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DEMOGRAPHIC RESPONSES TO FOOD AND SPACE COMPETITION BY JUVENILE STEELHEAD TROUT

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Abstract. I conducted two experiments in artificial stream channels, manipulating density of competitors, food abundance, and the possibility of emigration, to test whether density-dependence can operate through these factors in populations of a stream-dwelling salmonid fish, juvenile steelhead trout (*Oncorhynchus mykiss*). In the absence of emigration, increasing levels of per capita food competition increased mortality, decreased growth, and increased the variance in size distributions of surviving individuals. Smaller fish were more likely to occupy less profitable areas of the stream channel than larger individuals and did so with increasing frequency as food abundance decreased and stocking density increased.

When I allowed fish to emigrate from the stream channels, food and stocking density again influenced mortality, growth, and size distributions of survivors. Emigration was more likely at increasing levels of per capita competition; emigrants were smaller and in poorer condition than nonemigrants. The ability to emigrate from a population appears to normalize final size distributions and increase mean fish size within the stream channels. Thus, although both food and space are important factors shaping the demography of stream salmonid populations, neither appears to limit salmonid abundance exclusively.

Key words: body mass differentiation; competition, food and space; density-dependence; emigration; growth of juvinile fish; intraspecific competition; Oncorhynchus mykiss; *population dynamics; regulation; steelhead trout.*

INTRODUCTION

A central question in ecology is: what regulates population size (Murdoch 1994)? Theoretical models often argue that density-dependent changes in population size provide stability and persistence to a population (May 1976) and empirical studies have found that density-dependence is an important component of regulation in many taxa (e.g., Fowler 1987, Sinclair 1989, Watkinson 1997). Both classical and individual-based models predict that as a population exceeds its local carrying capacity, density-dependence acts to bring the population towards a stable equilibrium (May 1976, Łomnicki 1988).

However, unlike early models that assumed all individuals could be described equally, individual-based models argue that differences in competitive abilities lead to differential monopolization of resources among individuals (Łomnicki 1978, 1980). A consequence of unequal resource partitioning, in addition to average density-dependent responses, is that the variance in population characteristics often changes with increasing levels of competition (Łomnicki 1988). Hence, individual-based models make several unique demographic predictions. For instance, increasing levels of intraspecific competition should produce greater levels of skewness in size-frequency distributions because those individuals monopolizing food acquire an increasingly disproportionate share, leading to a few individuals with large body sizes and many suppressed weaklings (Łomnicki 1978, 1980). Unfortunately, tests of this prediction have been largely confined to qualitative analyses of published literature (Begon 1984, Uchmański 1985, Latto 1992) and no study has experimentally manipulated resource abundance and competitor density to test this hypothesis with an animal population.

An additional consequence of density-dependence based on unequal resource partitioning is emigration. Although emigration has been implicated in population regulation (Łomnicki and Slobodkin 1966, Łomnicki and Krawczyk 1980, McMahon and Tash 1988), the selective advantage for some individuals to expose themselves to potentially hostile environments is unclear when all individuals are considered to have equal characteristics (Łomnicki 1980). In contrast, when unequal resource partitioning occurs, it may be of selective advantage for subordinates to escape into new habitats with lower levels of competition, even if the risk of mortality is high.

In populations of stream-dwelling salmonid fish, where individuals compete for feeding territories, density-dependent competition is thought to occur whenever a habitat becomes saturated with territories of a given size (Chapman 1966, Allen 1969, Grant and Kramer 1990). Although mortality, growth or emigration

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are commonly reported density-dependent responses (Grant and Kramer 1990), no study has been able to determine how each of these potential mechanisms contributes independently to population regulation in stream-dwelling salmonids. Experimental studies that monitor population changes in response to density often ignore or prevent emigration (e.g., LeCren 1965, 1973) and studies that monitor emigration cannot often assess density-dependent mortality (e.g., Chapman 1962, Mesick 1988). Similarly, studies of natural populations that monitor population declines assume that changes in population size are a result of density-dependent mortality (Gee et al. 1978, Ward and Slaney 1993). In reality, declines in population size may be the result of density-dependent mortality or emigration (Elliott 1994, Post et al. 1999) and the magnitude of a population decline may be moderated by density-dependent growth (Jenkins et al. 1999).

In this study, I conducted two experiments to test how density-dependence operates through mortality, growth, or emigration in a stream-dwelling salmonid and how unequal resource partitioning influences the variance in success of individuals in a population. I studied juvenile steelhead trout (*Oncorhynchus mykiss*), the anadromous form of the rainbow trout (Scott and Crossman 1973). Steelhead trout are good candidates for such a study because they aggressively compete for feeding territories (Keeley and McPhail 1998) and undergo density-dependent mortality and growth (Fraser 1969). To manipulate levels of competition, I selected densities of fish that fell within the range found in natural populations of salmonids (Elliott 1994) yet represent a fully saturated habitat, based on individual territory size requirements (Grant and Kramer 1990). I compared these base densities, to densities that were two and four times higher. To assess independently effects of food abundance on trout demography, I fed each of the three fish densities at ration levels that were either similar to mean levels of food abundance in natural streams, or at levels two or four times higher (Dill et al. 1981, Keeley and Grant 1997). In a second experiment, I again manipulated food and competitor density, but I allowed fish to emigrate if they chose to do so. By monitoring how demographic characteristics change in response to increasing levels of competition in confined and unconfined populations, I examined how growth, mortality, and emigration can contribute to density-dependent changes in populations of stream-dwelling salmonids.

In populations limited by food or space, a reduction in competition for these resources should lead to a corresponding decrease in mortality, increase in growth, or a decrease in emigration from a population (Łomnicki 1988). However, if populations are limited by food only, an increase in food abundance should support a proportionally greater biomass in salmonid abundance (Marschall and Crowder 1995). Alternatively, in space-limited populations, territory size is inflexible and no additional individuals should be able to settle if the habitat is fully saturated (Grant and Kramer 1990). Finally, if individual differences in competitive abilities lead to a differential monopolization of resources, then as the intensity of competition increases, the skewness of size-frequency distributions should increase with increasing numbers of competitors or decreasing levels of food abundance (Łomnicki 1978, 1980).

METHODS AND MATERIALS

Collection and rearing of experimental animals

On 5 May 1995 and 17 April 1996, I collected eight male and two female adult steelhead trout from the Chilliwack River, British Columbia, Canada (49°4.8′ N, 122°42.8′ W) to use as broodstock for experiments 1 and 2, respectively. For each collection date, I divided the eggs from each female into eight equal parts and fertilized each part with the sperm from one of the eight males. Hence, I used 16 crosses as the source of juvenile trout in both experiments 1 and 2. I incubated the trout embryos in a single upwelling incubation bottle, supplied by 8°C groundwater at the Fraser Valley Trout Hatchery (49°0.9′ N, 122°16.4′ W) near Abbotsford, British Columbia. When the embryos reached the eyed stage of development, I moved them to the Cultus Lake Laboratory (49°3.3′ N, 122°1.4′ W), where I placed them in metal baskets suspended in a fiberglass trough that was supplied with 10°C water drawn from Cultus Lake, British Columbia (49°3.3′ N, 122°1.0′ W). All fish were kept in the trough until they were past the point of absorbing their yolk sac and had begun to feed exogenously.

Experimental setup

I constructed 18 artificial stream channels at the Cultus Lake Laboratory. Each channel measured 5 m long by 0.92 m wide and 0.40 m deep. Channels were constructed from plywood sheets supported by match lumber, lined with polyurethane tarpaulins, then sealed with silicone to make them watertight. To reduce the large volume of water required to simulate flow from a natural stream, I arranged the 18 channels in a blocked, staircase design (Keeley 1998, 2000). Channels were grouped into six columns of three, with water introduced to the upper channels supported by cinder blocks 117 cm high. The second group of channels, 78 cm off the ground, was connected to the first with plastic troughs, 68 cm long and 32 cm across. Hence, water could flow from the uppermost channels to the next highest channels, and then to a third set of channels that was placed level with the ground. The downstream end of each connecting trough was screened with 3-mm mesh to prevent the escape of any fish placed into the channel.

To simulate natural substrate, I placed a single layer of stream gravel, 5–10 cm in diameter, into each chan-

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nel. To prevent mortality due to aerial predators, I placed a canopy of burlap, supported by a wooden frame 132 cm high, above the top edge of each channel. The burlap also equalized the shade over the channels, while still permitting enough light to pass through to the water to allow the fish to feed and interact with each other.

To estimate numbers of fish being excluded from foraging in the channels, I attached a Plexiglas box, 62 cm long × 29.5 cm wide × 26 cm high, (hereafter called an emigration box) to the side and downstream end of each channel. The emigration box was accessible from the main channel through a pipe 8.9 cm in diameter and 5 cm long. Fish were able to move in and out of the emigration box through the access pipe. A piece of tubing, 3 cm in diameter and 100 cm long, drained the box into the downstream trough at a rate of ~1 L/min. The outlet tube maintained water temperature and oxygen levels in the emigration box at levels found in the channel, but did not have the unidirectional flow and food supply found in the main channel. The upstream end of the outlet tube was screened to prevent fish from leaving the channel.

Water was supplied to the channels from a 1700-L tank filled from two large reservoirs supplied by water from both above and below the thermocline of nearby Cultus Lake. By mixing the two sources, I maintained the experimental water temperature at 13.3° ± 1.1°C (mean ± 1 SD). Each channel received 435 L of water/min, producing a flow that averaged 7 cm/s and 10 cm deep. I filtered water entering the 1700-L tank using 250-μm nylon screening. In addition, I placed nets constructed from the nylon screening in the troughs connecting each channel to prevent any excess food from drifting between experimental units.

Experiment 1: effects of food abundance and stocking density on trout demography—confined populations

On 31 July 1995, I stocked the stream channels at one of three densities and introduced food at one of three levels of food abundance. Stocking densities represented 100%, 200%, or 400% saturation if occupied by territories of a size based on Grant and Kramer's (1990) allometric regression model of territory size. Levels of food abundance represented an average level of the dry mass of invertebrates drifting per area of stream profile (Dill et al. 1981, Keeley and Grant 1997) as well as levels two and four times higher. These three rations represent 72, 143, and 287% of the maximum ration predicted by Marschall and Crowder's (1995) model for salmonids. A channel thus received either 582, 291, or 146 fish and a daily ration of 5.76, 2.88, or 1.44 g/d of dry extruded pelleted food.

Using invertebrate drift as the model, I chose a size grade of pelleted food that represented the mean size of invertebrates encountered by stream salmonids (15% size grade 1, Biodiet; 85% size grade 2, Biodry; Bioproducts, Warrenton, Oregon, USA). I introduced the daily ration of food over a 12-h period (beginning at 0700) to simulate a natural encounter rate (Keeley and Grant 1997), using automated belt feeders attached to the top of each channel.

I assigned treatment levels using the channel position as a blocking factor (cf. Neter et al. 1990) to remove any potential upstream–downstream effects of treatment position. Each treatment level appeared once each in the upper, middle, and lower channel positions in the first three columns and once again in the next three columns.

Every 12 h, I checked and observed each channel to ensure water continued to flow equally in all channels and cleaned small debris from downstream screens and from the nets filtering the water between channels. At the end of the 56-d experiment, I removed and counted all fish remaining in each channel. To calculate size distributions, I haphazardly sampled 80 individuals from each channel and measured fish for length and mass, except for one channel where only 59 fish survived.

Experiment 2: effects of food abundance and stocking density on trout demography—unconfined populations

From 10 June to 5 August 1996, I repeated the previous experiment, except that I modified the stream channels to allow fish to emigrate from the channels into one-way traps. This modification also enabled me to capture and mark or selectively remove individuals. Emigration traps consisted of 4-L buckets and covers. Fish were able to emigrate into a trap through a tube, 3.2 cm in diameter and 1 m long, connected to the downstream end of the emigration box. By placing the connecting tube several centimeters above the water level in the trap, fish could move into the trap but not back into the channel. In addition, I placed a PVC pipe, 10 cm in diameter and 40 cm long, into each emigration box, and covered the opening of the tube leading to the trap, forcing fish to actively seek this downstream route from the stream channel. Inside each of the pipes, I also cemented pieces of PVC sheeting so that half of the pipe was blocked on alternating sides spaced 10 cm apart.

Data collection

To monitor mortality, dead or dying fish that were found on downstream screens were collected and measured for length and mass. To determine if dying fish lost or gained length or mass while on downstream screens, I measured unused fish from my original stocking pool immediately after being euthanized with an anesthetic and after 12 h of being on pieces of screening covering the outlet trough of the lowermost channels. Measurements after 12 h differed in length by 0.65% (paired $t = 1.94$, $n = 42$, $P = 0.06$) and in mass by 0.42% (paired $t = 0.15$, $n = 42$, $P = 0.88$) in com-

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parison to the original measurements. Thus, any gain or loss of mass or length during that period would have been small.

To monitor their use, each emigration box was checked for presence and number of fish once daily between 1100 and 1300. To estimate the size of fish over the course of the experiment, I used an S-VHS video camera to record images of fish once every two weeks. From these images, I measured body sizes of 10–15 fish in the central area of each stream channel, as well as of any fish that were using the emigration boxes at the time. To convert lengths on the video screen into actual lengths in cm, I used a correction factor 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.

In experiment 1, fish were removed only after dying. In experiment 2, when a fish was caught in an emigration trap, I anesthetized it, marked it with an adipose fin clip, and returned it to the channel after it recovered from the anesthetic (<5 min). If a marked fish was caught a second time in the trap, I considered it to be an emigrant and removed it from the experiment. Emigrant fish were measured for fork length and weighed. To monitor emigration rates, I recorded daily numbers of fish captured in each trap, but in figures I report mean daily numbers of fish caught in a trap averaged over weekly intervals.

Statistical analyses

I used two-factor repeated-measures analyses of variance (ANOVAR) to assess the effects of food abundance and stocking density on the demography of the steelhead trout held in the stream channels. All tests of significance are based on type-III sum-of-squares. When the assumption of sphericity of the variance–covariance matrix was not met, I applied a Huynh-Feldt correction of P values for hypothesis testing (SAS Institute 1989). When responses were measured on a specific group of fish at only a single point during the experiment, such as for those fish that were removed at the end of the experiment, I used univariate two-factor analyses of variance (ANOVA) to assess treatment effects. If I detected differences between treatment levels, whose trends were not clearly reflected in figures, I used a contrast transformation procedure (SAS Institute 1989) to determine which repeated-measures effects were different from each other.

To assess the condition of fish among and within treatments, I used a $\log_{10}$(length) × $\log_{10}$(mass) least-squares regression to calculate adjusted mass values, controlling for the effect of body length differences between groups (Sokal and Rohlf 1995). I quantified the degree of size inequality or hierarchy in a population as the degree to which biomass is concentrated among a few individuals (Weiner and Solbrig 1984). Size inequality is best demonstrated by using the relative mean size difference between all pairs of individuals (the Gini coefficient) rather than the traditional statistic of skewness (Weiner and Solbrig 1984; also see Hutchings 1997).

To make a posteriori comparisons between experiment 1 and 2, I used analyses of covariance (ANCOVA) between studies. For graphical comparisons, I plotted percentage differences to illustrate between-year effects after statistically controlling for treatment effects. To compare the probability of mortality or emigration in each of the stream channel experiments, I used a logistic regression analysis (SAS Institute 1989).

RESULTS

Experiment 1: effects of food abundance and stocking density on trout demography—confined populations

Of the 6114 fish that were initially stocked into the channels at the beginning of experiment 1, I was able to account for 95% of these individuals either from collecting mortalities or by removing them at the end of the experiment. The proportion of surviving fish depended on both the level of food abundance and stocking density (Fig. 1a–c). Numbers of fish declined in all treatments over time (ANOVAR, $F_{7,63} = 160.35$, $P < 0.0001$), but mortality was highest in the high stocking density and low level of food abundance and lowest in the low stocking density and high level of food abundance (Fig. 1a, c). The magnitude of treatment differences increased over the duration of the experiment. Hence, there were interactions of time × food abundance (ANOVAR, $F_{14,63} = 14.00$, $P < 0.0001$), time × fish density (ANOVAR, $F_{14,63} = 9.84$, $P < 0.0001$), and time × food × fish density (ANOVAR, $F_{14,63} = 3.10$, $P = 0.0001$). The tests of the between-subject effects of the repeated-measures analysis of variance are equivalent to comparisons, among treatments, of fish counts integrated over time. Overall, the survival of fish increased with decreasing stocking density (ANOVAR, $F_{2,9} = 17.47$, $P = 0.0005$) and increasing food abundance (ANOVAR, $F_{2,9} = 19.61$, $P = 0.0005$). In contrast to the within-subject effects, the overall experimental effects did not interact with each other (ANOVAR, $F_{4,9} = 0.98$, $P = 0.47$).

Indices of competition.—Growth of fish in the channels was also strongly affected by stocking density and by the amount of food available. From an initial mean stocking size of 3.18 ± 0.13 cm fork length (mean ± 1 SD) and 0.25 ± 0.050 g wet mass (mean ± 1 SD), mean fish length increased over the 8-wk experiment in all treatment combinations (ANOVAR, $F_{4,36} = 128.98$, $P < 0.0001$; Fig. 2a–c). Furthermore, the rate of growth increased with increasing food abundance, producing time × food abundance interactions (ANOVAR, $F_{8,36} = 3.11$, $P = 0.018$; Fig. 2a–c), and decreased with increasing stocking density, producing time × density interactions (ANOVAR, $F_{8,36} = 2.76$,

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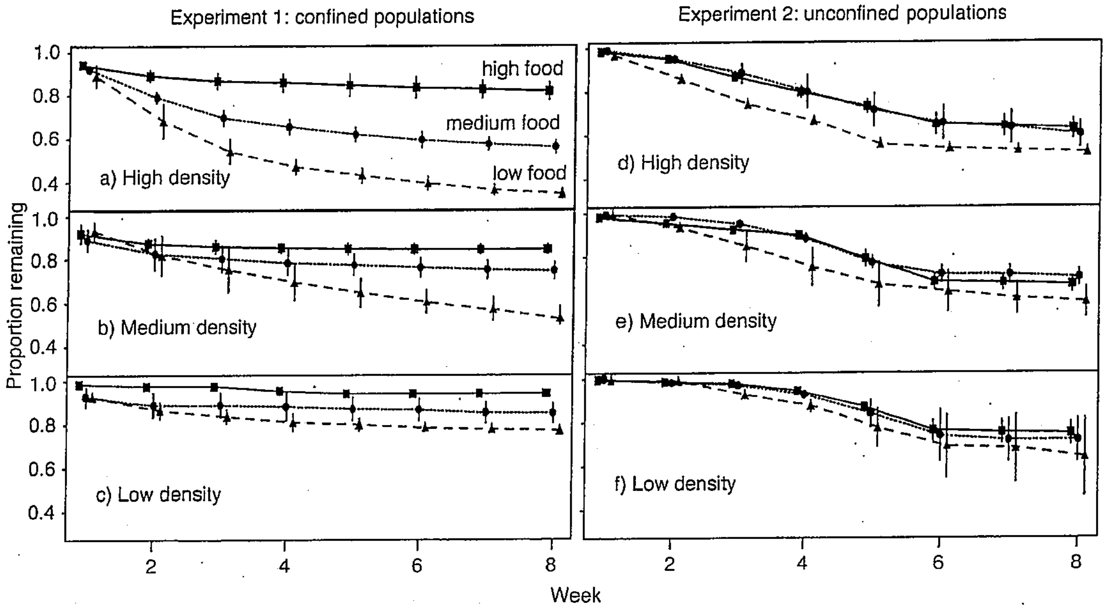

FIG. 1. Proportion of the total number (±1 SE) of juvenile steelhead trout present in stream channels over an 8-wk period in the (a) high, (b) medium, and (c) low stocking densities of experiment 1 or in the (d) high, (e) medium, and (f) low stocking densities of experiment 2. Squares and solid lines represent high food levels; circles and dotted lines represent medium food levels; and triangles and dashed lines represent low food levels.

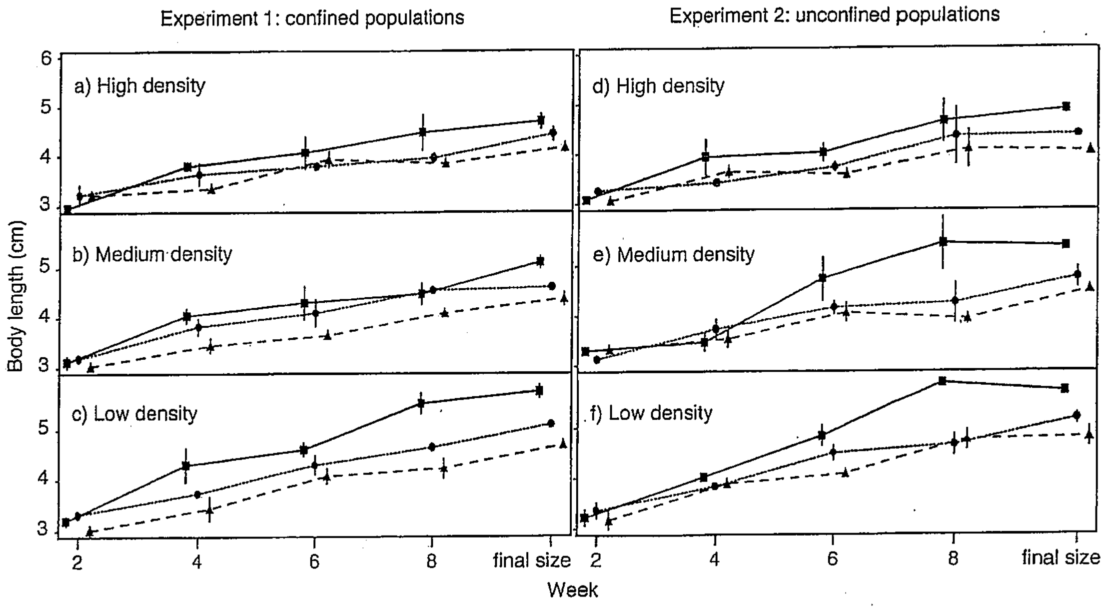

FIG. 2. Mean body length (±1 SE) of steelhead trout in stream channels of experiment 1 and 2. Sizes were estimated by video images or physically measured at the end of the experiment (final size) in (a) high, (b) medium, and (c) low stocking densities of experiment 1 and in (d) high, (e) medium, and (f) low stocking densities of experiment 2. Squares and solid lines represent high food levels; circles and dotted lines represent medium food levels; and triangles and dashed lines represent low food levels.

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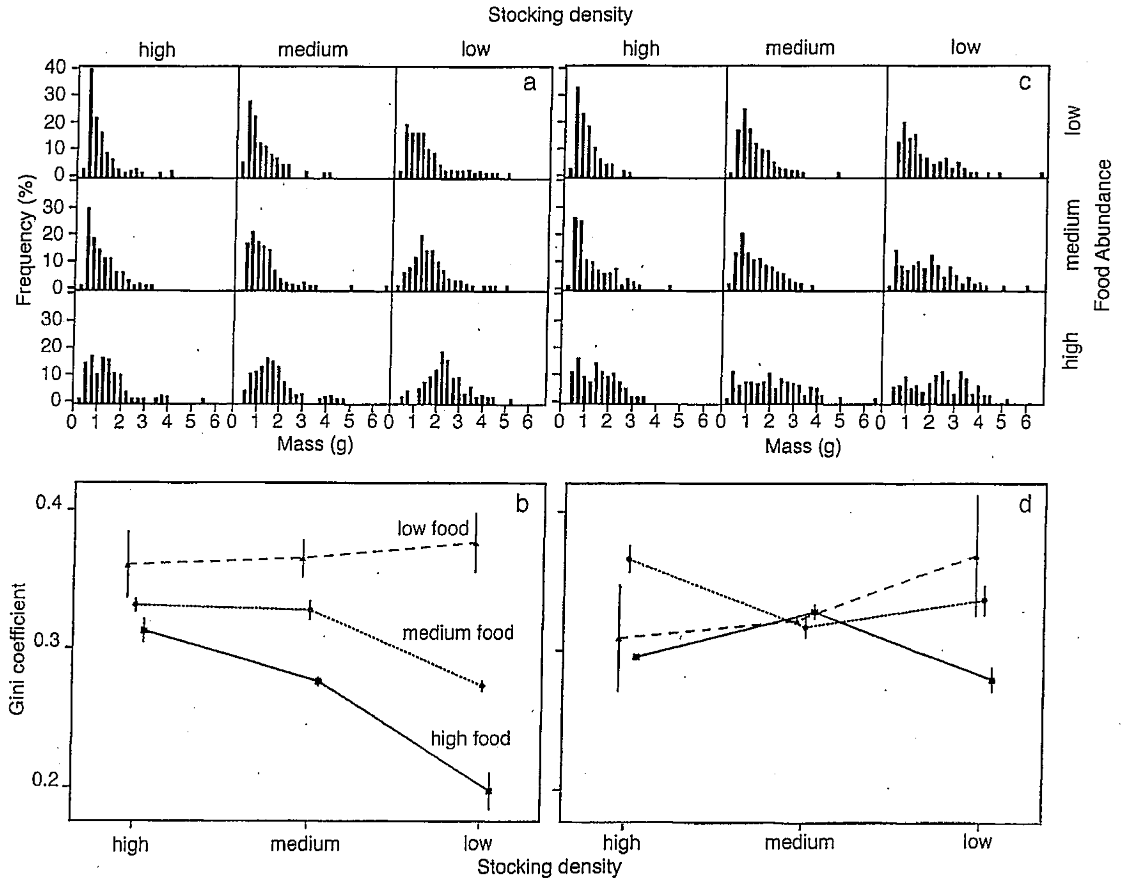

FIG. 3. (a; upper left panels) Final mass-frequency distributions for steelhead trout under the nine experimental conditions of experiment 1. Treatment levels for stocking density and food abundance are depicted on the top and right margins, respectively. (b; lower left panel) Mean (±1 SE) Gini coefficients for mass-frequency distributions in (a). (c; upper right panels) Final mass-frequency distributions for steelhead trout under the nine experimental conditions of experiment 2. (d; lower right panel) Mean (±1 SE) Gini coefficients for mass-frequency distributions in (c). Squares and solid lines represent high food levels; circles and dotted lines represent medium food levels; and triangles and dashed lines represent low food levels in (b) and (d).

P = 0.0089; Fig. 2a–c). Overall, fish size increased with increasing food abundance and decreased with increasing stocking density, whether mean final fish sizes were used as a measure of growth (food abundance effect, ANOVA, $F_{2,17}$ = 28.45, $P < 0.0001$; stocking density effect, ANOVA, $F_{2,17}$ = 22.10, P = 0.0003) or when size estimates were integrated over the whole experiment using the video tape measurements (food abundance effect, ANOVAR, $F_{2,9}$ = 84.05, $P < 0.0001$; stocking density effect, ANOVAR, $F_{2,9}$ = 53.79, $P < 0.0001$).

Using the videotaped images, I compared fish lengths in emigration boxes with those in the main stream channels, paired by treatment combination and filming date, because fish were not always present in the emigration boxes. Fish in the main stream channels were longer than those in the emigration boxes (paired t = 2.22, n = 29, P = 0.034). When averaged over the experiment, channel fish were 11.20% longer than those in emigration boxes.

In addition to mean effects, mass-frequency distributions showed greater levels of size inequality with increasing stocking density (Fig. 3a). Gini coefficients increased with stocking density (ANOVA, $F_{2,17}$ = 13.77, P = 0.0018; Fig. 3b). In contrast, increasing food abundance tended to normalize the size frequency distributions by reducing the amount of size inequality; consequently, Gini coefficients decreased with increasing food abundance (ANOVA, $F_{2,17}$ = 50.77, $P < 0.0001$; Fig. 3b). However, as Fig. 3b suggests, there was an interaction between food abundance and stocking density (ANOVA, $F_{4,17}$ = 7.09, P = 0.0073). Size inequality among channels that received low food rations was relatively unaffected by increasing stocking densities. Medium and high feeding regimes were strongly affected by stocking densities, particularly at low densities.

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The mean size of fish that died also increased over the course of the experiment (ANOVAR, $F_{3,24} = 9.70$, $P = 0.0003$), but did so at a much slower rate than average size of live fish foraging in the stream channel (ANCOVAR, $F_{3,60} = 19.48$, $P < 0.0001$). In contrast to survivors, there was no effect of either food abundance (ANOVAR, $F_{2,8} = 1.06$, $P = 0.39$) or stocking density (ANOVAR, $F_{2,8} = 1.45$, $P = 0.29$) on the size of fish that died.

When compared by treatment, condition of survivors was always higher than the condition of mortalities (ANCOVA, $F_{1,30} = 61.21$, $P < 0.0001$, Fig. 4a). In addition to between-group differences, the condition of both mortalities and survivors was inversely related to stocking density (ANOVA, $F_{2,30} = 218.14$, $P < 0.0001$, Fig. 4a) and positively related to food abundance (ANOVA, $F_{2,30} = 102.13$, $P < 0.0001$, Fig. 4a).

The mean number of fish observed in emigration boxes was related to both stocking density (ANOVAR, $F_{2,9} = 31.07$, $P < 0.0001$) and food abundance (ANOVAR, $F_{2,9} = 138.51$, $P < 0.0001$; Fig. 5a–c). The number of fish using the emigration boxes was greatest during the first few weeks of the experiment (Fig. 5a–c) but declined over time (ANOVAR, $F_{14,63} = 93.79$, $P < 0.0001$). In addition, the magnitude of the decline increased with increasing stocking density, but was reduced with increasing food abundance. This produced time × treatment interactions (ANOVAR, $F_{14,63} = 28.33$, $P < 0.0001$, food effect; ANOVAR, $F_{14,63} = 6.74$, $P < 0.0001$, density effect).

Experiment 2: effects of food abundance and stocking density on trout demography—unconfined populations

The proportion of fish remaining in a channel was dependent on both the level of food abundance and initial stocking density. Numbers of fish declined through mortality and emigration over time in all treatments (ANOVAR, $F_{7,63} = 202.48$, $P < 0.0001$), but showed the strongest decline in the low food level and high stocking density (Fig. 1d–f). The magnitude of these differences did not increase over the course of the experiment and therefore did not produce interactions between treatment factors (ANOVAR, $P = 0.35–0.99$) despite the decline in numbers over time.

Overall, treatment effects produced differences in the proportion of fish surviving that were inversely related to both food abundance (ANOVAR, $F_{2,9} = 4.04$, $P = 0.05$ and stocking density (ANOVAR, $F_{2,9} = 8.35$, $P = 0.0089$; Fig. 1d–f). While food abundance showed increasing effects among treatment levels, the lowest level of food abundance had a lower proportion of survivors compared to the intermediate level (ANOVAR, $F_{1,8} = 6.37$, $P = 0.033$) and high food levels (ANOVAR, $F_{1,8} = 5.73$, $P = 0.04$), but the latter two levels of food abundance did not differ from each other (ANOVAR, $F_{1,8} = 0.02$, $P = 0.90$; Fig. 1d–f). Similarly, the proportion of fish remaining in the highest stocking density was lower than in the low stocking density (ANOVAR, $F_{1,8} = 16.70$, $P = 0.0027$), but I could not detect differences between high and medium densities (ANOVAR, $F_{1,8} = 4.41$, $P = 0.065$) or low and medium densities (ANOVAR, $F_{1,8} = 3.93$, $P = 0.078$; Fig. 1d–f).

Indices of competition.—Over the course of the 8-wk experiment, mean fish size increased in all treatment levels (ANOVAR, $F_{4,36} = 132.75$, $P < 0.0001$; Fig. 2d–f). The rate of growth was influenced by both food abundance (ANOVAR, $F_{8,36} = 4.16$, $P = 0.0013$) and stocking density (ANOVAR, $F_{8,36} = 2.58$, $P = 0.025$; Fig. 2d–f). As food abundance increased, the rate of fish growth increased whereas fish growth slowed as stocking density increased (Fig. 2d–f). From the initial stocking size of 3.014 ± 0.14 cm (fork length; mean ± 1 SD) and 0.21 ± 0.035 g (wet mass; mean ± 1 SD), overall fish size increased with increasing food abundance and decreased with decreasing stocking density, whether final fish sizes were used as a measure of growth (Fig. 2d–f; ANOVA, $F_{2,17} = 52.16$, $P < 0.0001$, food abundance effect; ANOVA, $F_{2,17} = 41.93$, $P < 0.0001$, stocking density effect), or size estimates were integrated over the course of the whole experiment using the video tape measurements (ANOVAR, $F_{2,9} = 13.88$, $P = 0.0018$, food abundance effect; ANOVAR, $F_{2,9} = 13.63$, $P = 0.0019$, stocking density effect).

As in experiment 1, the mass-frequency distributions showed a wide range of size inequality among treatments (Fig. 3c). However, the overall measure of size inequality by Gini coefficients was not related to stocking density (ANOVA, $F_{2,17} = 0.07$, $P = 0.93$) or food abundance (ANOVA, $F_{2,17} = 3.23$, $P = 0.09$, Fig. 3d). Size distributions tended to be more bimodal in experiment 2 than experiment 1 (Fig. 3a and c).

In contrast to the fish that were observed foraging in the central area of the channels, fish that died or emigrated into downstream traps were generally smaller and in poorer condition. The mean size of mortalities increased over the course of the experiment (ANOVAR, $F_{3,15} = 25.58$, $P < 0.0001$), however, the rate was lower than for fish occupying the central area of the channels (ANCOVAR, $F_{3,63} = 4.02$, $P = 0.011$), and was unaffected by stocking density (ANOVAR, $F_{6,15} = 1.61$, $P = 0.21$) or food abundance (ANOVAR, $F_{6,15} = 1.34$, $P = 0.30$). The adjusted mass (condition) of survivors was higher than that of mortalities (Fig. 4b, ANCOVA, $F_{1,30} = 10.63$, $P = 0.0028$). The condition of both survivors and mortalities was inversely related to stocking density (Fig. 4b, ANOVA, $F_{2,30} = 86.94$, $P < 0.0001$) and positively related to food abundance (Fig. 4b, ANOVA, $F_{2,30} = 39.08$, $P < 0.0001$).

Fish that emigrated into downstream traps also increased in size over the course of the experiment (ANOVAR, $F_{3,18} = 28.42$, $P < 0.0001$), but did so at a lower rate than those fish occupying the channel (ANCOVAR, $F_{3,66} = 6.96$, $P = 0.0004$). Although the condition of emigrants and survivors was inversely related to stocking density (Fig. 4b, ANOVA, $F_{2,30} = 140.95$,

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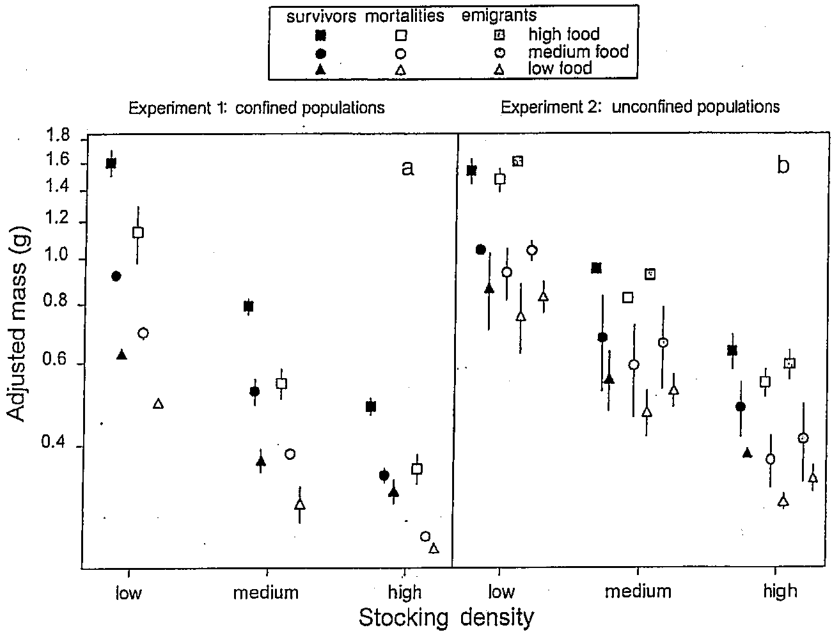

FIG. 4. (a) Adjusted mass (±1 SE) of juvenile steelhead trout that survived to the end of experiment 1 or were removed as mortalities. (b) Adjusted mass (±1 SE) of juvenile steelhead trout that survived to the end of experiment 2 or were removed as mortalities or emigrants.

$P < 0.0001$) and positively related to food abundance (Fig. 4b, ANOVA, $F_{2,30} = 82.83$, $P < 0.0001$), there was no difference between emigrants and survivors (Fig. 4b, ANCOVA, $F_{2,30} = 1.50$, $P = 0.23$).

The distribution of fish between the main stream channels and the emigration boxes suggested that there were differences in the level of competition among stream channels. The mean number of fish observed in emigration boxes peaked then declined over the 8-wk period (Fig. 5d–f). However, the peak and decline were related to the initial stocking density, as shown by a density × time interaction (ANOVAR, $F_{14,63} = 4.07$, $P = 0.0028$). In the high stocking treatment, the peak and decline occurred after 2–3 wk (Fig. 5d), but the pattern was lower in magnitude and delayed by 1–2 wk in the medium and low stocking levels (Fig. 5e and f). In contrast, the within-subject effects showed no interaction with food abundance (ANOVAR, $F_{14,63} = 1.57$, $P = 0.26$). When combined in the overall, between-subject tests, this same pattern occurred; only stocking density influenced emigration box use (ANOVAR, $F_{2,9} = 4.04$, $P = 0.0031$).

The number of fish that were captured twice and considered emigrants also increased and then declined over the course of the experiment (Fig. 5g–i). The peak and subsequent decline in emigrants occurred earliest, with the greatest magnitude, and over the longest time at high stocking levels (Fig. 5g). The magnitude and peak of the numbers captured in traps decreased in the medium and low stocking densities and occurred later in the experiment (Fig. 5h and i). This produced a time effect and a time × density interaction (ANOVAR, $F_{14,63} = 6.19$, $P < 0.0001$), as well as an overall effect of stocking density on the number of fish captured in traps (ANOVAR, $F_{14,63} = 16.12$, $P = 0.0011$). Food abundance had different influences on the numbers of emigrating fish. There was no overall effect of food abundance on the numbers of fish captured as emigrants (ANOVAR, $F_{2,9} = 1.06$, $P = 0.39$), however, there was a time by food abundance interaction (ANOVAR, $F_{14,63} = 4.29$, $P < 0.0001$). Low food levels produced the earliest peaks in emigrant numbers, after controlling for the effect of stocking density (Fig. 5h–i).

Comparison of confined and unconfined populations

In both experiments, experimental populations of steelhead trout showed declines in relation to food abundance and stocking density; however, there were important differences between experiments. Under conditions where fish could emigrate from stream channels (experiment 2), populations remained higher in the first half of the experimental period, but then declined (Fig. 6a; ANCOVAR, $F_{7,182} = 28.01$, $P < 0.0001$), after controlling for the effects of both treatment factors. Unlike confined populations, declines in trout densities were of equal magnitude across treatments and did not produce the time × treatment interactions (Fig. 2d–f) evident in confined populations (Fig. 2a–c).

The fish used in experiment 2 were initially 5.51% smaller in length than fish stocked in confined populations, however, both after 2 wk and when compared over the entire 8-wk intervals, fish were larger in un-

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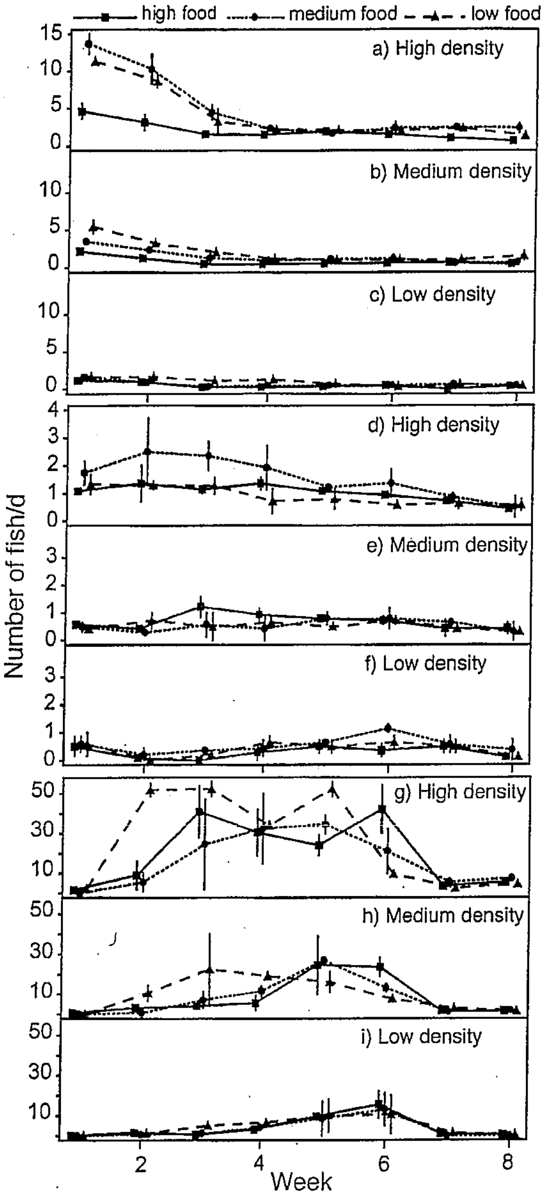

FIG. 5. (a–c) Mean daily number of juvenile steelhead trout (±1 SE) based on emigration boxes of stream channels, at weekly intervals, for (a) high, (b) medium, or (c) low stocking densities of experiment 1. (d–f) Mean daily number of juvenile steelhead trout (±1 SE) based on emigration boxes of stream channels, at weekly intervals, for (d) high, (e) medium, or (f) low stocking densities of experiment 2. (g–i) Mean daily number of juvenile steelhead trout (±1 SE) captured as emigrants in downstream traps of stream channels of experiment 2, at weekly intervals, for (g) high, (h) medium, and (i) low stocking densities. Squares and solid lines represent high food levels; circles and dotted lines represent medium food levels; and triangles and dashed lines represent low food levels.

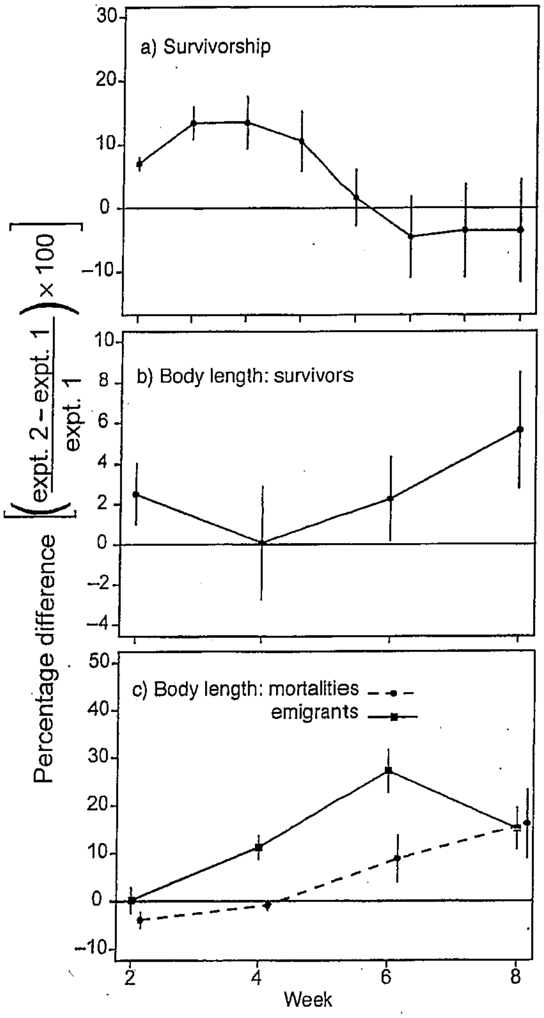

FIG. 6. (a) Percentage difference (mean ± 1 SE) between the proportion of fish surviving in stream channels in unconfined (experiment 2) relative to confined (experiment 1) populations, over eight weeks. (b) Percentage difference (mean ± 1 SE) in the length of fish (cm) measured in stream channels in unconfined (experiment 2) relative to confined (experiment 1) populations, over eight weeks. (c) Percentage difference (mean ± 1 SE) in the length of fish (cm) that died in stream channels from unconfined (experiment 2) relative to confined (experiment 1) populations, over eight weeks (dashed line and circles) or the percentage difference in length of fish that were removed as emigrants from channels in experiment 2 vs. those that died in experiment 1 (solid line and squares). For graphical purposes, differences are paired by treatment levels to illustrate differences between experiments.

confined stream channels (Fig. 6b; ANCOVAR, $F_{1,26}$ = 4.57, P = 0.042). Similarly, fish that died were smaller (Fig. 6c; ANCOVAR, $F_{1,20}$ = 44.09, P < 0.0001) and in poorer condition (ANCOVA, $F_{1,30}$ = 23.53, P < 0.0001) in experiment 1 than in experiment 2. Emigrants removed in experiment 2 were longer than fish that died in experiment 1 (Fig. 6c; ANCOVAR,

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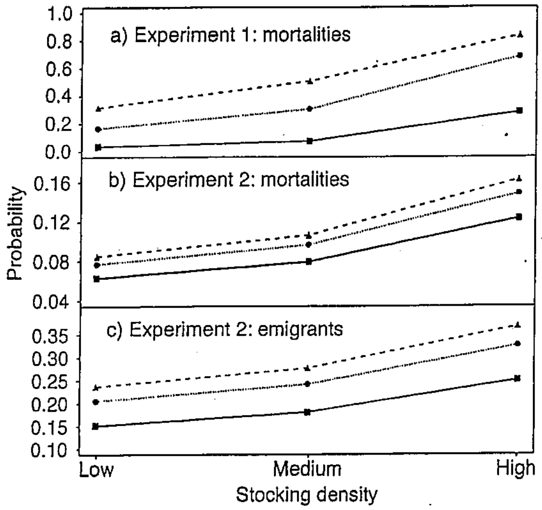

FIG. 7. The probability of steelhead trout mortality in stream channels vs. stocking density, in (a) experiment 1 and (b) experiment 2. The logistic equations for (a) and (b), respectively, are as follows: $\mathrm{logit}(p) = 0.79$ (stocking density) $- 0.85$(food abundance) $- 0.71$, $\chi^2 = 890.91$, $P < 0.0001$, 65.7% concordant; $\mathrm{logit}(p) = 0.23$(stocking density) $- 0.11$(food abundance) $- 1.98$, $\chi^2 = 18.93$, $P < 0.0001$, 45.1% concordant. (c) The probability of steelhead trout emigrating from experimental stream channels in experiment 2. The logistic equation is as follows: $\mathrm{logit}(p) = 0.20$(stocking density) $- 0.19$(food abundance) $- 1.11$, $\chi^2 = 50.36$, $P < 0.0001$, 48.6% concordant. Squares and solid lines represent high food levels; circles and dotted lines represent medium food levels; and triangles and dashed lines represent low food levels in (a)–(c). Note the different scales on the y-axis among the three figures.

$F_{1,20} = 4.66$, $P = 0.043$) and in better condition (ANCOVA, $F_{1,20} = 72.46$, $P < 0.0001$).

In both experiments, the probability of an individual fish dying increased with decreasing food abundance (experiment 1, Wald's $\chi^2 = 399.06$, $P < 0.0001$; experiment 2, Wald's $\chi^2 = 4.68$, $P = 0.031$) and increasing stocking density (experiment 1, Wald's $\chi^2 = 85.30$, $P < 0.0001$; experiment 2, Wald's $\chi^2 = 14.17$, $P = 0.0002$; Fig. 7a and b). The probability of death was about four times higher in confined channels than in unconfined channels (Wald's $\chi^2 = 107.75$, $P < 0.0001$). However, final densities of fish were similar at the end of the experiments (Fig. 6a) because, although fewer fish were dying in the unconfined population, they were emigrating in a manner similar to the pattern of mortality in the confined population. The probability of emigrating from stream channels in experiment 2 increased with decreasing food abundance (Wald's $\chi^2 = 27.06$, $P < 0.0001$) and increasing stocking density (Wald's $\chi^2 = 23.30$, $P < 0.0001$; Fig. 7c).

The final biomass of fish removed at the end of the experiments was related to both treatment factors (Fig. 8a and b), but there was no difference in biomass between experiments (ANCOVA, $F_{1,35} = 0.01$, $P = 0.93$). Biomass of fish increased with increasing food abundance (ANOVA, $F_{2,35} = 53.79$, $P < 0.0001$; Fig. 8a), but at a rate lower than expected by a relationship with a slope of one ($t = 70.56$, $P < 0.001$). Biomass of fish also increased with initial stocking density (ANOVA, $F_{2,35} = 12.85$, $P < 0.0001$; Fig. 8b) and there was no interaction between stocking density and food abundance (ANOVA, $F_{4,35} = 0.10$, $P = 0.98$).

DISCUSSION

Although density-dependent interactions have long been thought to regulate population size in many organisms, it is often difficult to determine the exact mechanism by which density dependence may operate. When populations approach a carrying capacity, they respond to density-dependent pressures in a variety of ways (Sinclair 1989). In stream salmonids, growth, mortality, and emigration are commonly observed den-

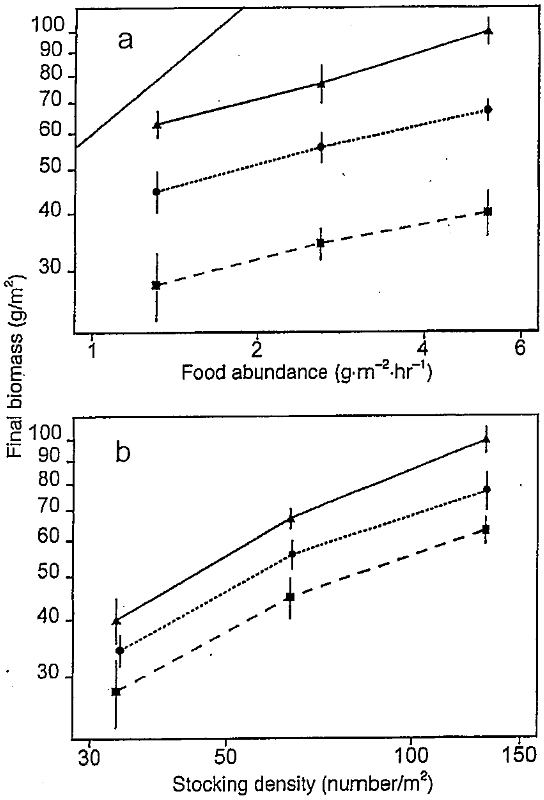

FIG. 8. (a) Mean final biomass of steelhead trout (±1 SE) removed from stream channels in experiment 1 and 2 (combined) vs. the amount of food delivered to the channels. The solid line and triangles represent low stocking densities; the dotted line and circles represent medium stocking densities; and the dashed line and squares represent high stocking densities. The solid line without symbols represents a line with a slope of 1. (b) Mean final biomass of steelhead trout (± 1 SE) removed from stream channels in experiment 1 and 2 (combined) vs. the initial stocking densities of fish. Lines and symbols are as in (a) for high, medium, and low levels of food abundance, respectively.

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sity-dependent responses (Grant and Kramer 1990). However, salmonid populations do not always have the same density-dependent response to increasing levels of competition. In some studies mortality is strongly density-dependent but growth is not (McFadden et al. 1967, Elliott 1984*a, b*) and in other studies the opposite is found (Mills 1969).

As predicted for populations that are regulated by density-dependent interactions, my experimental populations showed increasing density-dependent responses as initial stocking densities increased or as levels of food abundance decreased. By comparing experimental populations over a range of densities and resource levels, and by comparing confined and unconfined populations, my study provides insight into how growth, mortality, and emigration contribute, often simultaneously, to density-dependent population regulation.

In both the closed and open populations, density-dependence operated to regulate population size towards a carrying capacity by decreasing growth and increasing mortality. The intensity of density-dependent mortality and growth depended on the proportion of the population that was unable to acquire sufficient resources to maintain growth or prevent starvation. In the confined populations, density-dependence could only operate by growth or mortality similar to results of earlier experimental studies that prevented emigration (LeCren 1965, 1973, Fraser 1969). In unconfined populations, steelhead trout continued to exhibit decreased growth and increased mortality with increasing levels of competition. However, the ability to emigrate from a stream channel decreased the magnitude of density dependence on growth and mortality by allowing density-dependent emigration. Likewise, studies of unconfined salmonid populations often find density-dependent declines in population size that occur from mortality or emigration, but not from density-dependent growth (Gee et al. 1978, Elliott 1984*a, b*). Hence, my experiments suggest that the relative importance of growth, mortality, and emigration in regulating populations of salmonids in streams depends on the opportunity of some individuals to emigrate.

As in previous studies of stream salmonids (Grant 1990, 1997, Nielsen 1992), and consistent with models of population regulation by density-dependent competition (Łomnicki 1988), my data indicate that a disproportionate share of food went to large, aggressive individuals that were able to monopolize resources by occupying and successfully defending the most profitable areas of the stream channels. Although competitive differences predict the success of individuals within a population, increases in population density or decreases in resource abundance result in a situation where the proportion of individuals receiving a minority of resources tends to increase. Increasing levels of crowding produce striking differences in the shape of size-frequency distributions of populations (Uchmański 1985, Latto 1992, Hutchings 1997). A pattern of increasing size inequality is thought to be related to the intensity of competition (Begon 1984). My study provides experimental evidence to support this idea. In confined populations, the degree of size inequality increased with increasing stocking density and decreased with increasing levels of food abundance. When fish were given the opportunity to emigrate from the stream channels, size-frequency distributions continued to show an increasing asymmetry in the shape of the distributions with decreasing availability of per capita resources. But, as in other studies (Héland 1980*a, b*, Elliott 1986, Titus and Mosegaard 1991), emigrating individuals were smaller and in poor condition and the loss of individuals tended to normalize size-frequency distributions or created distributions that were polymodal. The occurrence of secondary peaks may represent individuals using alternate foraging tactics that minimize energy expenditure (Puckett and Dill 1985, Grant and Noakes 1988). Nonaggressive individuals may not be as successful at acquiring food and may have a smaller body size than aggressive fish. However, by avoiding the cost of aggression, some individuals can maintain their body condition (Puckett and Dill 1985, Nielsen 1992) and minimize risks to themselves until better opportunities for growth occur (Thorpe et al. 1992).

Although emigrating fish were in poorer condition than individuals using the main stream channel, they were larger and in better condition than individuals removed as mortalities in both years. Łomnicki (1978) has argued that emigration could be of selective advantage to individuals with little access to resources, if emigrating individuals have a better probability of survival in unoccupied areas. Adult female salmonid fish are often highly selective of spawning sites and densities of emerging juveniles can be very high in localized spawning areas (Groot and Margolis 1991). Density-dependent emigration may space individuals into adjacent unoccupied habitats that may not be useful for spawning, but are suitable for rearing. The dispersal of emigrants may therefore allow individuals to find new habitats and, as my data suggest, may reduce density-dependent pressures on individuals that remain in source habitats (Łomnicki and Slobodkin 1966, McMahon and Tash 1988).

Because of the occurrence of feeding territories in stream salmonids, competition for space has often been linked to changes in density-dependent population characteristics (McNicol et al. 1985, Elliott 1990, Keeley and Grant 1995). The space hypothesis (Allen 1969) assumes that a minimum territory size is inflexible and therefore determines the maximum density of salmonids in a stream. Once territories occupy all the usable area in a stream, density dependence will operate to maintain numbers at carrying capacity. In contrast, the food limitation hypothesis (Marschall and Crowder 1995) assumes that territories are only the proximate mechanism for capturing food, so salmonid abundance

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should be directly proportional to food abundance (Grant et al. 1998).

My data indicate that competition for both food and space are important components of demographic changes in stream salmonid populations, but do not support the hypotheses that food or space exclusively limits salmonid abundance. Final biomass of steelhead trout increased in relation to food abundance, but at a rate much slower than the directly proportional relationship predicted by the food hypothesis. Similarly, the space hypothesis was also rejected. Although final biomass did not increase in direct proportion to stocking density, biomass did remain higher at high stocking densities, contrary to that expected if space is limited once all habitat becomes fully occupied by territories of a minimum size (Grant and Kramer 1990).

If territory size influences salmonid abundance and is affected by both food and competitor abundance, then densities of fish will be influenced by both food and space competition. Territory size of steelhead trout in the stream channels was inversely related to food abundance and stocking density but not in direct proportion to either (Keeley 2000). Salmonid abundance appears to be constrained by changes in territory size that decrease relatively slowly with increasing levels of food abundance (Grant et al. 1998).

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