

Effects of Rearing Density upon Cutthroat Trout Hematology, Hatchery Performance, Fin Erosion, and General Health and Condition

ERIC J. WAGNER, TIM JEPPSEN, RONNEY ARNDT, M. DOUGLAS ROUTLEDGE,
AND QUENTIN BRADWISCH

Fisheries Experiment Station, Utah Division of Wildlife Resources
1465 West 200 North, Logan, Utah 84321, USA

Abstract.—Cutthroat trout of the Bear Lake Bonneville strain, *Oncorhynchus clarki utah*, were used in two separate density experiments. In the first, fish were reared for 212 d in outdoor raceways at four densities; fish were allowed to grow into their final rearing density and were fed 7 d/week. Final rearing densities averaged 768, 1,597, 2,073, and 2,998 fish/m³, and corresponding density indices (DI = fish weight, lb/[fish length, in × water volume, ft³]) were 0.40, 0.90, 1.10, and 1.46. In experiment 2, crowding screens were adjusted monthly, and fish were fed 5 d/week; final rearing densities were 338, 739, and 1,634 fish/m³ (DIs of 0.19, 0.39, 0.75). Feed conversion and mortality did not significantly differ among densities for either experiment. Final mean weights did not differ among the four densities of experiment 1, but mean total length was significantly longer in fish reared at the lower densities. In experiment 2, final mean weight was significantly reduced in the highest density and specific growth rates for all densities were lower than in experiment 1. Frequencies of agonistic behaviors did not differ among densities in experiment 2. Hemoglobin, total white blood cell (WBC) counts, differential WBC counts, and hepatosomatic indices did not differ among densities in either experiment. Red blood cell (RBC) counts and the splenosomatic index (SI) did not differ among densities of experiment 1. However, in experiment 2, the RBC count was higher at the lowest density than at the highest, and the SI was significantly higher at the highest density than the lowest. Condition factor, plasma protein, hematocrit, and relative dorsal fin length differences among densities were observed, but were inconsistent over time. Adverse effects of high density on mesenteric fat levels and pectoral fin condition were observed in experiment 2. Saltwater challenge tests resulted in greater mortality for fish from high densities. The data indicated that rearing cutthroat trout at a DI of 0.75 or higher (about 1,600 fish/m³) may compromise fish health when densities are adjusted monthly and fish are fed 5 d/week; the data also indicated that even lower densities are needed for maximum growth.

Densities of cutthroat trout *Oncorhynchus clarki* in Utah hatcheries have primarily been modeled after culture practices for rainbow trout *O. mykiss*. Rainbow trout have been domesticated for nearly a century, especially many of the strains used in Utah. Conversely, cutthroat trout cultured in Utah hatcheries are derived from wild parents and are

only one generation removed from wild parents. Although cutthroat trout are reared at densities similar to those for rainbow trout, a recent survey indicated that pectoral fin erosion in cutthroat trout was more severe than in rainbow trout (Bosakowski and Wagner 1994). Fin condition may have an impact on survival after stocking (Nicola and

Cordone 1973), is aesthetically unappealing, and may provide a site for bacterial infection.

Density can be a factor in fin erosion of salmonids (Mäkinen and Ruohonen 1990). This relationship is probably associated with aggressive behaviors such as fin nipping (Abbott and Dill 1985). For example, steelhead (anadromous rainbow trout) in isolation did not develop dorsal fin erosion, whereas counterparts did at a density of 9,400 fish/m³ (Kindschi et al. 1991a). Aggressive behavior can be dependent upon density; some species, such as the Arctic char *Salvelinus alpinus*, exhibit less aggression at higher densities (Brown et al. 1992), but others express more aggression (Cole and Noakes 1980).

This study was initiated to determine the effect of density upon fin erosion, aggressive behavior, and other variables related to hatchery performance and general health of cutthroat trout. Hatchery performance was determined by comparing growth, mortality, and feed conversion. General health in this study was defined by necropsy-based observations (Goede and Barton 1990), hepatosomatic and splenosomatic indices, counts of various blood cell types, and survival in salt challenge tests. Many of these variables are known to be affected by density (Pickering and Pottinger 1987; Vijayan et al. 1990; Banks 1994). The study consisted of two experiments. In the first, fish were allowed to grow into the final projected density. In the second experiment, fish densities were maintained at the target level by adjusting crowding screens monthly.

Methods

Experiment 1

Cutthroat trout of the Bear Lake Bonneville strain *O. clarki utah* were stocked into outdoor concrete raceways (water volume = 6.04 × 1.14 × 0.35 m) on 1 October 1993. Equal weights of fish were put into each raceway (about 2,385 fish per raceway; mean weight, 1.2 g) and reared for 212 d. Four densities were evaluated, with two raceways per treatment. Densities were adjusted with crowding screens at the beginning of the experiment and left until the fish grew into the final densities. The density index of Piper (1972) was calculated in English units from the formula: DI = fish weight, lb/(fish length, in × volume of rearing unit, ft³). Final rearing densities were 757–779 fish/m³ (DI = 0.41), 1,589–1,605 fish/m³ (DI = 0.86–0.95); 2,064–2,082 fish/m³ (DI = 1.09–1.12); and 2,998–2,999 fish/m³ (DI = 1.44–1.49).

These densities are hereafter referred to respectively as D1, D2, D3, and D4 for experiment 1.

Fish were initially hand fed a dry commercial trout diet (Silvercup) at 5.2% of body weight. This ration was reduced incrementally as waste feed was observed. By the second month of rearing, fish were fed 2.2% of body weight and 1.19% at the end of the experiment. Fish were fed 7 d/week. Feeding was begun at a frequency of 6 times/d and was reduced to 4 times/d after 66 d and to 3 times/d on day 132. Water flow rates were increased incrementally each month to achieve similar loading rates; flows began at 19 L/min and reached 163 L/min at the end of the experiment.

Water quality of the well water supplying the raceways was monitored with standard methods (APHA et al. 1989). Incoming water had a total alkalinity of 205–222 mg/L as CaCO₃, total hardness of 222 mg/L as CaCO₃, dissolved oxygen of 6.5–6.9 mg/L, temperature of 14.0 ± 0.5°C, and total gas saturation of 106–108%. At the end of experiment 1, outflow dissolved oxygen was 3.8–4.4 mg/L, pH was 7.2–7.3, carbon dioxide was 24–29 mg/L, and un-ionized ammonia nitrogen did not exceed 0.0042 mg/L.

Necropsy-based health and condition profiles (HCP; Goede and Barton 1990) were conducted on 3 December 1993, 28 January 1994, 28 February 1994, and 29 April 1994. Ten fish per raceway were dipnetted, placed into a lethal solution of tricaine methanesulfonate anesthetic (MS-222), and subsequently examined by a single person to avoid observer bias. The treatment from which the fish came was not revealed to the observer until after the observations were recorded. The fin index was modified such that the values ranged from 0 (no erosion) to 2 (severe erosion), and fin length, as well as hemorrhaging, was considered in the categorizing decision. Maximum fin length measurements were also made on the same dates with the same fish, and the measurements were converted to relative fin lengths (100·maximum fin length/total length; Kindschi 1987).

Experiment 2

On 11 July 1995, 1,500 Bear Lake Bonneville cutthroat trout (mean weight, 1.2 g) were hand counted into each of nine raceways. Three raceways were assigned to each of three density index treatments: 0.2, 0.4, or 0.8. Target densities were achieved by adjusting crowding screens monthly so that target densities would be reached at the end of the following month. On day 161, the raceways were thinned to 1,100 fish/raceway to maintain

TABLE 1.—Comparison of mean cutthroat trout density expressions for both experiments during each month.

Experiment day	Density index ^a				Fish/m ³				Kg/m ³			
	D1	D2	D3	D4	D1	D2	D3	D4	D1	D2	D3	D4
Experiment 1												
30	0.04	0.09	0.12	0.13	631	1,356	1,744	2,818	1.58	3.85	4.97	4.48
60	0.08	0.16	0.21	0.28	630	1,352	1,741	2,813	4.44	8.95	12.14	14.51
91	0.12	0.22	0.28	0.40	629	1,350	1,736	2,800	8.58	14.80	19.03	25.39
122	0.20	0.38	0.52	0.68	780	1,622	2,103	3,046	16.58	31.44	44.12	53.88
150	0.28	0.52	0.68	0.90	777	1,618	2,098	3,040	27.04	47.74	63.69	81.05
181	0.36	0.74	0.90	1.20	773	1,607	2,086	3,018	41.62	83.66	98.43	124.84
211	0.40	0.90	1.10	1.46	768	1,597	2,073	2,998	49.84	113.35	134.13	172.40
Experiment 2												
18	0.15	0.30	0.55		2,937	5,880	11,755		5.73	11.16	19.12	
49	0.13	0.25	0.44		1,465	2,932	5,860		6.07	11.52	19.41	
80	0.19	0.37	0.66		1,453	2,910	5,816		11.64	21.99	37.40	
110	0.16	0.29	0.57		916	1,933	4,009		11.41	18.86	35.76	
141	0.16	0.30	0.55		704	1,489	3,049		12.30	22.58	38.91	
171	0.14	0.28	0.48		513	1,081	2,228		13.21	24.16	39.38	
202	0.18	0.35	0.60		487	1,025	2,114		19.20	35.05	55.94	
231	0.18	0.36	0.70		383	810	1,888		21.20	41.00	71.45	
263	0.19	0.39	0.75		338	739	1,634		24.64	50.48	90.29	

^a Density index = fish weight, lb/(fish length, in × volume of rearing unit, ft³), from Piper (1972).

target densities. Actual density indices among individual raceways over the course of the experiment (261 d) ranged from 0.12–0.20, 0.24–0.40, and 0.42–0.79 in the low (D1), medium (D2), and high (D3) densities, respectively. Densities expressed as either fish or weight per unit volume are compared in Table 1 for both experiments.

The incoming water was identical to that described for experiment 1. At the end of the experiment, un-ionized ammonia nitrogen concentrations in the outflow did not exceed 0.0095 mg/L, effluent dissolved oxygen was 5.2–5.8 mg/L, and carbon dioxide was 21–27 mg/L. Values for pH and total gas concentration were within the ranges reported for experiment 1.

Necropsy-based HCPs were conducted on 29 September 1995 (day 79), 30 November 1995 (day 141), 30 January 1996 (day 202), and 27 March 1996 (day 289) with the protocol described for experiment 1. Maximum fin lengths were measured on the same dates with the same fish.

Fish were fed initially at 3.7% of body weight, which was reduced incrementally over the course of the experiment to 1.5% as waste feed was observed. Any changes in ration were applied across all raceways. Fish were initially fed 6 times/d, and the frequency was reduced to 4 times/d when the fish reached an average size of 15.1 g (day 147 for D1 and D2, day 155 for D3). Mean weights were determined monthly by crowding fish to the head of the raceway and averaging five samples of dipnetted fish. Water flow to each raceway was

initially 39 L/min; it was increased to 59 L/min on day 68 and incrementally reached 76 L/min by the end of the experiment.

Saltwater Challenge

A saltwater stress challenge was conducted to determine if crowding affected a fish's ability to osmoregulate when it was transferred to a saline solution. For experiment 1, challenge tests were conducted at 17°C in 30-L opaque containers supplied with compressed air through an air stone. Noniodized rock salt was dissolved in the tank before introducing the fish. Preliminary tests revealed that the fish could survive a salt solution of 10 g/L for 24 h. A subsequent 24-h test was conducted at a salt concentration of 15 g/L on 8 June 1994. In each test, three fish were put into each tank, and two tanks were used per treatment.

For experiment 2, 24-h challenge tests were conducted in 800-L indoor circular tanks on 10 January 1996 and replicated on 11 January 1996. Thirty fish (mean weight, 25.2 g) were put into each of six tanks, which were aerated as in experiment 1. For each replicate test, three tanks were used as controls (no salt added) and three had 18 g/L salt. Fish from one density treatment were added to one test tank and one control tank. No water exchange was made during each replicate. A small number of fish had jumped from a few of the tanks overnight, but these were not included in the analysis.

Specific conductivity, temperature, and dis-

solved oxygen (DO) were monitored shortly after stocking and also the following day. Dissolved oxygen concentrations dropped as low as 4.9 mg/L after stocking the fish but recovered to final concentrations that ranged from 6.2 to 7.4 mg/L. Temperatures during the test were stable ($14.4 \pm 0.3^\circ\text{C}$). Specific conductivity was 0.4–0.5 mS/cm in control tanks and ranged from 12.5 to 26.7 mS/cm in replicate 1 and from 23.6 to 28.6 mS/cm in replicate 2. After each of the 24-h tests, blood was collected with an ammonia-heparinized syringe from the caudal vasculature of anesthetized fish for analysis of plasma chloride. The blood was centrifuged in microcentrifuge tubes and the plasma was transferred to another tube for freezing until the assay. Chloride was assayed with a chloridometer (Haake-Buchler); a commercially prepared standard was used for calibration and quality control.

Hematology

On day 146 of experiment 1, six fish per treatment (three per raceway) were collected by dip net and immediately put into a 150 mg/L solution of tricaine methane sulfonate (MS-222). Blood was collected from the caudal vasculature with an unheparinized syringe. After the needle was removed, unheparinized microhematocrit tubes were filled and broken at 10-s intervals, and the elapsed time at which a clot strand remained suspended between broken sections of microhematocrit tubes was noted with a digital timer. An additional heparinized tube was used for determination of hematocrit (Hesser 1960). A blood smear was made according to standard methods (Hesser 1960) and later stained with the Leishman–Giemsa stain. Differential blood cell counts were made from the slide, and the smear was examined for the number of lymphocytes, neutrophils, thrombocytes, and other white blood cells. Counts were made at the margin of the smear (where cells did not overlap) at $100\times$ magnification until 100 white blood cells were counted.

Erythrocyte and white blood cell counts were made with a diluting pipette (1:200 dilution), Rees–Ecker solution, and an improved Neubauer hemocytometer (Houston 1990). Hemoglobin was determined with a Spencer hemoglobinometer. After blood collection, the weight of the whole fish, spleen, and liver were recorded to the nearest 0.001 g. Gall bladders were removed before weighing. Splenosomatic and hepatosomatic indices were calculated as follows: $SI = 100 \cdot \text{spleen weight} / \text{total}$

weight, $HSI = 100 \cdot \text{liver weight} / \text{total weight}$ (Goede and Barton 1990).

For experiment 2, the protocol differed slightly in that clotting time and hemoglobin were not determined. The blood was taken on 20, 25, and 26 March 1996 with heparinized syringes. Three fish at a time were captured for blood collection, and the sampling was distributed so that each density treatment was sampled each day. Six fish were sampled per raceway, which produced 18 blood samples per treatment.

Behavioral Observations

For experiment 2, the behavior of the fish from each density treatment was observed in either pairs or five-fish groups. Either two (paired tests) or five (group tests) fish from one treatment were placed into an aquarium ($60.7 \times 38 \times 30.2$ cm) that was covered on three sides and had supplemental aeration. After 4 h of acclimation, fish were viewed by video camera for 60 min (JVC GR-SZ7 Compact Super VHS camcorder). After 30 min of the trial, the camera was stopped and the fish fed floating pellets. Fish were allowed to eat and settle down for 3 min before videotaping was resumed for another 30 min. Length and weight of each fish were recorded after each trial. In all, there were 27 h of observation (3 replicates \times 3 raceways \times 3 density treatments) for each group size. To prevent possible resampling, fish were not returned to the raceways after the trial. During the experiment, water temperature ranged from 14.3 to 15.9°C. Each aquarium was drained and refilled with fresh water between each observation.

The videotape was observed later and fish behavior was categorized into seven behaviors.

Chase.—One fish actively pursues another (Keenleyside and Yamamoto 1962).

Strike.—One fish aggressively lunges at another in a short burst of speed, but this burst is not followed through with a chase (Abbott and Dill 1985).

Nip.—Aggressive physical contact is made by the mouth of one fish on the body or fins of another fish, usually preceded by a strike or chase (Abbott and Dill 1985).

Yawn.—A fish engages in a frontal threat display, in which the hyoid region is lowered and opercles flared (Nilsson and Northcote 1981).

Lateral display.—A fish holds a curved position with the dorsal fin usually laid flat while the caudal, pelvic, and pectorals are generally extended.

The convex side of the fish is often positioned towards the bottom while the concave side is towards another fish. This behavior is similar to the lateral display observed by Jenkins (1969) and Chiszar et al. (1975).

Displace.—One fish is moved out of its place by another with no signs of aggressive behavior (i.e., one fish swimming too close will cause another to flee, termed “direct aggressive responses” by Jenkins (1969) and Chiszar et al. (1975).

Activity level.—Individual fish generally fell into one of three categories that described their overall activity level: stable (averaged less than one move every 5 min), active (averaged more than one move every 5 min but less than five moves every 1 min), or nervous (averaged more than five moves every 1 min). A move is counted as a complete 180-degree turn.

Each individual fish was observed for activity level, and these levels were averaged for the overall level of the pair or group in the aquarium. Observations of a specific behavior were counted as a pair or group behavior, not a single fish behavior. For example, one aquarium with five fish could have a total of five strikes, of which all could be from a single fish or all from different fish.

Statistical Analysis

Raceway mortality data were arcsine-transformed before one-way analysis of variance (ANOVA). Feed conversion and mean weight were also analyzed with the same ANOVA model. Health condition profile (HCP) continuous variables (e.g., plasma protein, hematocrit, leucocrit, length, and condition factor) were tested for normality and rank-transformed if not normally distributed. These values were then tested in a 3-way full factorial ANOVA with date, density, and replicate (raceway) as factors. Many variables varied significantly by date and did not differ between replicates. These were subsequently analyzed separately for each sampling date by using one-way ANOVA with density as a factor. Chi-square analysis was used for the categorical variables of the HCP and for the salt challenge test mortality data. Differences among the two salt challenge trials were first tested in contingency tables and were not significant; so data were pooled to analyze density effects and salt treatment effects. Hematology data were analyzed in a full-factorial two-way ANOVA, factoring for density and raceway effects. Clotting time, neutrophil, and other white blood cell counts were normalized with a \log_e transformation before analysis, and a constant was

TABLE 2.—Final mean weight (\pm SD), feed conversion (weight of food fed/weight gain), mortality, and specific growth rate of cutthroat trout reared at four (experiment 1) or three (experiment 2) densities. See Table 1 for description of densities. For each experiment, means within a column followed by the same letter or no letter are not significantly different ($P > 0.05$).

Density	Mean weight (g)	Feed conversion	Mortality (%)	Specific growth rate (%/d)
Experiment 1				
D1	83.4 \pm 8.60	0.93	2.6	1.99
D2	80.3 \pm 0.40	0.92	2.9	1.97
D3	76.2 \pm 9.93	0.98	3.1	1.95
D4	65.8 \pm 5.78	1.05	3.2	1.88
Experiment 2				
D1	72.8 \pm 4.71 z	0.94	2.7	1.57 z
D2	68.3 \pm 3.33 z	0.94	3.1	1.55 z
D3	55.3 \pm 4.17 y	1.00	4.0	1.47 y

added if necessary. Thrombocyte counts were normalized with an arcsine transformation. Specific growth rates (SGR) were calculated by the formula:

$$\text{SGR} = (\log_e W_f - \log_e W_i) \times 100/D,$$

where W_f is the final average weight of fish in a raceway, W_i is the initial weight, and D is the number of days of rearing. A significance level of 0.05 was used for each test.

Results

Experiment 1

Feed conversion, mean weight, and mortality did not significantly differ among the four densities (Table 2). Feed conversion was at or below 1.05 for all groups, indicating an efficient conversion of food to fish mass at all densities. Mortalities were relatively low (<3.2%) for all groups. Mean weight decreased with increasing density, but not significantly.

Many of the HCP variables did not vary among densities or dates. Kidney, bile, liver, spleen, gills, hindgut, leucocrit, and opercles were indicative of normal, healthy fish. With the exception of two fish, eyes were also normal. The percentage of normal pseudobranchs ranged from 85 to 100%, the mean thymus index ranged from 0.0 to 0.6, and the mean fat index from 2.2 to 2.6. None of the three variables differed among densities or sampling dates.

There were some HCP variables that differed significantly. Plasma protein was significantly higher at intermediate densities (D2, D3) than at

TABLE 3.—Mean values for select health and condition profile variables from cutthroat trout held at four densities. Within a column, means within a sampling date followed by the same letter or no letters are not significantly different ($P > 0.05$). See Table 1 for description of densities in experiment 1.

Density	Total length (mm)	Condition factor ^a	Hematocrit (%)	Leucocrit (%)	Plasma protein (g/dL)	Fin index	Fat index
Experiment 1: day 119							
D1	129.5 z	0.910 z	41.4	1.0	4.07 z	0.2 z	2.5
D2	132.7 z	0.910 z	41.4	1.4	4.61 y	0.6 zy	2.4
D3	119.8 y	0.870 y	41.3	1.4	4.33 zy	0.3 zy	2.3
D4	125.3 zy	0.920 z	41.5	1.2	4.22 z	0.8 y	2.3
Experiment 1: day 150							
D1	155.8	0.880 z	43.2	1.1	4.27	0.4	2.6
D2	143.5	0.910 zy	43.9	1.2	3.98	0.5	2.2
D3	144.7	0.910 zy	42.6	1.0	4.18	0.7	2.3
D4	144.3	0.930 y	40.4	1.1	4.27	0.8	2.3
Experiment 1: day 210							
D1	205.4 z	0.890	48.6 z	1.0	3.98 z	0.6 z	2.4
D2	196.3 zy	0.910	51.9 y	1.1	4.62 y	1.2 y	2.4
D3	194.7 zy	0.910	55.2 x	1.0	5.28 x	1.3 y	2.6
D4	189.1 y	0.880	43.6 w	1.2	3.92 z	1.1 y	2.5

^a Condition factor = $10^5 \times (\text{weight, g})/(\text{length, mm})^3$.

low or high densities on day 119 and day 210, but not on day 150 (Table 3). Hematocrit was significantly higher at the intermediate densities in the last sample, but did not differ among densities in the other two samples. Both hematocrit and plasma protein differed significantly among dates. Mean total length and condition factor were significantly lower at D3 than the two lower densities in the first sample. However by the third sample, mean length of D3 fish did not differ from D1 and D2 fish. After 210 d of rearing, mean length tended to decrease as density increased, and D1 fish and D4 fish were significantly different in size (Table 3). Condition factor tended to be positively correlated with density in the second sample, but after 210 d condition factor was greatest at intermediate densities (D2, D3; Table 3), but the differences were not significant.

Mean comparisons (Duncan's test) of fin index values analyzed in a 3-way ANOVA model indicated that the fin index increased with density and that values were significantly lower at the lowest density (D1) than at higher densities, which did not differ from each other (Table 3). Relative fin length data were analyzed separately for each sampling date. There were some significant differences in relative fin length related to density, but the differences were variable over the experimental period (Figure 1). In the initial sample, dorsal, adipose, and anal fin lengths were greatest at the higher densities. After 119 d of outdoor rearing, the dorsal and ventral fins of fish from the D3

density were significantly longer than fins at the lowest two densities. This difference was transitory, and by day 150, there were no significant differences among densities, except for the adipose and right pectoral fins. The adipose was longer for the highest density fish, but the right pectoral fin was significantly shorter at the highest density, D4, than at the lowest density. At the end of the rearing period, the lowest density produced fish with significantly longer right pectoral fins than the other three densities. Final right ventral fin length was shortest at the highest density. Final anal fin lengths were greatest at the D2 and D4 densities.

When pooled across densities in a three-way ANOVA model, a few HCP variables differed significantly among dates. Bile was significantly higher on day 119 (0.61) than day 150 (0.30) or 210 (0.35), but values were generally indicative of active feeding. Fin index values were significantly higher in the last sample (1.08) than in the previous samples (0.50 to 0.62). Plasma protein values were also significantly higher in the last sample (4.42 g/dL) than in previous samples (4.18, 4.30 g/dL). Mean hematocrit increased significantly over time, with each sampling period differing from the other.

The salt challenge resulted in significant differences in survival from freshwater controls (Table 4). Fish from the highest density (D4) and intermediate density (D2) exposed to salt had significantly higher mortality than control fish.

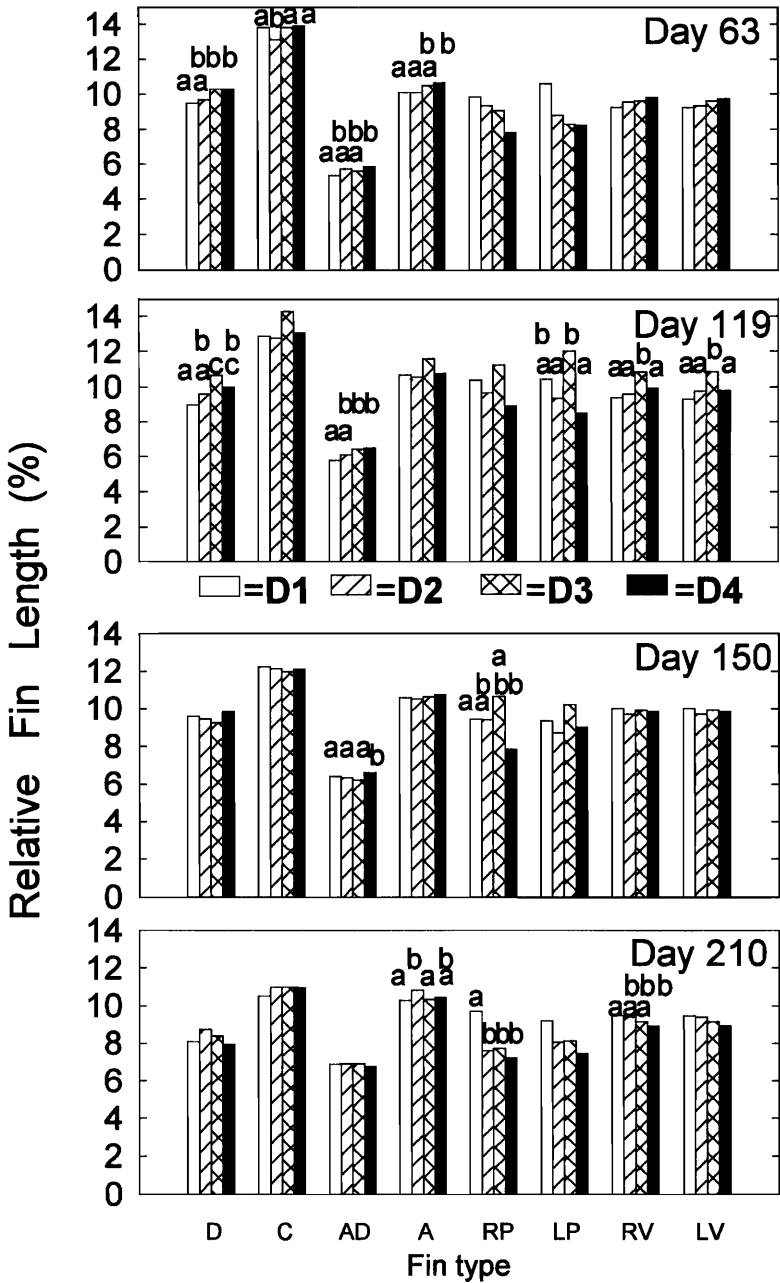


FIGURE 1.—Comparison of relative fin length (percent of total length) of cutthroat trout held at four densities (D1, D2, D3, and D4) in experiment 1 and sampled on four occasions. Numbers in upper right corners refer to days of outdoor rearing. Fin abbreviations are D = dorsal, C = caudal, AD = adipose, A = anal, RP = right pectoral, LP = left pectoral, RV = right ventral, and LV = left ventral. For each fin, bars with a common letter or no letters above them are not significantly different ($P > 0.05$).

None of the hematological variables analyzed differed significantly among densities (Table 5). Red blood cell counts ranged from 65.4×10^4 (D4) to $112.5 \times 10^4/\text{mm}^3$ (D1). The HSI and SI indices

did not differ among densities. Lymphocyte and thrombocyte cells were sometimes difficult to distinguish and some of the variation in the counts may be attributed to this problem.

TABLE 4.—Survival of cutthroat trout reared at four densities and transferred to 15 g/L (experiment 1) or 18 g/L (experiment 2) salt solution for 24 h. Control fish were held in freshwater at the same temperature and fish density. An asterisk indicates survival that differed significantly from that of control fish.

Density	Number surviving	Percent survival
Experiment 1		
D1	2	33
D2	1	17*
D3	3	50
D4	0	0*
Control	5	83
Experiment 2		
D1	57	98.3
D2	60	100.0
D3	51	89.5*
Control	179	99.4

Experiment 2

There were no significant differences in mortality (range, 2.7–4.0%) or feed conversion (0.94–1.00) among the three densities tested. Final mean weight decreased at higher densities and was significantly lower in the highest density (55.3 g, Table 2) than in the lower two densities (68.3 g for D2 and 72.8 g for D1). Specific growth rates decreased with density and mean values ranged from 1.57 for D1 to 1.47 for D3. When densities were pooled, specific growth rates were significantly lower (*t*-test, $P < 0.001$) in experiment 2 than in experiment 1.

The fin index was significantly different among densities in a one-way ANOVA for each sampling date (Table 6). In the first three samples, fin index values were significantly higher (shorter fins) at the highest density than the other two densities, which were not significantly different. In the last

sample (day 289), fin index values were significantly different among all three densities and were positively correlated with density.

Relative fin lengths were significantly affected by sampling date for all fins. Density affected the relative length of the ventral, pectoral, and dorsal fins (Figure 2). Ventral fins did not differ among densities in the first three samples, but in the last sample, they were significantly shorter for fish in D1 than in D2. The left and right pectoral fins were significantly shorter in the highest densities in all four samples, with fin condition improving (i.e., longer fins) as the fish density decreased. Relative dorsal fin length differed among densities only in the second sample in which fish from D3 had longer fins than fish from D1 or D2. Relative caudal and anal fin lengths did not differ among densities when analyzed separately for each sampling time.

Some HCP variables differed among density treatments. Fat index values were significantly and consistently lower at the highest density in the first three samples but not the last (Table 6). Condition factor differed significantly among densities, but the relationship changed as the experiment progressed. In the first and second samples, the condition factor was negatively correlated with density. In the third sample (day 202), the relationship reversed and condition factor was positively correlated with density. In the last sample, there were no significant differences in condition factor among the densities.

There were no significant differences in the coefficient of variation ($CV = 100 \cdot SD/mean$; one-way ANOVA by sampling date) for total weight among densities with the CV for 10 fish from each raceway sampled for the HCP. For these groups, CV values ranged from 15% (day 79) to 62.2%

TABLE 5.—Means (\pm SD) of hematological variables ($N = 6$) of cutthroat trout after 146 d of rearing at four densities. The lymphocyte, neutrophil, thrombocyte, and other white blood cell (WBC) counts are expressed as a percent of WBC; RBC = red blood cell; splenosomatic index = $100 \cdot \text{spleen weight}/\text{total body weight}$; hepatosomatic index = $100 \cdot \text{liver weight}/\text{total body weight}$. Densities (D1–4) are the final densities for experiment 1 in Table 1.

Variable	Density			
	D1	D2	D3	D4
Clotting time (s)	228 \pm 27.8	459 \pm 93.6	290 \pm 42.7	287 \pm 36.0
Hemoglobin (g/dL)	8.84 \pm 0.50	7.90 \pm 0.44	7.85 \pm 0.33	7.63 \pm 0.64
RBC count (per $\text{mm}^3 \times 10^{-4}$)	112.5 \pm 6.68	71.8 \pm 18.20	81.2 \pm 6.13	65.4 \pm 23.3
WBC count (per mm^3)	60,833 \pm 6,679	55,500 \pm 18,220	68,300 \pm 4,981	45,600 \pm 19,911
Lymphocytes	58.0 \pm 4.4	53.7 \pm 3.3	54.5 \pm 2.7	53.1 \pm 6.8
Neutrophils	1.50 \pm 0.79	0.70 \pm 0.25	1.00 \pm 0.22	1.00 \pm 0.29
Thrombocytes	39.9 \pm 4.02	44.8 \pm 3.49	43.2 \pm 2.31	45.3 \pm 6.83
Other WBC	0.50 \pm 0.16	0.80 \pm 0.30	1.33 \pm 0.40	0.50 \pm 0.18
Splenosomatic index	0.043 \pm 0.002	0.049 \pm 0.007	0.035 \pm 0.006	0.045 \pm 0.003
Hepatosomatic index	0.87 \pm 0.04	0.95 \pm 0.04	0.94 \pm 0.05	0.90 \pm 0.08

TABLE 6.—Mean values for select health and condition profile variables from cutthroat trout held at three densities (low, D1; medium, D2; high, D3; see Table 1) in experiment 2. Within a column, means within a sampling date followed by the same letter or no letter are not significantly different ($P > 0.05$).

Density	Total length (mm)	Condition factor ^a	Hematocrit (%)	Leucocrit (%)	Plasma protein (g/dL)	Fin index	Fat index
Experiment 2: day 79							
D1	93.1	0.940 y	45.8	0.0	4.37	0.2 z	2.8 z
D2	91.9	0.900 z	46.1	0.1	4.31	0.4 z	2.1 y
D3	85.0	0.900 z	43.8	0.1	4.31	1.3 y	1.7 x
Experiment 2: day 141							
D1	122.9	0.830 y	41.7	0.6	3.08	0.9 z	2.4 z
D2	118.8	0.850 y	40.4	0.6	3.31	0.9 z	2.1 zy
D3	104.5	0.810 z	40.5	0.3	3.06	1.6 y	1.8 y
Experiment 2: day 202							
D1	158.0	0.860 z	40.7	0.5	3.32	1.0 z	2.1 z
D2	156.9	0.860 zy	39.3	0.6	3.36	0.9 z	2.6 y
D3	141.1	0.880 y	38.6	0.5	3.38	1.6 y	2.0 z
Experiment 2: day 289							
D1	205.1	0.790	41.6 y	1.0	3.03	1.1 z	2.7
D2	190.3	0.800	39.9 z	0.9	3.20	1.5 y	2.5
D3	182.2	0.810	42.9 y	0.9	3.36	1.9 x	2.7

^a Condition factor = (weight in g)/(length in mm)³ × 10⁵.

(day 202). Larger sample sizes would have provided a more accurate account of size variation than presented here, but size variation did not seem to be a problem at the densities studied.

Leucocrit and plasma protein were influenced by sampling date, but not by density. Leucocrit increased over time. Plasma protein was significantly higher in the first sample than the other three. Of the latter three dates, plasma protein for the second sample was significantly lower than for the third sample. Hematocrit differed among densities only in the last sample ($P = 0.050$), in which fish from D2 had significantly lower hematocrit than those from D1 and D3.

Health and condition profile variables such as the eye, gill, liver, bile, kidney, spleen were generally normal across all densities. Among the four samples, only 3 of 360 fish had eye abnormalities (two with unilateral exophthalmia), and no significant differences were observed among densities. Shortened opercles were observed in two fish from D2 in the last sample, but there were no differences among densities. A small percentage of pseudobranchs were swollen (7–17%) in each sample, but this was unrelated to the density treatments. Thymus index values similarly did not differ among densities, but did differ among sampling dates.

Salt challenge test survival among salt water treatments was significantly lower ($P = 0.006$) in the high density treatment (89.5%; chi-square test)

than in D1 (98.3%) or D2 (100%). A comparison of survival between salt water and freshwater for each density treatment with Fisher's exact test resulted in significantly lower survival in salt water only in the high density treatment ($P = 0.012$; Table 4). Plasma chloride taken after the 24-h challenge test did not differ among density treatments for fish exposed to freshwater (controls; range 125.5–129.3 meq/L), but was significantly higher in fish from D3 (155.0 meq/L) than in D1 (132.6) or D2 (134.3 meq/L) in salt water.

Hematological variables measured on day 251 and analyzed with two-way ANOVA generally did not differ among densities. Exceptions included the splenosomatic index, which was significantly higher at D3 than at D1 (Table 7). Red blood cell counts were significantly higher at D1 than D3. Replicate effects were significant for white blood cell counts (higher counts in later replicates), but density did not significantly affect this variable.

Behavior variables from the five-fish groups were not influenced by replicate or feeding time effects (three-way ANOVA of rank-transformed data). Density had significant effects upon activity and lateral display in the five-fish groups (Table 8). Lateral display frequency was significantly higher ($P = 0.038$) in fish from D1 than D2, but did not differ from D3. Strike frequency differences among densities were nearly significant ($P = 0.062$), with lowest values for fish from D2, and highest for fish from D3.

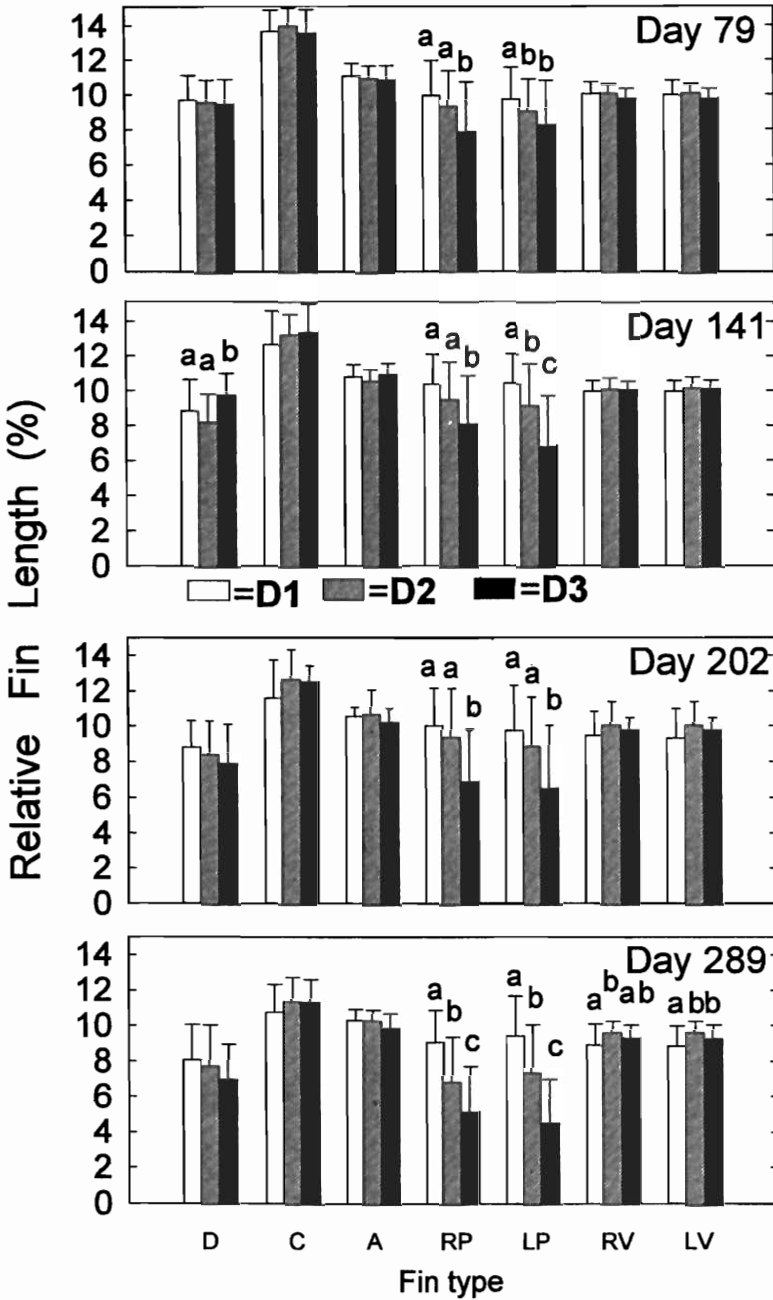


FIGURE 2.—Comparison of relative fin length (percent of total length) of cutthroat trout held at three densities (D1, D2, and D3) in experiment 2 and sampled on four occasions. Number in upper right corners refers to days of outdoor rearing. For fin abbreviations, see Figure 1. For each fin, bars with a common letter or no letters above them are not significantly different ($P > 0.05$).

In paired-fish trials, density significantly influenced activity, but not the other behaviors (Table 8). Activity frequencies were highest in D3 and lowest in D2. Displacement frequency was greatest

for D2 and lowest for D1. Feeding time had no influence upon any behavior except yawning. Replicate effects were significant for lateral display (replicate 1 > 2, $P = 0.033$).

TABLE 7.—Means (\pm SD) of hematological variables ($N = 15-18$) of cutthroat trout after 251 d of rearing at three densities (low, D1; medium, D2; high, D3; see experiment 2 in Table 1). The lymphocyte, neutrophil, thrombocyte, and other white blood cell (WBC) counts are expressed as percent of WBC; RBC = red blood cell. Splenosomatic and hepatosomatic indices are defined in Table 5. Values for each variable followed by a common letter or no letter are not significantly different ($P > 0.05$).

Variable	Density		
	D1	D2	D3
Red blood cell count (per $\text{mm}^3 \times 10^{-4}$)	152.1 \pm 25.2 z	14.3.3 \pm 18.4 zy	124.9 \pm 36.1 y
WBC count (per mm^3)	59,235 \pm 17,352	61,028 \pm 13,153	58,147 \pm 11,126
Lymphocytes	74.2 \pm 10.6	70.7 \pm 12.7	68.7 \pm 11.7
Neutrophils	1.2 \pm 1.6	0.8 \pm 1.3	0.8 \pm 0.9
Thrombocytes	23.5 \pm 11.0	27.4 \pm 13.2	29.2 \pm 12.4
Other WBC	1.1 \pm 1.3	1.1 \pm 1.1	1.3 \pm 1.9
Splenosomatic index	0.043 \pm 0.01 z	0.048 \pm 0.01 zy	0.054 \pm 0.01 y
Hepatosomatic index	0.775 \pm 0.09	0.801 \pm 0.09	0.772 \pm 0.07

Discussion

Hatchery Performance

In this study, high densities negatively affected growth. The negative effect of high densities upon growth of salmonids has been noted by a number of authors (Refstie and Kittelsen 1976; Trzebiatowski et al. 1981; Poston 1983; Martin and Wertheimer 1989). However, Bonham and Williams (1948) and Kibus et al. (1992) reported no significant effect upon growth at lower densities. Kindschi and Koby (1994) evaluated Snake River

cutthroat trout performance at densities ranging from 55 to 247 kg/m^3 and did not observe effects on growth and mortality until the DI exceeded 2.1. In experiment 2, growth was significantly reduced at the highest density (1,634 fish/m^3 , DI = 0.75). Also, mean length was significantly reduced in experiment 1. Growth was reduced in experiment 2 relative to growth in the first test. Primary differences in the approach between the two experiments were the number of days fed per week (7 d versus 5 d) and the crowding approach (crowding month-

TABLE 8.—Means ($N = 18$), SEs, and median frequencies for 30-min period (prefeed or postfeed, data pooled) for certain behaviors of cutthroat trout originating from three different rearing densities (low, D1; medium, D2; high, D3) and observed in either five-fish groups or pairs. Means within a behavior type with a common letter or no letters are not significantly different ($P > 0.05$).

Behavior and density	Five-fish group			Paired group		
	Mean	SE	Median	Mean	SE	Median
Activity						
D1	1.50 z	0.10	1.60	1.61 z	0.10	1.50
D2	1.79 zy	0.13	1.80	1.50 z	0.09	1.50
D3	2.03 y	0.09	2.00	2.09 y	0.09	2.00
Chase						
D1	0.06	0.06	0.06	0.03	0.17	0.00
D2	0.06	0.06	0.00	0.17	0.12	0.00
D3	0.67	0.67	0.00	0.41	0.17	0.00
Displace						
D1	3.67	1.07	2.00	0.28	0.14	0.00
D2	3.22	1.36	1.50	1.22	0.37	1.00
D3	3.56	0.87	2.00	0.53	0.26	0.00
Lateral display						
D1	3.39 y	1.10	1.50	0.94	0.57	0.00
D2	0.56 z	0.34	0.00	3.22	1.63	0.00
D3	1.83 zy	0.83	0.00	2.58	1.23	0.00
Strike						
D1	0.17	0.17	0.00	0.00	0.00	0.00
D2	0.00	0.00	0.00	0.06	0.06	0.00
D3	0.56	0.39	0.00	0.00	0.00	0.00
Yawn						
D1	6.61	1.07	6.50	8.39	1.00	7.50
D2	6.61	1.48	6.00	11.39	1.37	9.50
D3	8.44	1.30	8.50	9.88	1.42	9.00

ly versus allowing the fish to grow into the final density). Because there was no replication of the two approaches to maintaining densities, no definitive statements can be made. However, these preliminary results indicated that the approach used in experiment 1 may produce larger and healthier fish without compromising feed conversion.

Feed conversions were efficient (<1.05), mortality was low ($<4\%$), and both variables were unaffected across the range of densities tested in both experiments. Kindschi and Koby (1994) reported similar feed conversion values (1.07, 1.08) for Snake River cutthroat trout for density indices of 0.48 or 1.40; but at a density index of 2.30, feed conversion was significantly less efficient and mortality significantly higher. A similar increase in feed conversion rates has been reported for rainbow trout across densities ranging from 150 to 900 fish/m³ (Trzebiatowski et al. 1981). Bonham and Williams (1948) found no difference in feed conversion and growth of fingerling cutthroat trout between fish in aquaria at densities of either 92 or 927 fish/m³ (DI = 0.015 or 0.15). The above data suggests that feed conversion for cutthroat trout at a density index above 1.4 will likely be negatively affected and mortality will be affected at higher densities (DI approaching 2.3).

General Health and Condition

Condition factor differed significantly among densities in both experiments, but differences were inconsistent over the culture period and between the tests. For example, condition factor in the second experiment was negatively correlated with density during early rearing, but later changed to a positive correlation, and finally changed to no relationship with density at all. Fish from experiment 1 had better condition factors at intermediate densities at the end of the rearing period. At high densities, a decrease in the condition factor of coho salmon *Oncorhynchus kisutch* (Fagerlund et al. 1981) and Atlantic salmon *Salmo salar* (Refstie and Kittelsen 1976) has been reported. Other authors report no significant differences among densities in condition factor for rainbow trout (Kilambi et al. 1977; Kebus et al. 1992) or lake trout *Salvelinus namaycush* (Poston 1983; Soderberg et al. 1987).

Examination of mesenteric fat indicated no density effects when the fish were allowed to grow into the maximum density, but results from the experiment with monthly density adjustment indicated that crowding fish into a density index of 0.75 (1,634 fish/m³) significantly reduced mes-

enteric fat levels. Fagerlund et al. (1981) also noted reductions in fat levels of coho salmon at higher densities (>751 fish/m² or 10.5 kg/m³). Brook trout *Salvelinus fontinalis* reared at 120 kg/m³ had reduced liver glycogen, plasma glucose, and thyroxine levels compared with controls at 30 kg/m³ (Vijayan et al. 1990). Reductions in energy stores may compromise survival or reproduction (Markovich 1977; Storebakken and Austreng 1987; Rowe et al. 1991).

The effects of density upon the hepatosomatic index (HSI) and the splenosomatic index (SI) were measured in this study. A decrease in HSI has been associated with pulp mill pollution that also induced higher incidences of lesions and parasitic infections, as well as reduced lymphocyte counts and condition factor (Barker et al. 1994). Similar decreases in HSI have been observed for lake whitefish *Coregonus clupeaformis* below a hydroelectric dam control structure (Barnes et al. 1984). To use somatic indices for biomonitoring, it is important to determine how the indices vary temporally and environmentally and to evaluate factors such as temperature and photoperiod. Increased feeding rates and decreasing temperatures have been shown to increase the HSI (Heidinger and Crawford 1977). Seasonal HSI variations in brook trout have been observed in wild lacustrine populations (Larson 1973). Some of this variation is probably a result of energy being transferred to gonads during gametogenesis (Larson 1973). High densities reduced HSI in brook trout (Vijayan et al. 1990), although an earlier study indicated no significant differences in HSI, liver glycogen content, or SI as densities varied from 30 to 120 kg/m³ (Vijayan and Leatherland 1988). In this study, rearing density did not influence either the HSI or SI of cutthroat trout in experiment 1, but in experiment 2, the SI was significantly higher in the highest density treatment than the lowest.

Certain hematological variables were influenced by density, although results were inconsistent over time and across experiments. Hematocrit and plasma protein differed significantly among densities in some samples, but levels were within normal ranges reported for other salmonids (Snieszko 1961; Barnhart 1969) and did not follow any obvious trends related to density. Mazur and Iwama (1993) observed significant increases in hematocrit and plasma cortisol of chinook salmon *Oncorhynchus tshawytscha* at densities of 32 or 64 kg/m³ compared with a 8 kg/m³ (about 2,050 fish/m³). These fish were sampled 5 d after stocking, whereas the fish in this study were sampled late

in the rearing period. Pickering and Pottinger (1987) observed a reduction in circulating thrombocytes and lymphocytes in age-I brown trout *Salmo trutta* and rainbow trout as density increased from 18 to 123 kg/m³ (61 to 444 fish/m³), but erythrocyte and neutrophil numbers were unaffected. In this study the differential blood cell counts did not indicate any negative density effects on immune function, although further tests on non-specific immunity impairment should be conducted to fully evaluate effects of density upon the immune system.

Salt challenge test results indicated that fish from high-density treatments were compromised in their ability to withstand osmoregulatory challenges. Mazur and Iwama (1993) similarly noted that Chinook salmon from the highest densities (32 and 64 kg/m³) had fewer days to 50% mortality (5.5, 3.9 d) than at 8 kg/m³ (9.3 d). In seawater challenge tests, Banks (1994) noted reduced mortality and blood sodium concentrations in chinook salmon smolts reared at 585 fish/m³ (15 kg/m³) than at 1,169 or 1,754 fish/m³. Schreck et al. (1985) noted similar density effects in seawater tests with coho salmon. However, Blackburn and Clarke (1990) noted no difference in seawater adaptability of coho salmon across three densities.

Fin Erosion and Aggressive Behavior

Pectoral fin erosion in this study increased with density; the longest fins were from fish from the lowest density. Measurement of other fins showed that fin erosion grew worse over time, but density effects were inconsistent. Because the erosion was fin specific, density effects on fin erosion were probably behavioral modifications (e.g., nipping of pectoral fins) rather than physiological changes that theoretically would affect all fins. No significant differences in dorsal and pectoral fin erosion were reported for lake trout at final densities of 30–245 kg/m³ (DI = 0.25–2.0; Soderberg and Krise 1987). Similar densities also did not result in differences in dorsal or pectoral fin erosion for either rainbow trout (Kindschi et al. 1991b) or cutthroat trout (Kindschi and Koby 1994). Soderberg et al. (1993) reported that pectoral fins of Atlantic salmon were not significantly affected by rearing density (80–310 kg/m³) that but dorsal fins were more eroded at the highest density. Mäkinen and Ruohonen (1990) noted that fin erosion of rainbow trout was positively correlated with density and recommended rearing densities below 50 kg/m³.

Behavioral observations in this study did not indicate a strong density effect. Activity level was

higher in fish from high-density groups, but the frequency of agonistic behaviors did not increase with density. Density effects upon agonistic behavior appear to be dependent upon the species and actual density (e.g., Kaiser et al. 1995), with some authors reporting that density increases aggression (convict cichlid *Cichlasoma nigrofasciatum*, Fitzgerald and Keenleyside 1978; guppy *Poecilia reticulata*, Warren 1973; rainbow trout, Cole and Noakes 1980) and others reporting the reverse (Atlantic salmon, Fernö and Holm 1986; Arctic char, Brown et al. 1992).

Application of the results of this study depend on the objectives of the fish culturist. If maximum growth and a reduction in pectoral fin erosion is desired, the lowest densities tested are recommended because high density significantly reduced growth and increased pectoral fin damage. Conversely, the reduction in growth and possible decreases in poststocking survival may be offset by higher overall numbers or mass of fish produced. Data collected on aggressive behavior, feed conversion, most HCP variables, and hematological variables indicated that the highest densities of this study had little impact on general health and high numbers of fish were raised with little mortality. Raceway cleaning was also easier and less time consuming at the higher densities.

However, the salt challenge results indicated that the higher densities can compromise the fish's ability to survive in extreme conditions. Fish from high densities may survive and perform well in the hatchery or when stocked into ideal conditions but when seriously challenged may succumb rather than survive. As experience with chinook salmon has shown (Ewing and Ewing 1995), more is not necessarily better. For example, golden shiners *Notemigonus crysoleucas* (Schwedler and Plumb 1982) and chinook salmon (Mazur et al. 1993) had higher levels of viral or bacterial infection at higher densities than counterparts at lower densities. Physiological changes brought about by high densities, such as reductions in Na⁺, K⁺, -ATPase activity (Sower and Fawcett 1991), cortisol, thyroxine, and glucose (Vijayan and Leatherland 1988), can affect the immune system and other organ systems essential for survival. Erosion of pectoral fins, which aid fish in maneuvering away from predators, may also affect survival in certain situations. Therefore, stocking conditions as well as economics should guide decisions about rearing densities. Because of variation in these conditions, poststocking survival of fish reared at high densities should be evaluated for each species and

situation to determine the appropriate rearing density.

Acknowledgments

We thank Steve Intelmann for assistance in data collection. The research was supported by the Utah Division of Wildlife Resources and the Federal Aid in Sport Fish Restoration Program, project F-53-R.

References

- Abbott, J. C., and L. M. Dill. 1985. Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 42:1702-1706.
- APHA (American Public Health Association), American Water Works Association, and Water Pollution Control Federation. 1989. Standard methods for the examination of wastewater, 17th edition. APHA, Washington, D.C.
- Banks, J. L. 1994. Raceway density and water flow as factors affecting spring chinook salmon (*Oncorhynchus tshawytscha*) during rearing and after release. Aquaculture 119:201-217.
- Barker, D. E., R. A. Khan, and R. Hooper. 1994. Bioindicators of stress in winter flounder, *Pleuronectes americanus*, captured adjacent to a pulp and paper mill in St. George's Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 51:2203-2209.
- Barnes, M. A., G. Power, and R. G. H. Downer. 1984. Stress-related changes in lake whitefish (*Coregonus clupeaformis*) associated with a hydroelectric control structure. Canadian Journal of Fisheries and Aquatic Sciences 41:1528-1533.
- Barnhart, R. A. 1969. Effects of certain variables on hematological characteristics of rainbow trout. Transactions of the American Fisheries Society 98:411-418.
- Blackburn, J., and W. Clarke. 1990. Lack of density effect on growth and smolt quality in zero-age coho salmon. Aquacultural Engineering 9:121-130.
- Bonham, K., and R. W. Williams. 1948. Effect of population pressure upon rate of growth and feed conversion of fingerling cutthroat trout. Progressive Fish-Culturist 10:15-18.
- Bosakowski, T., and E. J. Wagner. 1994. Assessment of fin erosion by comparison of relative fin length in hatchery and wild trout in Utah. Canadian Journal of Fisheries and Aquatic Sciences 51:636-641.
- Brown, G. E., J. A. Brown, and R. K. Srivastava. 1992. The effect of stocking density on the behaviour of Arctic charr (*Salvelinus alpinus* L.). Journal of Fish Biology 41:955-963.
- Chiszar, D., D. W. Drake, and J. T. Windell. 1975. Aggressive behaviour in rainbow trout (*Salmo gairdneri* Richardson) of two ages. Behavioral Biology 13:425-432.
- Cole, K. S., and D. L. G. Noakes. 1980. Development of early social behaviour of rainbow trout, *Salmo gairdneri* (Pisces, Salmonidae). Behavioural Processes 5:97-112.
- Ewing, R. D., and S. K. Ewing. 1995. Review of the effects of rearing density on survival to adulthood for Pacific salmon. Progressive Fish-Culturist 57:1-25.
- Fagerlund, U. H. M., J. R. McBride, and E. T. Stone. 1981. Stress-related effects of hatchery rearing density on coho salmon. Transactions of the American Fisheries Society 110:644-649.
- Fernö, A., and M. Holm. 1986. Aggression and growth of Atlantic salmon parr. 1. Different stocking densities and size groups. Fiskeridirektoratets Skrifter Serie Havundersökelse 18:113-122.
- Fitzgerald, G. J., and M. H. A. Keenleyside. 1978. The effects of numerical density of adult fish on reproduction and parental behavior in the convict cichlid fish *Cichlasoma nigrofasciatum* (Günther). Canadian Journal of Zoology 56:1367-1371.
- Goede, R. W., and B. A. Barton. 1990. Organismic indices and an autopsy-based assessment as indicators of health and condition of fish. Pages 93-108 in S. M. Adams, editor. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, Maryland.
- Heidinger, R. C., and S. D. Crawford. 1977. Effect of temperature and feeding rate on the liver-somatic index of the largemouth bass, *Micropterus salmoides*. Journal of the Fisheries Research Board of Canada 34:633-638.
- Hesser, E. F. 1960. Methods for routine fish hematology. Progressive Fish-Culturist 22:164-170.
- Houston, A. H. 1990. Blood and circulation. Pages 273-334 in C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.
- Jenkins, T. M., Jr. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *S. gairdneri*) resident in mountain streams. Animal Behavior Monographs 2:57-123.
- Kaiser, H., O. Weyl, and T. Hecht. 1995. The effect of stocking density on growth, survival and agonistic behaviour of African catfish. Aquaculture International 3:217-225.
- Kebus, M. J., and five coauthors. 1992. Effects of rearing density on the response and growth of rainbow trout. Journal of Aquatic Animal Health 4:1-6.
- Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour 19:139-169.
- Kilambi, R. V., J. C. Adams, A. V. Brown, and W. A. Wickzer. 1977. Effect of stocking density and cage size on growth, feed conversion, and production of rainbow trout and channel catfish. Progressive Fish-Culturist 39:62-66.
- Kindschi, G. A. 1987. Method for quantifying degree of fin erosion. Progressive Fish-Culturist 49:314-315.
- Kindschi, G. A., and R. F. Koby, Jr. 1994. Performance and oxygen consumption of Snake River cutthroat trout reared at four densities with supplemental oxygen. Progressive Fish-Culturist 56:13-18.

- Kindschi, G. A., H. T. Shaw, and D. S. Bruhn. 1991a. Effects of baffles and isolation on dorsal fin erosion in steelhead trout, *Oncorhynchus mykiss* (Walbaum). *Aquaculture and Fisheries Management* 22:343–350.
- Kindschi, G. A., C. E. Smith, and R. F. Koby, Jr. 1991b. Performance of two strains of rainbow trout reared at four densities with supplemental oxygen. *Progressive Fish-Culturist* 53:203–209.
- Larson, G. L. 1973. Liver weight of brook trout in a high-mountain lake in Washington state. *Progressive Fish-Culturist* 35:234–236.
- Mäkinen, T., and K. Ruohonen. 1990. The effect of rearing density on the growth of Finnish rainbow trout (*Oncorhynchus mykiss* Walbaum 1792). *Journal of Applied Ichthyology* 6:193–203.
- Markevich, N. B. 1977. Some morphophysiological indices of the silverside, *Atherina mochon pontica*, in the Aral Sea in connection with the age structure of its population. *Journal of Ichthyology* 17:618–626.
- Martin, R. M., and A. Wertheimer. 1989. Adult production of chinook salmon reared at different densities and released as two smolt sizes. *Progressive Fish-Culturist* 51:194–200.
- Mazur, C. F., and G. K. Iwama. 1993. Effect of handling and stocking density on hematocrit, plasma cortisol, and survival in wild and hatchery-reared chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture* 112:291–299.
- Mazur, C. F., D. Tillapaugh, and G. K. Iwama. 1993. The effects of feeding level and rearing density on the prevalence of *Renibacterium salmoninarum* in chinook salmon (*Oncorhynchus tshawytscha*) reared in salt water. *Aquaculture* 117:141–147.
- Nicola, S. J., and A. J. Cordone. 1973. Effects of fin removal on survival and growth of rainbow trout (*Salmo gairdneri*) in a natural environment. *Transactions of the American Fisheries Society* 102:753–758.
- Nilsson, N. A., and T. G. Northcote. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1228–1246.
- Pickering, A. D., and T. G. Pottinger. 1987. Crowding causes prolonged leucopenia in salmonid fish, despite interrenal acclimation. *Journal of Fish Biology* 30:701–712.
- Piper, R. G. 1972. Managing hatcheries by the numbers. *American Fishes and U.S. Trout News* 17(3):10, 25–26.
- Poston, H. A. 1983. Effect of population density of lake trout in cylindrical jars on growth and oxygen consumption. *Progressive Fish-Culturist* 45:8–12.
- Refstie, T., and A. Kittelsen. 1976. Effect of density on growth and survival of artificially reared Atlantic salmon. *Aquaculture* 8:319–326.
- Rowe, D. K., J. E. Thorpe, and A. M. Shanks. 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* 48:405–413.
- Schreck, C., R. Patiño, C. Pring, J. Winton, and J. Holway. 1985. Effects of rearing densities on indices of smoltification and performance of coho salmon, *Oncorhynchus kisutch*. *Aquaculture* 45:345–358.
- Schwedler, T. E., and J. A. Plumb. 1982. Golden shiner virus: effects of stocking density on incidence of viral infection. *Progressive Fish-Culturist* 44:151–152.
- Snieszko, S. F. 1961. Microhematocrit values in rainbow trout, brown trout, and brook trout. *Progressive Fish-Culturist* 23:114–119.
- Soderberg, R. W., D. S. Baxter, and W. F. Krise. 1987. Growth and survival of fingerling lake trout reared at four densities. *Progressive Fish-Culturist* 49:284–285.
- Soderberg, R. W., and W. F. Krise. 1987. Fin condition of lake trout, *Salvelinus namaycush* Walbaum, reared at different densities. *Journal of Fish Diseases* 10:233–235.
- Soderberg, R. W., J. W. Meade, and L. A. Redell. 1993. Fin condition of Atlantic salmon reared at high densities in heated water. *Journal of Aquatic Animal Health* 5:77–79.
- Sower, S. A., and R. S. Fawcett. 1991. Changes in gill Na^+ , K^+ -ATPase, thyroxine, and triiodothyronine of coho salmon held in two different rearing densities during smoltification. *Comparative Biochemistry and Physiology* 99A:85–89.
- Storebakken, T., and E. Austreng. 1987. Ration level for salmonids. I. Growth, survival, body composition, and feed conversion in Atlantic salmon fry and fingerlings. *Aquaculture* 60:189–206.
- Trzebiatowski, R., J. Filipiak, and R. Jakubowski. 1981. Effect of stock density on growth and survival of rainbow trout (*Salmo gairdneri* Rich.). *Aquaculture* 22:289–295.
- Vijayan, M. M., J. S. Ballantyne, and J. F. Leatherland. 1990. High stocking density alters the energy metabolism of brook charr, *Salvelinus fontinalis*. *Aquaculture* 88:371–381.
- Vijayan, M. M., and J. F. Leatherland. 1988. Effect of stocking density on the growth and stress-response in brook charr, *Salvelinus fontinalis*. *Aquaculture* 75:159–170.
- Warren, E. W. 1973. The effects of relative density upon some aspects of the behaviour of the guppy—*Poecilia reticulata* (Peters). *Journal of Fish Biology* 5:753–765.

Received: July 24, 1996

Accepted: November 22, 1996