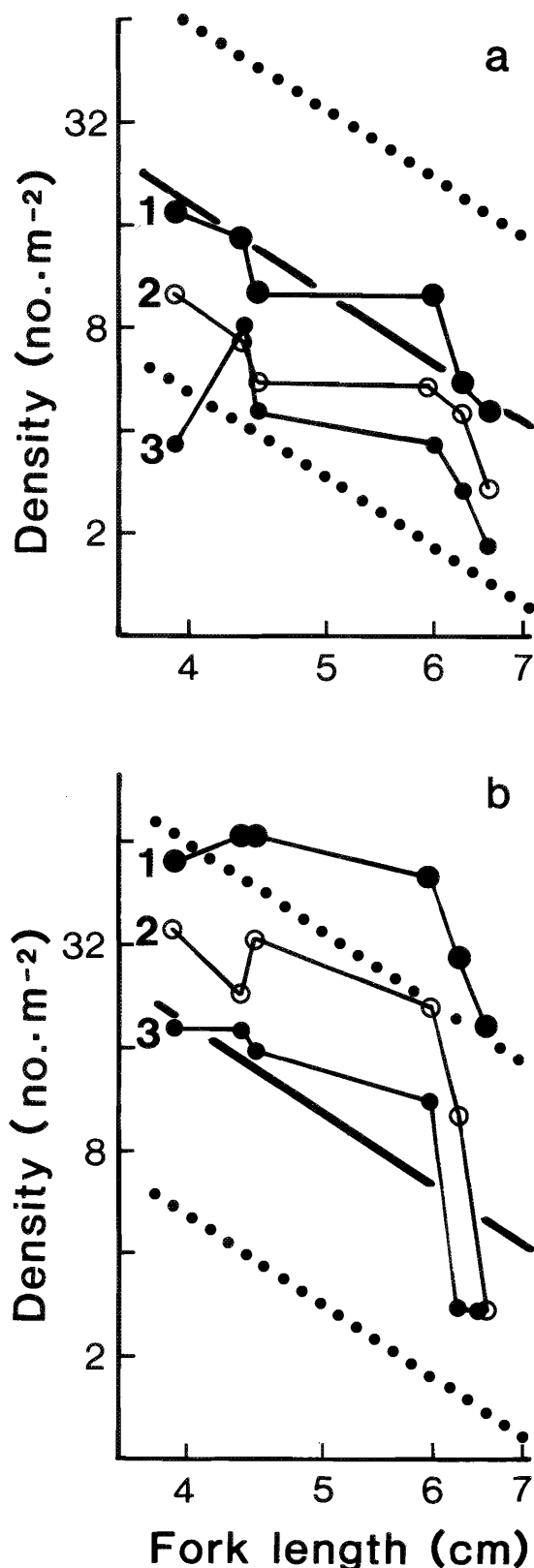


FIG. 4. Population density and mean size of juvenile coho salmon in (a) 3 riffles and (b) 3 pools of an artificial stream channel (Mason and Chapman 1965). The lines follow the number of fish in each compartment over a 4-mo experiment. The numbers refer to riffles 1, 2, and 3 and pools 1, 2, and 3 respectively (1 is upstream, 3 is downstream). The solid and dotted lines are as in Fig. 3.

the density-dependent starvation. Le Cren reported weights but not lengths of fish so we used Elliott's (1984b) relationship for brown trout to estimate length.

When Le Cren's data are replotted with our maximum-density regression, they provide strong support for the territory-size hypothesis (Fig. 3a). When initial densities were above the line, the number of survivors was just below that predicted by the maximum-density regression. When initial densities were well below the line, the cohort trajectories were virtually horizontal.

Fraser (1969) — Fraser stocked a mixture of juvenile coho salmon and rainbow trout into stream channels from which they could not emigrate, and counted the survivors 163 d later. The cause of death was unknown. The fish fed on natural drift entering and produced within the channel. Growth rate and survival rate of fish decreased with increasing density.

Fraser's data (Fig. 3b) were consistent with the hypothesis in Fig. 2a. At the three highest stocking densities, the cohort trajectories paralleled the maximum-density regression. When the stocking density was well below the line, the cohort trajectory was horizontal.

Mason and Chapman (1965) — Mason and Chapman stocked 300 coho salmon alevins into two stream channels that were each divided into six habitats: three riffles alternating with three pools. The coho salmon could move freely among the habitats or emigrate from the channel. Food entered the channel as natural drift at the upstream end (riffle 1, pool 1); drift density decreased downstream as the fish removed drift from the water. The number of fish was followed for 4 mo. Only data for the left channel are presented in detail (see their table III). The alevins in the right channel emerged from the gravel asynchronously, and therefore were considered in less detail below. Fork length was estimated from data in their table V.

Mason and Chapman's (1965) data for the three riffles (Fig. 4a) and three pools (Fig. 4b) are replotted with our regression. There were no significant differences among the slopes of regressions through the seven data sets ( $P = 0.65$ , ANCOVA), but the intercepts were different ( $P < 0.0001$ ). The adjusted mean density for riffle 1 was not significantly different from the maximum-density regression ( $P = 0.97$ , ANCOVA) and provided strong support for the territory-size hypothesis. Adjusted mean densities for riffle 2 and 3 were less than the maximum-density regression ( $P = 0.027$  and  $0.0002$ , respectively), demonstrating the influence of food availability on population density.

Data for pools 1 and 2 falsified the territory-size hypothesis since the adjusted mean density of coho salmon was greater than the maximum-density regression ( $P = 0.0001$  and  $0.025$ , respectively). The densities of coho salmon in pool habitats of Mason's (1969) experiments (not shown) were also above the upper 95% C.L. Food availability was also important in pools as population density decreased from pool 1 to pool 3 ( $P = 0.0003$ , ANCOVA).

Mason and Chapman's (1965) data also illustrate the importance of measuring local-habitat density rather than average-stream density for composite habitats. Even within this small stream channel ( $7.6 \times 0.9$  m), the density varied by an order of magnitude between pool 1 and riffle 3 (Fig. 4a, 4b).

Mason (1976) — Mason's influential study attempted to determine whether food or space limited the density of stream-dwelling salmonids during summer. Mason stocked juvenile coho salmon into small screened sections of a natural stream under two feeding regimes: natural food only or natural food

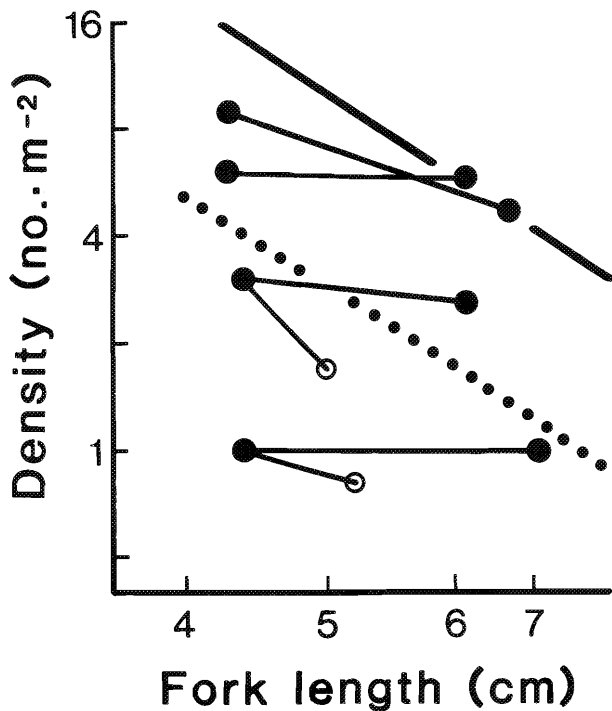


FIG. 5. Population density and mean size of coho salmon stocked and recovered from screened sections of a natural stream (Mason 1976). Solid circles show populations recovered from sections supplemented with food; the open circles show control populations. The solid line is the maximum-density regression with the lower 95% C.L.

supplemented with a daily ration of 15% per day. Fish were allowed to emigrate from the sections, and the number of survivors was recovered after either 50 or 62 d.

Supplemental feeding of coho salmon increased the growth rate and density of fish remaining in the sections compared to control populations (Fig. 5). Mason concluded that food and not space limited the density of juvenile coho. However, his results were also consistent with the territory-size hypothesis because the density of fish recovered from the two highest stocking densities were very close to the maximum-density line. Repeating these experiments at higher stocking densities and food densities would provide a stronger test of the territory-size hypothesis.

Other experimental studies — A number of authors stocked juvenile salmonids in stream tanks at high density, allowed some to emigrate, and reported “final” densities when emigration had ceased. We have collected these data in Fig. 6. To allow us to present all the data in one figure, the data are expressed as percent habitat saturation (PHS).

The data were generally consistent with the predictions since 13 of 16 recovered populations were within the 95% C.L. Ten of 16 populations were below saturation, but this did not differ from chance ( $P > 0.20$ , two-tailed binomial test). The variation in PHS of the final populations was probably due to factors other than just space. For example, all 10 fish emigrated from the low food + high cover treatment of Wilzbach’s (1985) experiment. Of particular interest are the two data points of Fausch (1984). His initial densities were close to the upper 95% C.L. and although emigration occurred, the final densities were well above 100 PHS, but within the C.L. However, 87% of the fish remaining in the stream channels lost weight during his experiment. Thus, fewer fish than expected emigrated, but they showed the effects of space-related competition by losing

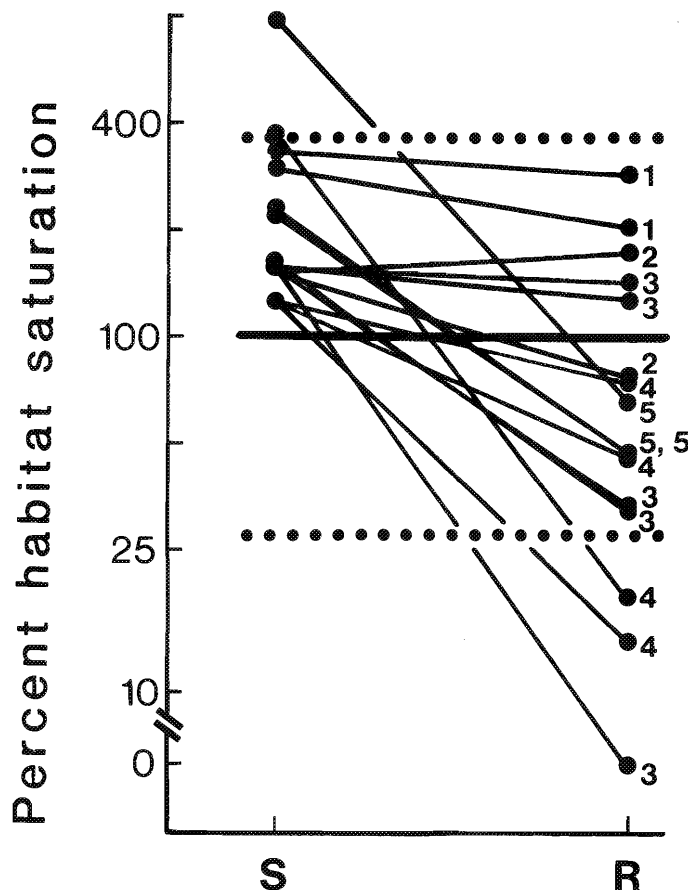


FIG. 6. Percent habitat saturation for juvenile salmonids stocked (S) and non-emigrants recovered (R) in experimental laboratory studies. Numbers refer to data from (1) Fausch (1984), (2) right riffle 1 and 2 from Mason and Chapman (1965), (3) Wilzbach (1985), (4) Slaney and Northcote (1974), and (5) Stein et al. (1972). The solid line represents a PHS of 100; the dotted lines are the approximate 95% C.L. from the maximum-density regression.

weight. These fish would presumably starve to death in a longer-term experiment that allowed no emigration.

#### Observational studies

Local-habitat density — Population density of young-of-the-year brook trout from three streams in southern Ontario are plotted in Fig. 7 (J. W. A. Grant, unpubl. data); the range in size is due to growth over the summer. Young-of-the-year trout rarely used the same microhabitat as older age-classes in these streams, so the data represent the total standing crop in these habitats. No density exceeded the upper 95% C.L. The density of small fish (<4 cm) was more often (76%) below the lower 95% C.L. than was the density of large fish (15%). The trajectory of the points was consistent with the predictions of Fig. 2a. The density of small trout did not appear to be limited by territory size, whereas space appeared to be more limiting for large young-of-the-year trout.

Other visual estimates of local-habitat density from the literature are shown in Fig. 8. Most of the points are within the 95% C.L. of the maximum-density regression. Of note are the data of Puckett and Dill (1985) who observed “floaters” living between the territories of other fish (point 4). If these floaters are excess fish that cannot acquire a permanent territory, then the population density of territorial fish alone (point 3) should be close to saturation. The large range in density of territorial

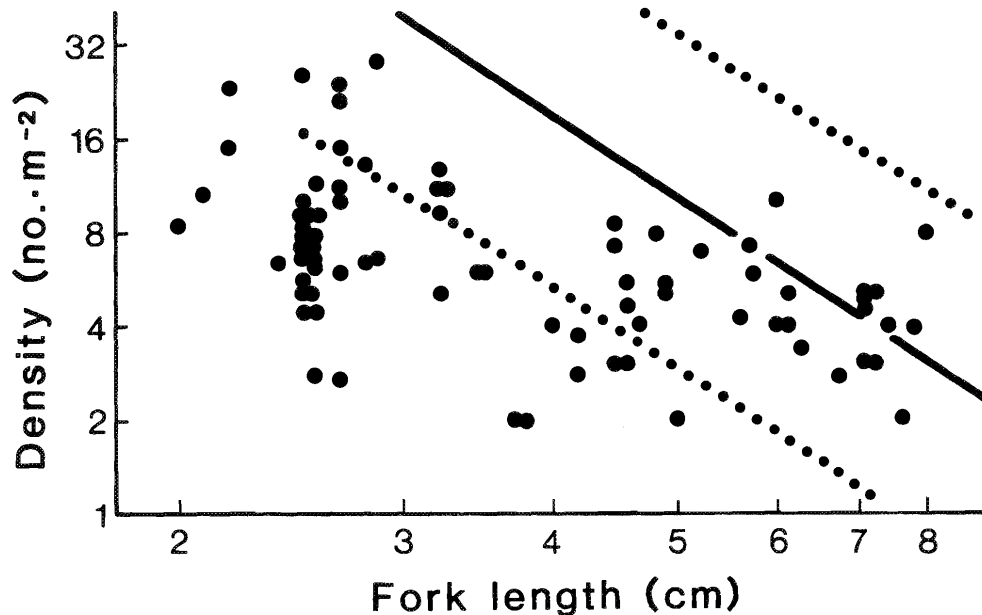


FIG. 7. Population density of young-of-the-year brook trout estimated from focal-animal observations in three southern Ontario streams. Each point represents the mean density of 1 d in one stream. The range in size is due to growth over the summer. Solid and dotted lines as in Fig. 3.

fish suggested that floaters might not always be individuals that cannot acquire a territory because of a lack of space, but rather are individuals that adopt an alternative foraging strategy. The total density of territorial fish plus floaters (point 5) was close to the regression line, supporting this latter interpretation.

**Average-stream density** — Allen (1969) collated density data for salmonids in streams from the literature. These data (Fig. 9) represent higher than average densities because Allen rejected studies where densities were so low as to suggest that factors other than space were limiting.

Sixteen of the 20 data points were below the lower 95% C.L. and the mean PHS was 18.6 (range = 4.5–68.6). If these data accurately represent higher than average densities of salmonids in the wild, then we would conclude that other factors such as food, spawning habitat, or predation must normally limit these populations. However, we think these data underestimate the actual density of fish in usable habitat because Allen (1969) deliberately combined data for separate stream sections to obtain average densities for large areas of stream. Furthermore, Allen plotted data for different size-classes in the same area separately. Different size-classes in the same area should be summed unless they occupy different microhabitats and densities are reported separately for those microhabitats. Otherwise, one needs an estimate of the total space used by all size-classes in the area sampled for population density. When we summed the densities of different size classes in an area, only four of 10 points fell below the lower 95% C.L., the mean PHS was 37.2 (range = 11.3–71.9), and none were above the upper 95% C.L. Hence, Allen's revised data were generally consistent with the territory-size hypothesis.

Elliott (1984a) measured the density of juvenile brown trout in Black Brows Beck, England for 17 consecutive years. There was strong density-dependent mortality within the first 2 mo after emergence when young trout were establishing feeding territories (Elliott 1984). When we replotted these data (Fig. 10) the density of emerging alevins was close to the regression. The steep drop in density reflects the strong density-dependent mortality observed by Elliott, after which the cohort trajectory

follows the lower 95% C.L. of the maximum-density line. The sharp drop in density after emergence is qualitatively consistent with the territory-size hypothesis, but these data underestimate total fish density because there was more than one year-class present at a time.

To present graphically more than one cohort at a time, we plotted PHS for all fish that were present at one time (Fig. 11); this was possible for 14 yr. For the May/June and Aug./Sept. samples, we summed the PHS for the 0+, 1+, and 2+ cohorts. Elliott did not sample the 1+ and 2+ cohorts during the emergence of 0+ fish, so we assumed that PHS for these fish did not change between emergence in April and the first sampling in May/June, i.e. that any growth during this short period was offset by mortality. The decrease in PHS between April and May/June was due entirely to the death of 0+ trout. All cohorts were below 100 in May/June ( $P=0.002$ , two-tailed binomial test), suggesting that the density-dependent mortality of 0+ trout overcompensated for the high density of alevins in April. However, the trout population responded to this overshoot as 13 of 14 cohorts increased in PHS between May/June and Aug./Sept. Eleven cohorts remained below saturation at the Aug./Sept. census ( $P=0.057$ , two-tailed binomial test).

All the points in the May/June and Aug./Sept. samples were within the 95% C.L. and clustered closely about the territory-size line. Hence, Elliott's data appear to provide strong support for the hypothesis.

**Biomass data** — An extensive review of salmonid biomass is beyond the scope of this paper, but Mann and Penczak (1986), who recently reviewed salmonid production in 85 streams, concluded that an approximate ceiling in production occurs at about  $30 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ . Assuming an average production/biomass ratio of 1.30 (Mann and Penczak 1986), this translates to a maximum biomass of  $23 \text{ g} \cdot \text{m}^{-2}$ , not far below our predicted maximum of  $30 \text{ g} \cdot \text{m}^{-2}$ . We are aware of two studies that exceed  $30 \text{ g} \cdot \text{m}^{-2}$ . Sand Creek, Wyoming, had a biomass of  $63.4 \text{ g} \cdot \text{m}^{-2}$ ; the biomass in the remaining 43 streams surveyed by Binns and Eiserman (1979) was less than  $30 \text{ g} \cdot \text{m}^{-2}$ . The biomass of brown trout in the Horokiwi stream apparently



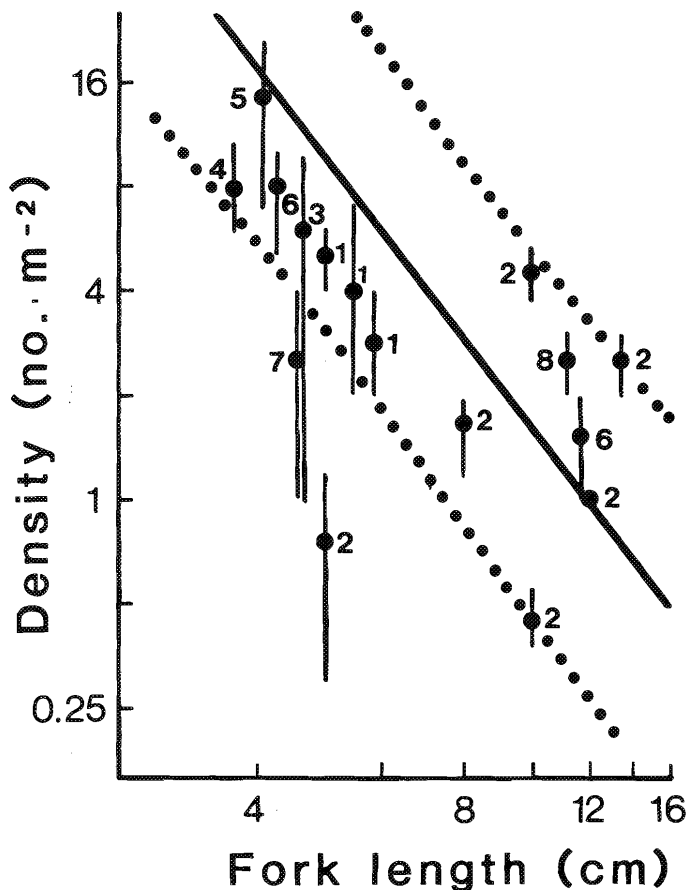


FIG. 8. Local-habitat densities (mean and range) of stream-dwelling salmonids from visual surveys. The numbers refer to data from the following papers: (1) Chapman (1962), (2) Wankowski and Thorpe (1979), (3) territorial fish, Puckett and Dill (1985), (4) floaters, Puckett and Dill (1985), (5) territorial fish + floaters, Puckett and Dill (1985), (6) nonterritorial fish, Puckett and Dill (1985), (7) McNicol et al. (1985), and (8) Stradmeyer and Thorpe (1987). Solid and dotted lines as in Fig. 3.

exceeds  $50 \text{ g} \cdot \text{m}^{-2}$ , but Le Cren (1969) suggests that this value is an overestimate. Given the approximations in the calculations, neither estimate is far above the suggested maximum. Moreover, higher values would be expected if fish were larger than 23 cm or if pools were common at a site (see below).

### Discussion

The territory-size hypothesis was clearly falsified in the pool habitats of Mason's (Mason and Chapman 1965; Mason 1969) stream channel. The coho salmon in these pools were distributed throughout the water column (also see Fausch and White 1986), but were found only near the substrate in riffles (see figures 9 and 10 in Mason (1969)). This falsification suggests that the hypothesis is not applicable in three-dimensional habitats such as pools. Apparently, more fish than predicted by the maximum-density regression can occupy sites if the fish are distributed in three dimensions. If the same pattern occurs in natural streams, then we would predict high standing crops of salmonids in pool habitats. There is some evidence of this: salmonid biomass was positively correlated with the percentage of stream area that was composed of pools (Bowby and Roff 1986) and pool volume (Nickelson et al. 1979 in Fausch et al. 1988).

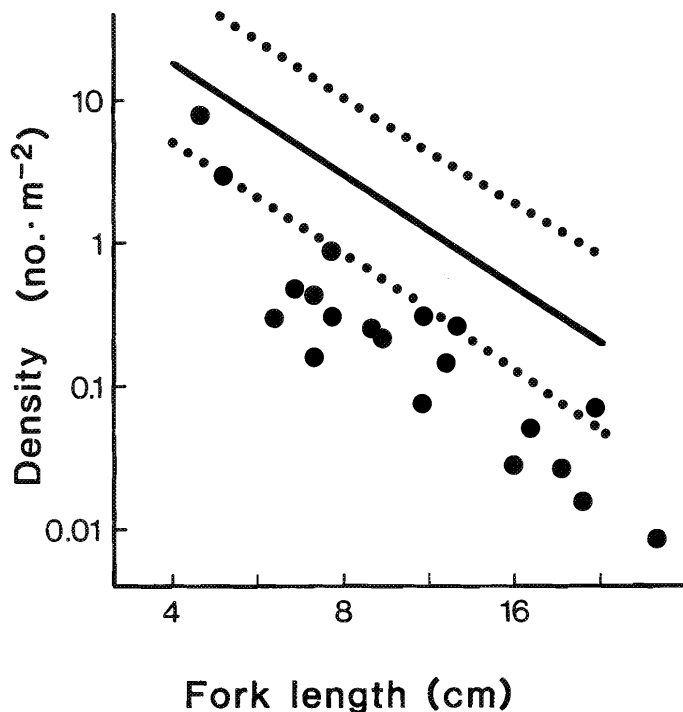


FIG. 9. Average-stream density for resident populations of stream-dwelling salmonids from table 1 of Allen (1969). Solid and dotted lines as in Fig. 3.

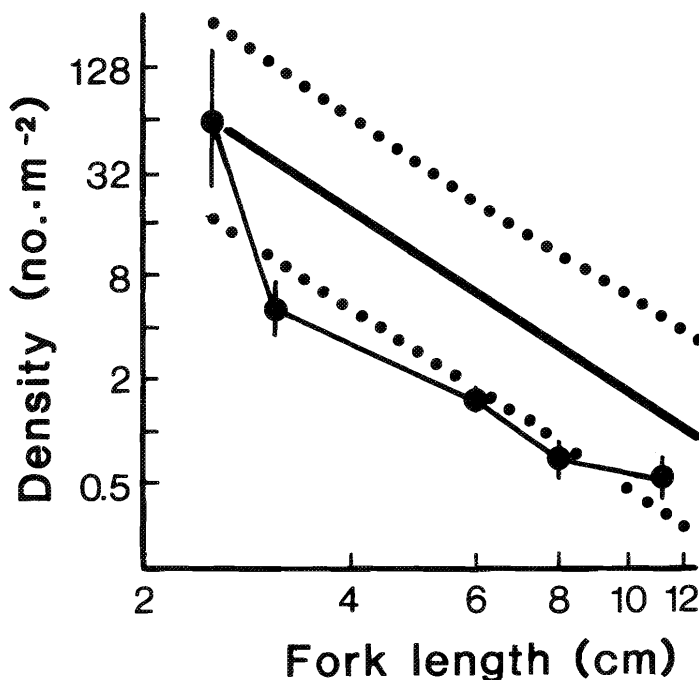


FIG. 10. Average-stream density (mean and SD) of brown trout in Black Brow's Beck (Elliott 1984a, 1984b, 1985). Successive points follow cohorts from emergence as alevins, to 0+ in May, to 0+ in August, to 1+ the following May, to 1+ the following August. Solid and dotted lines as in Fig. 3.

When the comparisons are limited to shallow habitats, many of the experimental data (e.g. Fig. 3, 4a) and field data (e.g. Fig. 7, 8, 11) were consistent with the territory-size hypothesis and no data provided a clear falsification. However, more field estimates of local fish density in usable habitat are needed to test the hypothesis more rigorously.

TABLE 2. Studies reporting density-dependent or no density-dependent responses in relation to percent habitat saturation (PHS) calculated from the territory-size regression.

Source <sup>a</sup>	Age-class <sup>b</sup>	Species <sup>c</sup>	Comparison	PHS		Response <sup>d</sup>		
				Mean	Range	G	M	E
1	0+	<i>O.k.</i>	single density	161				+
1	0+	<i>O.k.</i>	single density	83				+
1	0+	<i>O.k.</i>	single density	14				-
2	0+	<i>S.s.</i>	different years	105	71-129	+	+	
3	0+	<i>S.s.</i>	different densities	56	35-107	+	+	
4,5,6	0+	<i>S.t.</i>	different years	74	41-115	-	+	
7,8	M	<i>S.t.</i>	different years	44	27-56	-	-	
9	M	<i>S.t.</i>	single density	298				+
9	M	<i>O.k.</i>	single density	329				+
10	0+	<i>O.k.</i> , <i>O.m.</i>	different densities	41	4-78	+	+	
11,12	M	<i>S.s.</i>	different stream sections	27	6-41	-	+	
13	0+	<i>S.s.</i> , <i>O.m.</i>	effect of <i>S.s.</i> on <i>O.m.</i>	19				-
13	0+	<i>O.m.</i>	single density	13				-
14	1+	<i>S.f.</i>	different years	43	35-52	+	+	
15	0+	<i>S.t.</i>	effect of <i>S.s.</i> on <i>S.t.</i>	49	42-57	+		
15	M	<i>S.t.</i> , <i>S.s.</i>	different years	63	57-69	+	+	
15	0+	<i>S.t.</i>	different years	37	28-42	-		
16	0+	<i>S.s.</i>	effect of <i>S.t.</i> on <i>S.s.</i>	68	59-76	+		
16	M	<i>S.s.</i>	different years	69	54-83	+	+	
17,18	0+	<i>S.t.</i>	different densities	140	5-535	+	+	
19	M	<i>O.m.</i>	different densities	404	135-673	+		
20	0+	<i>O.k.</i>	single density	273				+
20	0+	<i>O.k.</i>	single density	405				+
20	0+	<i>O.k.</i>	single density	79				-
20	0+	<i>O.k.</i>	single density	209				+
21	0+	<i>O.k.</i>	different densities, unfed	17	8-27	+		
21	0+	<i>O.k.</i>	single density	24				+
21	0+	<i>O.k.</i>	single density	48				+
21	0+	<i>O.k.</i>	single density	8				-
21	0+	<i>O.k.</i>	single density	24				-
21	0+	<i>O.k.</i>	single density	71				-
22	0+	<i>O.k.</i>	single density	137				+
22	0+	<i>O.k.</i>	single density	151				+
23	1+	<i>S.f.</i>	different years	41	32-55	-	+	
24	0+	<i>S.s.</i>	different densities	23	13-44	+	-	
25	0+	<i>S.t.</i>	different stream sections	20	6-35		+	
26	M	<i>S.s.</i>	different stream sections	9	4-12	-		
26	M	<i>S.s.</i>	different stream sections	5	3-8	-		
27	0+	<i>O.k.</i>	single density	74				+
27	0+	<i>O.k.</i>	single density	53				+
27	0+	<i>O.k.</i>	single density	86				+
27	0+	<i>O.k.</i>	single density	61				+
28	0+	<i>S.f.</i>	different years, Hunt Creek	17	15-22		+	
28	0+	<i>S.f.</i>	different densities	20	9-36		-	
29	0+	<i>O.m.</i>	single density	368				+
29	0+	<i>O.m.</i>	single density	127				+
29	0+	<i>O.m.</i>	equilibrium density	18				-
30	0+	<i>O.k.</i> , <i>O.t.</i>	single density	775				+
30	0+	<i>O.k.</i> , <i>O.t.</i>	single density	227				+
30	0+	<i>O.k.</i> , <i>O.t.</i>	single density	218				+
30	0+	<i>O.k.</i> , <i>O.t.</i>	single density	82				+
30	0+	<i>O.k.</i> , <i>O.t.</i>	single density	56				+
31	M	<i>O.c.</i>	single density	156				+

<sup>a</sup>1 = Chapman 1962; 2, 3 = Egglisshaw and Shackley 1977, 1980; 4, 5, 6, 7, 8 = Elliott 1984a, 1984b, 1985, 1987, 1988; 9 = Fausch 1984; 10 = Fraser 1969; 11, 12 = Gee et al. 1978a, b; 13 = Hearn and Kynard 1986; 14 = Hunt 1974; 15, 16 = Kennedy and Strange 1980, 1986; 17, 18 = Le Cren 1965, 1973; 19 = Li and Brocksen 1977; 20, 21 = Mason 1969, 1976; 22 = Mason and Chapman 1965; 23 = McFadden et al. 1967; 24 = Mills 1969; 25 Mortensen 1977; 26 = Randall and Chadwick 1986; 27 = Ruggles 1966; 28 = Shetter 1961; 29 = Slaney and Northcote 1974; 30 = Stein et al. 1972; 31 = Wilzbach 1985.

<sup>b</sup>M = more than one age-class.

<sup>c</sup>*O.k.* = coho salmon, *O.t.* = chinook salmon, *O.m.* = rainbow trout, *O.c.* = cutthroat trout, *S.s.* = Atlantic salmon, *S.t.* = brown trout, and *S.f.* = brook trout.

<sup>d</sup>G = growth rate, M = mortality rate, E = emigration rate; + = a significant decrease in growth rate or an increase in mortality rate with increasing density or more than 10% of the fish emigrated; - = no significant changes in growth or mortality rate with changes in density or less than 10% of the fish emigrated.

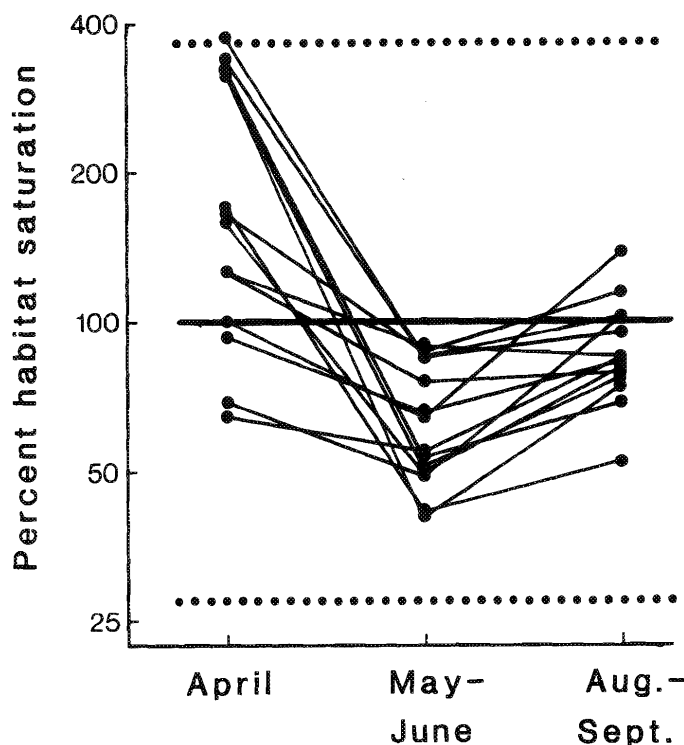


FIG. 11. Percent habitat saturation of brown trout (age 0+, 1+ and 2+) in Black Brow's Beck (Elliott 1984a, 1984b, 1985). Solid and dotted lines as in Fig. 6.

Although the data show that the territory-size regression can be used to predict maximum densities of stream-dwelling salmonids, this cannot be taken as evidence that territoriality is the actual mechanism that limits density. Not all individuals defend territories in the field (Puckett and Dill 1985; Grant and Noakes 1988) or even in some of the experimental studies that provided strong support for the territory-size hypothesis (e.g. riffle 1, Mason and Chapman 1965; Slaney and Northcote 1974; Fausch 1984). Hence, population density reported in many studies probably includes floaters or other individuals that do not defend space. We suspect that territoriality per se is not the mechanism that limits density, but rather that territory size predicts the spatial requirements of stream-dwelling salmonids, whether the space is defended or not. In territorial brook trout, foraging areas were similar to defended areas (Grant et al. 1989). Nonterritorial brook trout in the same streams had somewhat smaller foraging areas than territorial fish (Grant 1990), but their foraging areas may be sufficiently similar in size to be adequately predicted by the territory-size regression. When these spatial requirements are not met, density-dependent growth, mortality, or emigration should occur.

### Territory-Size Hypothesis and Density-Dependent Responses

#### Predictions

The territory-size hypothesis predicts the maximum densities of stream-dwelling salmonids. As a cohort approaches this saturation point, the hypothesis predicts that individuals will cease growing, emigrate or die. If space is the only factor affecting growth, emigration, and mortality, then the territory-size hypothesis predicts that these responses will be density-independent at densities below the lower 95% C.L. of the

maximum-density regression. As the habitat becomes increasingly saturated, the probability of observing density-dependent responses increases until it reaches 1.0 at a habitat saturation of 100%. If factors other than space affect growth, emigration, and mortality, then density-dependent responses can occur at densities less than the lower 95% C.L. of the maximum-density regression. However, the qualitative prediction of the territory-size hypothesis will still hold: the probability of observing a density-dependent response increases with increasing density or habitat saturation. It is also important for fisheries managers to know at what densities or levels of habitat saturation these responses occur.

#### Methods

To test the predictions of the territory-size hypothesis, we searched the literature for studies that reported either density-dependent or no density-dependent responses. A density-dependent response was defined as a statistically significant ( $P < 0.05$ ) decrease in growth rate or increase in mortality rate with increasing density, or as emigration by more than 10% of the fish. 'No emigration' was defined as less than 10% of the initial fish leaving to guard against a few individuals reacting abnormally to laboratory conditions or a low level of density-independent emigration in the field. Emigration was the most sensitive measure of density-dependent responses because we could score a response for a specific value of PHS. In contrast, we could only assess density-dependent growth or mortality by a significant change in the response at different values of PHS.

Many of the populations could be scored (yes or no) for more than one of the three potential responses: growth, mortality, and emigration. To insure independence of the data, a population contributed only one data point if it showed the same response for all measures. Populations that showed ambiguous responses (e.g. two yes, one no; one yes, two no; one yes, one no) contributed two data points: one yes and one no.

#### Results

Table 2 lists studies that report either density-dependent or no significant density-dependent responses in relation to PHS. Because we could not score the strength of a density-dependent response for all studies, we treated it as a categorical response: yes or no. There are as yet too few data to draw strong conclusions about whether growth, mortality, and emigration respond differently to increases in PHS. One interesting trend was that three studies that reported strong density-dependent mortality reported no density-dependent growth (McFadden et al. 1967; Gee et al. 1978a, b; Elliott 1984a, b).

We used PHS to predict whether or not density-dependent responses occurred: a datum was included for each row in Table 2. Because PHS is a continuous variable and density-dependence is a categorical variable, we analyzed the data using a linear logistic response model (Fienberg 1980; also called logistic regression, SAS Institute Inc. 1982). As predicted by the territory-size hypothesis, the probability of observing a density-dependent response increased with increasing mean PHS (Fig. 12). The logistic response function correctly predicted the response in 81% (46/57) of the cases (Fig. 12).

The inflection point in the response function represents the equal probability of observing density-dependent and no density-dependent responses. The PHS at the inflection point (27.2) was remarkably close to the lower 95% C.L. of the maximum-density regression (PHS = 27.8). At a PHS of 100, the

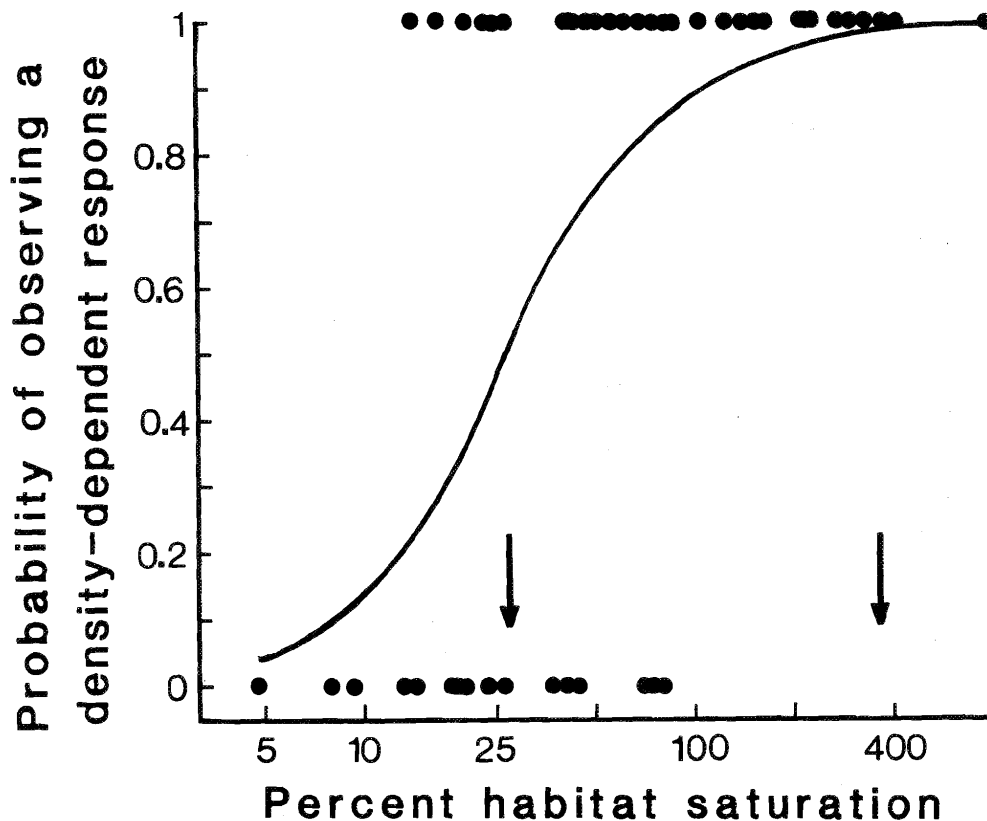


FIG. 12. Linear logistic response model relating the probability of observing a density-dependent response (growth, mortality, or emigration) in relation to percent habitat saturation (PHS). The line is  $\ln(p/1-p) = 4.07 \log_{10} \text{PHS} - 5.84$ , where  $p$  = probability of observing a density-dependent response ( $\chi^2 = 12.16$ ,  $n = 57$ ,  $df = 1$ ,  $P < 0.001$ ). The inflection point ( $P = 0.5$ ) is at a PHS of 27.2; the arrows show the approximate 95% C.L. of the territory-size regression. Individual data points are shown ( $P = 0$  or  $P = 1.0$ ).

logistic response function predicted that the probability of observing a density-dependent response was 0.91.

#### Discussion

The accuracy with which mean PHS was able to predict the occurrence of density-dependent responses (81%) was encouraging because PHS is a measure only of the spatial saturation of the habitat; we deliberately ignored other important factors like habitat productivity and predation which undoubtedly affect growth, mortality, and emigration. In addition, we have ignored the quality of the habitat and assumed that all space used by the fish is equivalent. The predictive power of PHS would probably increase if one could apply the technique only to suitable habitat (*sensu* Bovee 1982) for a given species or life stage or incorporate other factors in a multiple regression.

The close correspondance between the inflection point in the logistic regression and the lower 95% C.L. suggested that the territory-size regression delimits a zone of space-related competition. We believe that the territory-size regression and the concept of PHS have applied value for salmonid biologists. Percent habitat saturation may be a valuable index for comparing the density or standing crop between streams or within streams over years. Abundance is traditionally expressed as density ( $\text{no.} \cdot \text{m}^{-2}$ ) or as biomass ( $\text{g} \cdot \text{m}^{-2}$ ), thus ignoring the size of the fish. Biomass data integrate the number and size of fish but assume that the distribution of mass among individuals is not important. The territory-size hypothesis predicts that this

would not be the case: more space is used by two 1-g fish than by one 2-g fish. PHS provides an index that integrates the number, size, and space requirements of salmonid fish.

The territory-size regression and PHS can be used as rough guides for setting maximum stocking densities for stream-dwelling salmonids in relation to body size. For example, the logistic response function suggests that stocking fish into a stream where the PHS of the resident populations is greater than 27 will likely cause a density-dependent response in either the stocked or resident population.

The territory-size hypothesis predicts that a cohort of stream-dwelling salmonids in a saturated environment will experience a reduction in population density as individuals increase in size. This "self-thinning" phenomenon has been widely studied in plants (Westoby 1984) and recently in sessile marine invertebrates (Hughes and Griffiths 1988). Double logarithmic regressions of average plant mass vs. plant density often, but not always, have a slope close to  $-3/2$  (Weller 1987). Based on energetic allometries, Begon et al. (1986) have argued that mobile animal populations should exhibit a self-thinning slope of  $-4/3$ . Our empirical regressions suggested a slope of  $-1.16$  for stream-dwelling salmonids. If  $\log_{10} \text{density} = 2.83 - 2.61 \log_{10} \text{fork length}$ , and  $\log_{10} \text{mass} = 3.03 \log_{10} \text{fork length} - 1.93$ , then  $\log_{10} \text{mass} = 1.35 - 1.16 \log_{10} \text{density}$ . The validity of this salmonid thinning line remains to be tested.

#### Conclusions

Body length explained 87% of the variation in territory size of juvenile salmonids in streams, despite differences in species,

environmental conditions, and methods of measuring territory size. We used the inverse of this regression, the maximum-density regression, to test the hypothesis that territory size limits the maximum density of juvenile salmonids in streams. In shallow habitats such as riffles and raceways, no data clearly falsified the hypothesis and most either strongly supported or were consistent with the territory-size hypothesis. We suspect that territoriality is not the mechanism that actually limits density, but rather that territory size predicts the spatial requirements of stream-dwelling salmonids, whether the space is defended or not.

An index of habitat saturation (PHS), which was developed from the territory-size regression, was able to predict the occurrence of density dependent growth, mortality, or emigration in 81% of the cases. The predictive power of the territory-size regression and PHS was surprisingly strong because both assume that space is the only factor influencing density; we deliberately ignored other important factors like habitat productivity and predation. The territory-size regression and PHS should be valuable tools for predicting maximum population densities, the occurrence of density-dependent population responses, and stocking densities of stream-dwelling salmonids.

## Acknowledgments

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