

AN ABSTRACT OF THE THESIS OF

Sandra Marie Noble for the degree of Master of Science
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Title: Impacts of Earlier Emerging Steelhead Fry of Hatchery
Origin on the Social Structure, Distribution, and Growth
of Wild Steelhead Fry

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Abstract approved: _____
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Newly emerged steelhead fry (Oncorhynchus mykiss) of hatchery and wild origins were studied in laboratory stream channels and natural streams. Objectives of the study were to determine if and how earlier emerging hatchery fry influence the emigration, realized densities, growth, habitat use, social structure, and activity patterns of localized populations of wild steelhead fry when the hatchery fry have a competitive advantage conferred by larger size and prior residence.

During 1986 and 1987, the above variables were observed daily among hatchery and wild steelhead fry in laboratory stream channels for 8 weeks following emergence in June. The habitat use and social activities for fry of both origins were observed weekly in natural stream reaches from June through August in 1987 to corroborate lab findings. In lab channels, both hatchery and wild fry received 2 treatments: living alone (allopatry) and living together (sympatry). In the lab, fry of hatchery origin emerged 7 to 10 d prior to wild fry and remained larger in size during the 8 weeks of study both years. In natural stream reaches, fry of each origin were observed only in allopatric situations. Wild fry in the field emerged from natural redds while hatchery fry were released in stream reaches as unfed, newly emerged (swim-up) fry.

Hatchery and wild fry in lab sections were found to be very similar in their emigration rates, distances to nearest neighbor, growth rates, and use of habitat. Both fry types, regardless of treatment or environment (lab or field), established similar stable social structure

and used the same types of aggressive acts. Among all lab groups, once a fry became dominant, it retained that social status to the end of the study period.

Significant differences ($P < .05$ both years) among comparison tests were: 1) in allopatric lab sections, wild fry maintained larger densities than hatchery fry, 2) in sympatry, hatchery fry had a greater tendency to establish stable focal points and social hierarchies more readily, defend larger areas, have better condition, prefer pools with overhead cover more frequently, be more aggressive, and reach stable densities more quickly than the wild fry, 3) fewer hatchery fry in sympatry maintained nomadic positions than wild fry in both treatments, 4) in sympatry, hatchery fry directed more acts of overt aggression toward wild fry than other hatchery fry, 5) wild fry in sympatry usually used defensive or less offensive acts of aggression when interacting with other fry, 6) fry of both origins in natural stream reaches maintained greater distances to their nearest neighbor than fry in allopatric lab sections, 7) dominant hatchery fry in both treatments maintained larger focal areas than subdominant fry, 8) hatchery fry maintained longer lengths than wild fry through the duration of the study, and 9) hatchery fry were more aggressive in sympatry than in allopatry.

Potential differences ($P < .05$ in one year and $P < .1$ in the other year) were: 1) wild fry in sympatry had lower realized densities, maintained smaller focal areas, had greater proportions of nomadic individuals, and established stable social hierarchies slower than wild fry in allopatric lab sections, 2) wild fry in sympatry had poorer condition than all other fry groups in lab sections, 3) in sympatry, wild fry were the recipients of the majority of aggressive acts perpetrated by hatchery fry and other wild fry and usually assumed the subordinate positions within the social hierarchy, 4) all fry in the lab showed a high preference for pools with overhead cover and low preference for gravel and fines and run areas, and 5) wild fry in allopatric lab sections were more socially active than hatchery fry while the reverse was observed in the natural streams.

Any influences that could be attributed to inherent differences

between stock origins were probably masked by size differences between fry types. The study would have been more complete had I included sympatric lab sections where wild fry emerged first and where fry types emerged simultaneously, and sympatric reaches in natural streams. Results were further confounded by the limited number of wild adults used for broodstock in the lab segment of this study. Progeny produced from so few adults (5 adults of each sex each year) would have very limited genotypic variation compared to what occurs in natural streams. This may partially explain why some findings from lab sections and natural stream reaches differed. Likewise, genotypic expression among wild fry in lab sections may have varied greatly between years. This could explain differences found between years in behavior of wild fry in similar lab treatments.

Although this study does not simulate all possible scenarios, results support suspicions that introductions of hatchery fry of larger size and earlier emergence into streams containing wild stocks could disrupt the social structure and negatively influence the realized densities, spatial distribution, growth, and behavior of wild juveniles in recipient streams.

Impacts of Earlier Emerging Steelhead Fry of Hatchery Origin
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This thesis is dedicated to my husband William O. Noble.

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TABLE OF CONTENTS

| | <u>Page</u> |
|--|-------------|
| CHAPTER I GENERAL INTRODUCTION..... | 1 |
| CHAPTER II EFFECTS OF SIZE AND PRIOR RESIDENCE OF EARLY EMERGING HATCHERY STEELHEAD FRY ON THE DISPERSAL, DISTRIBUTION, AND GROWTH OF WILD STEELHEAD FRY IN LABORATORY STREAM CHANNELS..... | 4 |
| ABSTRACT..... | 4 |
| INTRODUCTION..... | 6 |
| METHODS..... | 7 |
| Conditions of the Experiment..... | 7 |
| Treatment of Data..... | 12 |
| RESULTS..... | 15 |
| Dispersal..... | 15 |
| Emigration..... | 15 |
| Density..... | 19 |
| Spatial Distribution..... | 19 |
| Spacing..... | 19 |
| Use of Habitat..... | 24 |
| Growth..... | 26 |
| DISCUSSION..... | 29 |
| REFERENCES..... | 34 |
| CHAPTER III VARYING INFLUENCES OF EARLIER EMERGING STEELHEAD FRY OF HATCHERY ORIGIN ON THE SOCIAL STRUCTURE OF WILD STEELHEAD FRY..... | 38 |
| ABSTRACT..... | 38 |
| INTRODUCTION..... | 40 |
| METHODS..... | 41 |
| Conditions of the Experiment..... | 41 |
| Laboratory Channels..... | 41 |
| Natural Streams..... | 42 |
| Treatment of Data..... | 46 |
| RESULTS..... | 47 |
| Social Hierarchy..... | 47 |
| Distance to Nearest Neighbor and Size of Focal Area..... | 52 |
| Social Interactions..... | 55 |
| Overall Results..... | 55 |
| Effects of Feeding..... | 57 |
| Social Status..... | 59 |
| DISCUSSION..... | 62 |
| REFERENCES..... | 67 |
| CHAPTER IV GENERAL SUMMARY..... | 70 |
| BIBLIOGRAPHY..... | 73 |

LIST OF FIGURES

| <u>Figure</u> | <u>Page</u> |
|--|-------------|
| 1. Diagram of laboratory streams: two channels each arranged as above..... | 9 |
| 2. Example of map drawn to scale of a back pool in a lab section showing overhead cover, substrate type, feeding pipe, and emigrant box. Direction of flow is left to right..... | 11 |
| 3. Average emigration rates through time for wild and hatchery fry in allopatry and sympatry, 1986 and 1987..... | 17 |
| 4. Average distances to nearest neighbor through time for both fry types in each treatment, 1986 and 1987..... | 22 |
| 5. Average size of focal areas through time for fry types in each treatment, 1986 and 1987..... | 23 |
| 6. Map of natural streams used in study during 1987..... | 44 |
| 7. Mean condition factors and their 95% confidence intervals for dominant (Dom) and subordinate (Subor) fry in allopatry and sympatry in lab sections. Numbers above 95% CI bars are the sample size in each category at the end of the study each year..... | 51 |
| 8. Average size of focal areas through time for dominant (Dom) and subdominant (Sub) fry in allopatry and sympatry in lab sections, 1986 and 1987..... | 54 |
| 9. Average high and low intensity acts for both fry types in allopatric and sympatric lab sections (in sympatry, fry type that an act was directed toward is shown), and the field reaches..... | 56 |
| 10. Average high and low intensity acts through time for fry in allopatric lab sections and field reaches..... | 58 |
| 11. Average number of high and low intensity acts delivered by each fry type (Wild = wild fry, Hatch = hatchery fry) in allopatry and sympatry in lab sections before (Pre) and after (Post) feeding periods..... | 60 |

Figure

Page

12. Average high and low intensity acts for both fry types in both treatments in the lab by social status (D or Dom = dominant fry, S or Sub = subdominant fry, and N or Nomad = nomadic fry). In sympatry, fry type toward which act was directed is shown (Wild = wild fry, Hatch = hatchery fry)..... 61

LIST OF TABLES

| <u>Table</u> | <u>Page</u> |
|--|-------------|
| 1. Days to peak emigration and stable densities, and realized densities for test sections in 1986 and 1987. W = wild fry; H = hatchery fry; I = replicate 1 and II = replicate 2 within each year; numbers in parentheses refer to number of days or densities of specific fry types in sympatry..... | 16 |
| 2. Spearman rank correlations showing effects of time and density on emigration rates for each test section, 1986 and 1987. In sympatry, H = effects of hatchery fry density and W = effects of wild fry density; I = replicate 1 and II = replicate 2 within each year..... | 18 |
| 3. The number and proportion of total density of nomadic fry in each test section at the beginning of the fifth week following emergence when densities had stabilized and focal points and areas were established in each section, 1986 and 1987. I is replicate 1 and II is replicate 2 in each year of study..... | 21 |
| 4. Relative preference and results from comparison tests among substrate types (RUB=rubble, COB=cobble, and GRF=gravels and fines) for each fry type in both treatments. Averages are given for weeks 1-4 and 5-8..... | 25 |
| 5. Relative preference and results from comparison tests among habitat types (COVP=pool with overhead cover, NCOVP=pool without overhead cover, and RUN=a run area) for each fry type in both treatments. Averages are given for weeks 1-4 and 5-8..... | 27 |
| 6. Average lengths, weights, and condition factors (Q), and overall instantaneous growth rates (G) for each treatment and fry type in both years using data from the first week following emergence (Week 1) and the end of the study (End) and combining data from replicate sections within years. In parentheses are sample size (n) and standard deviation (s) for averages..... | 28 |
| 7. Watershed and reach characteristics of streams used in the field studies, 1987..... | 45 |

Table

Page

| | | |
|-----|---|----|
| 8. | Total number of nomads for each fry type and treatment through time in lab sections during 1986 and 1987..... | 49 |
| 9. | Average fork length (mm), sample size (n), standard error (se), and results from tests for significant differences (* = significant at the .05 level; ns = not significant) for dominant and subordinate fry of each fry type and treatment in lab sections, 1986 and 1987..... | 50 |
| 10. | Average size (m ²), sample size (n), and standard error (se) of focal areas through time for both fry types in allopatric lab sections and natural stream reaches..... | 53 |

**IMPACTS OF EARLIER EMERGING STEELHEAD FRY
OF HATCHERY ORIGIN ON THE SOCIAL STRUCTURE, DISTRIBUTION,
AND GROWTH OF WILD STEELHEAD FRY**

CHAPTER I

GENERAL INTRODUCTION

Enhancement and protection of wild steelhead (Oncorhynchus mykiss) stocks and their genetic diversity and integrity are central goals among many fishery management groups. The urgency to work toward these goals has been pronounced in recent years since many wild stocks are rapidly declining or face extinction. Since the early 1900's, supplementation (the stocking of presmolts or fry) of wild steelhead stocks with steelhead juveniles of hatchery origin has been a common practice used to stimulate smolt production among depressed wild stocks and increase the number of returning adults that spawn in natural streams (McIntyre 1983, Leider et al. 1986b). A popular practice in supplementation efforts is the release of unfed fry of hatchery origin. This practice decreases rearing costs at hatcheries and provides a means for public involvement in fishery programs through the use of low maintenance, streamside incubators. The success of these supplementation efforts are often measured by the number of adult spawners returning to release streams. Since the unfed hatchery fry released in these programs usually are not marked for identification upon return, managers do not have the opportunity to evaluate the impact these releases may have on the wild segment of a population. It remains unknown whether the hatchery fry deter or expedite the decline of wild steelhead populations in recipient streams.

Theoretically, if a hatchery stock is genetically and behaviorally similar to the supplemented wild stock, the potential for adverse influence on the wild population is reduced. Significant differences between hatchery and wild salmonid stocks from the same or proximate drainage basins have been noted in survival (Reisenbichler and McIntyre

1977, Kreuger and Menzel 1979, Leider et al. 1986b), life history strategies (Peterson 1978, Hiss et al. 1986, Leider et al. 1986a), behavior (Symon 1969, Bieber 1977, Sosiak et al. 1979, Dickson and MacCrimmon 1982, Bachman 1984), and genetic frequencies (Kreuger and Menzel 1979, Allendorf and Phelps 1980, Stahl 1983, Reisenbichler and Phelps 1989). Although some hatcheries have begun to reduce the differences between their stocks and wild stocks by incorporating wild adults in their broodstock, selection (intentional or not) of early returning hatchery adults for broodstock continues to be practiced. It has resulted in the development of hatchery stocks that emerge as swim-up (unfed, newly emerged) fry earlier than wild progeny in the same or proximate watersheds (Leider et al. 1986a). When used in supplementation programs, the earlier emergent hatchery fry may have a competitive advantage conferred by larger size and early arrival at rearing sites and could actively displace wild juveniles from quality rearing habitat (Chapman 1962, Solazzi et al. 1983, Nickelson et al. 1986). The advantage of larger size is enhanced when hatchery juveniles are released as unfed fry since they have not accrued potentially maladaptive behaviors as a result of exposure to the hatchery environment that could weaken their adaptability to natural stream conditions (Jenkins 1971, Sosiak et al. 1979).

Investigators have reported negative influences on the densities and growth of wild fry supplemented with earlier emerging, and subsequently larger, hatchery fry. Nickelson et al. (1986) reported significantly lower average densities among newly emerged wild coho salmon (Oncorhynchus kisutch) fry in streams stocked with slightly larger hatchery fry than in unstocked streams. Chandler and Bjornn (1988) observed lower densities and depressed growth among later emerging steelhead fry when in the presence of earlier emerging steelhead fry than in their absence.

Other investigators have reported the importance of social status in the survival of juvenile salmonids. Among social, territorial animals, such as juvenile steelhead, the hierarchial position held by an individual is intricately linked to its potential for survival.

Juveniles that obtain the more dominant positions within a localized population have shown superior growth rates (Brown 1946, Chapman 1962, Yamagishi 1962, Carline and Hall 1973, Li and Brocksen 1977, Abbott and Dill 1989), higher levels of aggression (Keenleyside and Yamamoto 1962, Abbott et al. 1985, Abbott and Dill 1989), and relatively greater fitness (Ejike and Schreck 1980). Dominance among juvenile salmonids is usually positively correlated with size and/or prior residence (Stinger and Hoar 1955, Kalleberg 1958, Chapman 1962, Mason 1966, Carline 1968, Jenkins 1969, Noakes 1980, Jobling and Wandsvik 1983).

Since juvenile steelhead are socially oriented animals that form relatively stable linear social dominance hierarchies early in their life history, they are potential candidates to be strongly influenced by size differences that occur between wild fry and earlier emerging hatchery fry used in supplementation programs. In response to the increasing use of unfed hatchery fry in supplementation programs, I conducted a study to identify the impacts that these programs could have on the social structure, distribution, and growth of local wild steelhead populations. The objectives of the study were to determine the influence of earlier emerging hatchery fry on the emigration, density, growth, spacial distribution, and social structure and activities of wild steelhead fry. The study focussed on the first 8 weeks of life following emergence when dispersal is high and social dominance hierarchies and territories are being established.

CHAPTER II

EFFECTS OF SIZE AND PRIOR RESIDENCE OF EARLY EMERGING HATCHERY STEELHEAD FRY ON THE DISPERSAL, DISTRIBUTION, AND GROWTH OF WILD STEELHEAD FRY IN LABORATORY STREAM CHANNELS

ABSTRACT

Emigration, density, spacing, growth, and habitat use among steelhead fry, Oncorhynchus mykiss, of hatchery and wild origins were observed in laboratory stream channels during June through August of 1986 and 1987. Fry from both origins received 2 treatments: living alone (allopatry) and living together (sympatry). Hatchery fry emerged 7-10 d prior to wild fry and remained larger in size during the 8 weeks of study both years. All fry groups had similar emigration rates, lengths and weights upon emergence, distances to their nearest neighbor, growth rates, low preference for gravel and fines and run areas, and depths of focal points. Significant differences of comparison tests ($P < .05$ both years) were: 1) in allopatry, wild fry maintained larger densities than hatchery fry, 2) in sympatry, hatchery fry had a greater tendency to establish stable focal points more readily, defend larger areas, have better condition, prefer pools with overhead cover for location of focal points, and reach stable densities more quickly than wild fry, 3) fewer hatchery fry maintained nomadic positions than wild fry in both treatments, and 4) hatchery fry maintained longer length than wild fry through the duration of the study period each year. Although not significant at the 0.05 level both years, potential differences were: 1) wild fry in sympatry had lower realized densities, maintained smaller focal areas, and adopted a nomadic existence more frequently than wild fry in allopatry, 2) wild fry in sympatry had poorer condition than all other fry, and 3) all fry expressed a high preference for pools with overhead cover and low preference for gravels and fines and run areas for establishment of focal points. Larger size and prior residence gave hatchery fry in the sympatric sections a competitive advantage over the wild fry. Such an advantage in natural

streams could allow hatchery fry to displace wild fry from quality rearing habitat, thereby lowering the potential for survival among the wild fry. Subsequently, it is important for managers to consider the timing of emergence and subsequent size of wild steelhead fry that reside in prospective recipient streams when planning supplementation projects that use unfed hatchery fry.

INTRODUCTION

Supplementation (the stocking of presmolts or fry) of wild steelhead (Oncorhynchus mykiss) stocks with steelhead juveniles of hatchery origin has been an integral part of fishery management since the early 1900's (Leider et al. 1986b). The intent of supplementation is to stimulate smolt production among depressed wild anadromous stocks and ultimately increase the number of returning adults that spawn in natural streams (McIntyre 1983). Wild populations often have not responded as intended. Such efforts have elicited declines or no change in the number of wild adults (Peterson 1978, Smith et al. 1985, Nickelson et al. 1986, Lichatowich and McIntyre 1987), no increase in the number of smolt-sized migrants (Bjornn 1978), and declines in densities of wild juveniles (Nickelson et al. 1986).

The negative responses of wild stocks to enhancement programs have stimulated concern about the adverse influences that supplementation may have on the wild segment of populations. Investigators have reported significant differences between hatchery and wild salmonid stocks from the same or proximate drainage basins in survival (Reisenbichler and McIntyre 1977, Krueger and Menzel 1979, Leider et al. 1986b), life history strategies (Peterson 1978, Hiss et al. 1986, Leider et al. 1986a), behavior (Symon 1969, Bieber 1977, Sosiak et al. 1979, Dickson and MacCrimmon 1982, Bachman 1984), and genetic frequencies (Kreuger and Menzel 1979, Allendorf and Phelps 1980, Stahl 1983, Reisenbichler and Phelps 1989). Theoretically, if a hatchery stock is genetically and behaviorally similar to the supplemented wild stock, the potential for adverse influences on the wild population is reduced.

Some hatcheries have recently begun to reduce the differences between their stocks and wild stocks by incorporating wild adults in their broodstock. Unfortunately, many hatcheries continue to select (intentionally or not) for early spawners as broodstock. This practice ensures that egg quotas for the hatchery are likely to be filled. It has resulted, however, in the development of hatchery stocks that emerge as fry earlier than wild progeny in the same or proximate watersheds

(Leider et al. 1986a). When used in supplementation programs, the earlier emergent hatchery fry may have a competitive advantage conferred by larger size and first arrival to rearing areas and may actively displace wild juveniles from quality rearing habitat (Chapman 1962, Solazzi et al. 1983, Nickelson et al. 1986). The advantage of larger size is enhanced when hatchery juveniles are released as unfed fry; they then have not accrued potentially maladaptive behaviors as a result of exposure to the hatchery environment that could weaken their adaptability to natural stream conditions (Jenkins 1971, Sosiak et al. 1979).

The use of unfed fry in supplementation programs continues to gain popularity. It releases hatcheries from the economic burdens of rearing juveniles to fingerling or smolt stages and allows volunteers to participate in supplementation programs through the use of low-maintenance streamside incubators. In response to the increasing use of unfed hatchery fry in supplementation efforts, I conducted a study to identify the effects that could occur on the dispersal, spatial distribution, and growth of coexisting hatchery and wild steelhead fry when hatchery fry have the competitive advantage of larger size and prior residence. Similar studies have been conducted using only hatchery fry (Chandler and Bjornn 1989) and fry of 2 species (Allee 1974). In both these studies, fry were placed into experimental channels several days after emergence. In this study, I used fry of both hatchery and wild origins to address specific supplementation concerns involving the introduction of unfed hatchery fry into streams containing wild populations. To reduce potential alterations in behavior induced by handling and to more closely mimic supplementation efforts using streamside incubators, fry in this study emerged into experimental channels.

METHODS

Conditions of the Experiment

During May-August in 1986 and 1987, laboratory observations were conducted in 2 identical, oval artificial channels, as described by

Reeves et al. (1983). Water temperature was maintained in both channels between 11.1 and 13.3 degrees Celsius by a cooling/heating system and was checked periodically each day. Photoperiod was controlled at a 15 hour daylight/9 hour darkness schedule that simulated sunrise and sunset at the beginning and end of each lighted period. Each channel was divided into 3 study sections, for a total of 6 sections each year, in which habitat types (pools and runs), overhead cover, and substrate types were similarly arranged (Figure 1). Each study section measured 2.1 m x 0.76 m. The 2 pool areas in each section averaged between 25.6-31.1 cm in depth and 0.7-3.5 cm/sec in velocity. Two run areas, 1 consisting of the redd and the other located between the 2 pools in each section, average 15-18.2 cm in depth and 5.8-9.7 cm/sec in velocity. Boxes were attached to the downstream divider of each section to allow for voluntary emigration. Food was forced through a perforated pipe in the substrate that spanned the length of each channel. This apparatus allowed food to be distributed equally within each section and simulated emergence and drift of food items. Fry were fed frozen brine shrimp and chironomids twice daily to satiation. Excess food was removed from the surface and section divider screens after each feeding.

Wild and hatchery fish used in the study were identified by biologists of the Oregon Department of Fish and Wildlife. Within this study, "hatchery" fry were defined as progeny from adults that returned to hatchery racks and were artificially spawned. "Wild" fry were progeny from adults produced naturally in streams. Both hatchery and wild fry (fry types) were progeny from winter steelhead within the Santiam River drainage, Oregon. All fry were received as eyed eggs, and all eggs received similar treatment before they were put into test sections. Hatchery adults were spawned 7-10 d before wild adults to ensure that hatchery fry would emerge first. In 1987, half of the wild adults used for broodstock in this study tested positive for the infectious hematopoietic necrosis virus (IHNV). Fertilized eggs from all wild adults were used in the channels since these were the spawn from wild adults available and I could find no information that suggested fry from IHNV positive parents would behave differently from

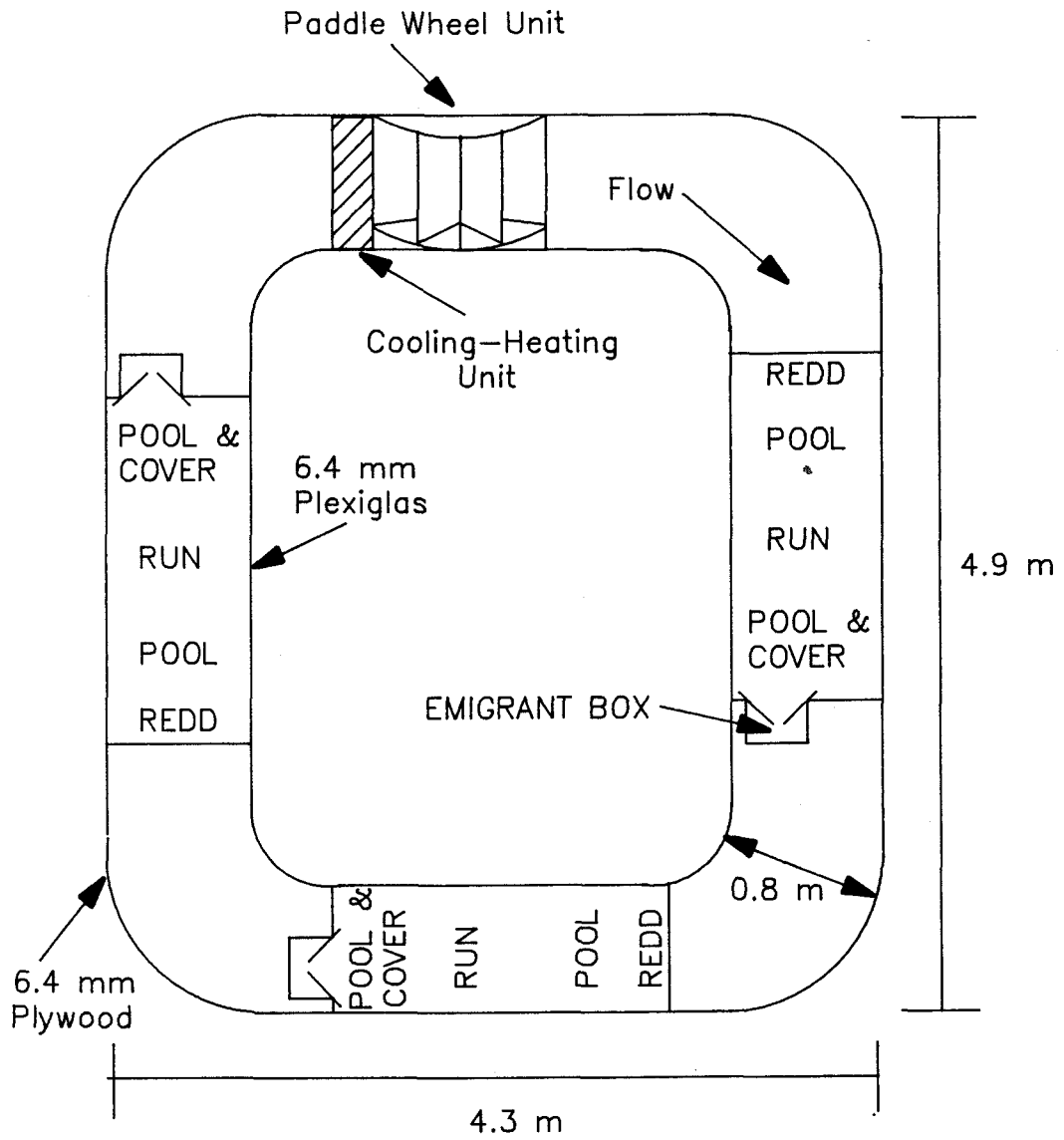


Figure 1. Diagram of laboratory streams: two channels each arranged as above.

fry of IHNV negative parents.

Two treatments were tested on the 2 fry types: hatchery fry and wild fry living alone (allopatry) and hatchery and wild fry living together (sympatry). Since each channel contained 3 study sections, both treatments for both fry types (i.e. hatchery fry in allopatry, wild fry in allopatry, and hatchery and wild fry in sympatry) were represented in each channel both years of the study. This allowed replication of treatments within years for both fry types.

Eyed eggs were contained in Vibert boxes which were placed in an artificial redd adjacent to the upstream divider in each test section. Redds contained 650 eggs each (in sympatric sections, 325 eggs per stock) to ensure full seeding while allowing for potential pre-emergence mortality. Observations began at the onset of emergence and continued daily for 7-8 weeks.

Fry types in sympatric sections were differentiated initially by size, since hatchery fry emerged first and remained slightly larger. Fry in each test section were observed through screened openings in black plastic curtains that shielded the observer from view. Eventually, individual fry could be identified by their coloration, pigmentation, body shape, and location within a section.

Fry were removed daily and counted from emigrant boxes. A subsample of emigrants of each fry type from each section was measured daily for length and weight. All fry remaining at the end of the study were also measured. Densities within sections were recorded daily.

Maps were drawn to scale of pool and run areas in each section, showing substrate and overhead cover placement (Figure 2). These maps were used to record the location of fry to gain information on habitat use, distance to nearest neighbor, and size of focal area. "Focal area" was defined as the area that contained the focal point of a fry (the point location where a fry usually rested and returned to after interactions or feedings) and regularly patrolled. Focal area was used in lieu of "territory" because the boundaries of the focal area were not always defended by overt aggression. Each focal point was marked with a colored marble to aid in noting any changes in point location of a fry

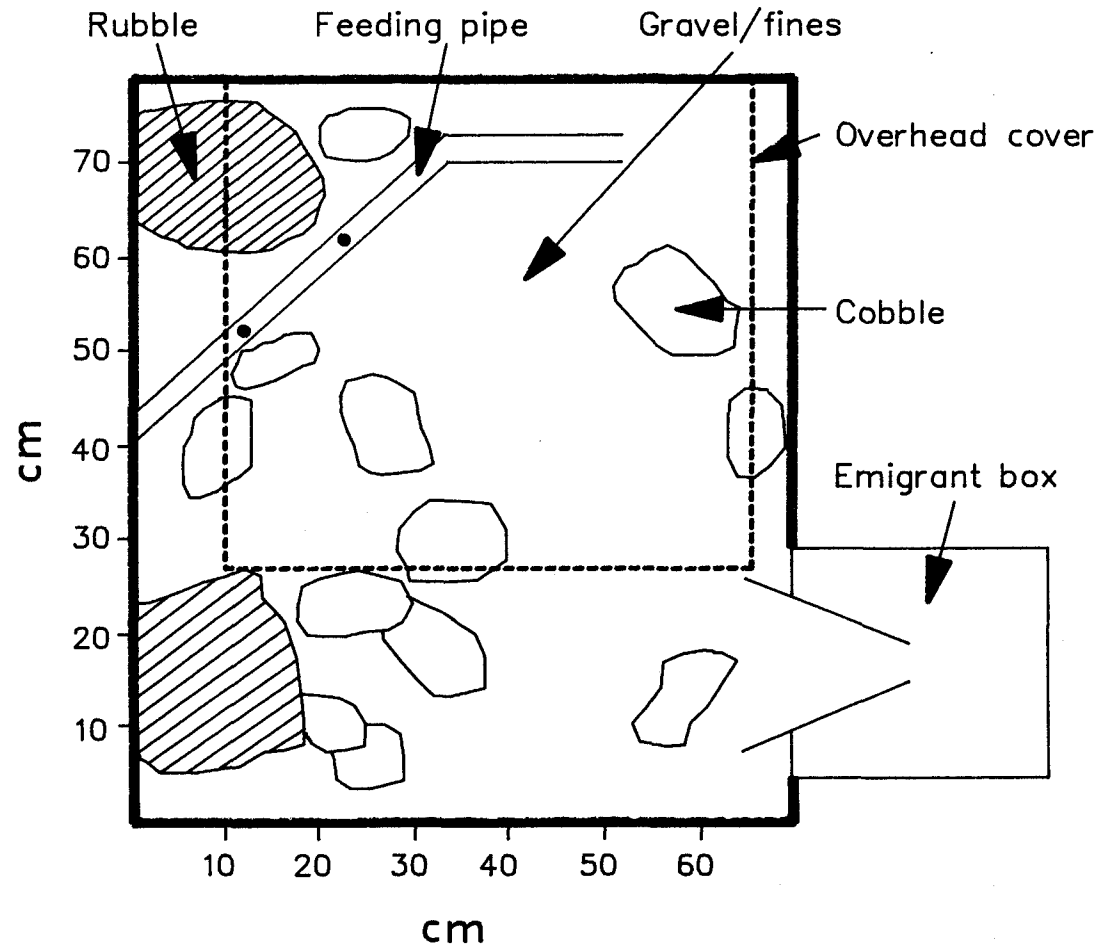


Figure 2. Example of map drawn to scale of a back pool in a lab section showing overhead cover, substrate type, feeding pipe, and emigrant box. Direction of flow is left to right.

through time. Maps of focal areas were revised weekly following the initial mapping session during the fourth and fifth weeks following emergence in each section by both fry types.

Treatment of Data

Analyses were made using data averaged for individual days or weeks. Weeks were counted from the onset of emergence (week 1) in each section for each fry type. Tests for similarities between treatments for each fry type (allopatry vs. sympatry) and between fry types (hatchery vs. wild) were made among fry of the same age (time from start of emergence). Observations for replicate sections within years were often pooled when preliminary tests on data revealed that replicate sections within years were similar. Although care was taken to keep environmental variables similar among sections in both years of study, I found that variation between years was greater than within years for most data. Therefore, I usually tested data from 1986 and 1987 separately and compared results for similar trends. Results from comparison tests are reported as "significant" when probability values were at the .05 level of confidence in both years; tests resulting in $P < .05$ in 1 year and $P < .1$ in the other are reported as "potential" differences or trends. Averages were gained by first summing measurements or calculations gained on individual fry within a given treatment for a specific time period.

Daily emigration rates were calculated as:

$$\text{Em.rate} = \text{emigrants}_{ij} / (\text{emigrants} + \text{fry in section})_{ij}$$

for each day (i) in each section (j). Wilcoxon Signed Ranks tests were used to compare emigration rates through time between fry types and treatments for each fry type when I found that emigration rates were not normally distributed and transformations did not normalize data. In these tests, data were paired by day from the onset of emergence for each fry type in both treatments. Average emigration rates for fry in both treatments or for fry types were calculated by averaging daily rates for replicate sections per year of observation.

"Realized densities" were defined as the densities at which emergence had ceased and emigration had decreased to zero for at least 3 consecutive days. These densities were relatively stable and assumed to represent the carrying capacity of a section. For statistical tests, realized densities in each replicate section in both years were treated as separate data points. Student's t tests were used to compare densities between fry types and treatments for each fry type.

Growth information is reported as average lengths, weights, and Fulton's condition factor (Q), and overall instantaneous growth rates (G) for each fry type and treatment in both years of observation. Only lengths and weights recorded for emigrant fry during week 1 and fry at the end of the study were used in analyses. During the interim, fry were not removed from sections for measuring since such disturbance could influence observations on behavior. Also, emigrant fry removed after week 1 were not used in analyses because I was uncertain if they were representative of all fry remaining in a section once potential differential feeding had occurred and social hierarchies had been established. An instantaneous growth rate (G) was calculated for each fry type and treatment in each study year as:

$$G = \ln Wx_e - \ln Wx_b / t_e - t_b$$

where Wx = the average weight of a fry type in a treatment (2 sections per year) during week 1 (b) and at the end of the study (e), t_b = week 1, and t_e = the end of the study in weeks from the onset of emergence. Fulton's condition factor (Q) was calculated as a means of comparing overall "robustness" of fry in each treatment (Ricker 1975). Q was calculated for each fry emigrating during week 1 and at the end of the study as:

$$Q = W \times 10^5 / L^3$$

where W = live weight (g) and L = fork length (mm).

Spatial distribution was compared between both fry types in each treatment for both years of study. It is reported as the weekly average distance of a fry to its nearest neighbor, weekly average size of its focal area, and overall average use of habitat variables. Distances to the nearest neighbor were measured from focal point of the fry being

observed (or the current position of a fry that did not have a defined focal point) to the focal point of the next closest fry. Focal areas for each fry were mapped weekly according to methods described by McNicol and Noakes (1981) and actual area regularly patrolled by each fry. In this method, points of interactions between a focal fry (a fry under observation) and other fry and areas repeatedly patrolled are recorded on a map. This area designates the "territory" or focal area of the fry under observation. Focal areas were digitized by computer to determine the size of each. Comparisons of focal areas were made between fry types and treatments for each fry type using Student's *t* tests.

Use of habitat was determined from focal point information recorded weekly on section maps during the second week following emergence until the end of the study in both years. Substrate types included rubble (15 - 30.5 cm), cobble (7.5 - 15 cm), and gravel and fines (<7.5 cm). Habitat types were represented by pools with overhead cover, pools without overhead cover, and runs. Runs with overhead cover were too small in area (<5% of section total area) to include as a separate habitat type. Use per week of each habitat variable for fry types in each section was calculated as the number of fry maintaining focal points within or over a habitat characteristic divided by the total number of fry in the section. Availability of a habitat variable was calculated as the total area occupied by the variable divided by the total area in the section. Within sympatric sections, availability of a habitat variable for each fry type was in proportion to the total density in the section represented by each fry type. To determine preference for each habitat variable, I used a ranking technique and subsequent statistical tests proposed by Johnson (1980). For both years, tests for preference were run on 2 groups of weekly observations: weeks 2-4 of the study period were grouped to represent information on habitat use before focal points and areas were firmly established in each study section while weeks 5-8 represented habitat use after the establishment of relatively stable focal points and areas.

RESULTS

Dispersal

Emigration

During both years of observation, emigration began immediately upon the onset of emergence and peaked within 10 d in all study sections. The number of fry emigrating declined to zero for 3 consecutive days (referred to as realized densities) in all sections by d 35 in 1986 and d 27 in 1987 (Table 1). Days to peak emigration and then to stable numbers did not differ significantly among treatments or fry types with 1 exception: in sympatry, hatchery fry reached stable numbers in significantly fewer days ($P < 0.01$ both years) than did the wild fry.

Hatchery and wild fry appeared to emigrate at similar rates through time in both treatments (Figure 3). Tests on emigration rates revealed no differences in both years between hatchery and wild fry in allopatry and between treatments for hatchery fry. In 1986, emigration rates of wild fry in sympatry were significantly faster ($P < 0.01$) than those of wild fry in allopatry. Tests were not significant for emigration rates between treatments for wild fry in 1987.

In summary: 1) emigration rates were similar between newly emerged hatchery and wild steelhead fry, and 2) when in sympatry, hatchery fry reached stable numbers faster than wild fry.

Both time (relative to emergence) and density strongly influenced emigration rates. Spearman rank correlation tests indicated that time had a strong inverse correlation with emigration rates whereas density showed a strong positive correlation in all test sections in both years. All tests were significant ($P < .001$) except for 1 test comparing the density of hatchery fry to the emigration rates of wild fry in 1 sympatric section in 1987 (Table 2). As densities decreased, so did emigration rates in all sections for both fry types. The strength of correlations between densities and emigration rates of fry types in different treatments varied between years and between sections within years. In sympatric sections, correlations were stronger between hatchery fry densities and their emigration rates than between wild fry

Table 1. Days to peak emigration and stable densities, and realized densities for test sections in 1986 and 1987. W = wild fry; H = hatchery fry; I = replicate 1 and II = replicate 2 within each year; numbers in parentheses refer to number of days or densities of specific fry types in sympatry.

| | Allopatric Populations | | | | Sympatric Populations | |
|---------------------------|------------------------|------|----------|------|-----------------------|---------------|
| | Hatchery fry | | Wild fry | | 1986 | 1987 |
| | 1986 | 1987 | 1986 | 1987 | | |
| Days to peak emigration: | | | | | | |
| I | 7 | 8 | 6 | 10 | W(6) = H(6) | W(8) = H(8) |
| II | 6 | 7 | 8 | 6 | W(7) > H(4) | W(6) < H(9) |
| Days to stable densities: | | | | | | |
| I | 18 | 21 | 35 | 24 | W(23) > H(22) | W(22) > H(20) |
| II | 17 | 26 | 35 | 22 | W(24) > H(20) | W(23) > H(19) |
| Realized densities: | | | | | | |
| Actual in I | 7 | 8 | 31 | 15 | W(17) > H(10) | W(8) > H(3) |
| Actual in II | 10 | 12 | 20 | 19 | W(17) > H(13) | W(9) > H(6) |
| Fry/ m ² in I | 5 | 5 | 21 | 10 | W(11) > H(7) | W(5) > H(2) |
| Fry/ m ² in II | 7 | 8 | 14 | 12 | W(11) > H(8) | W(6) > H(4) |

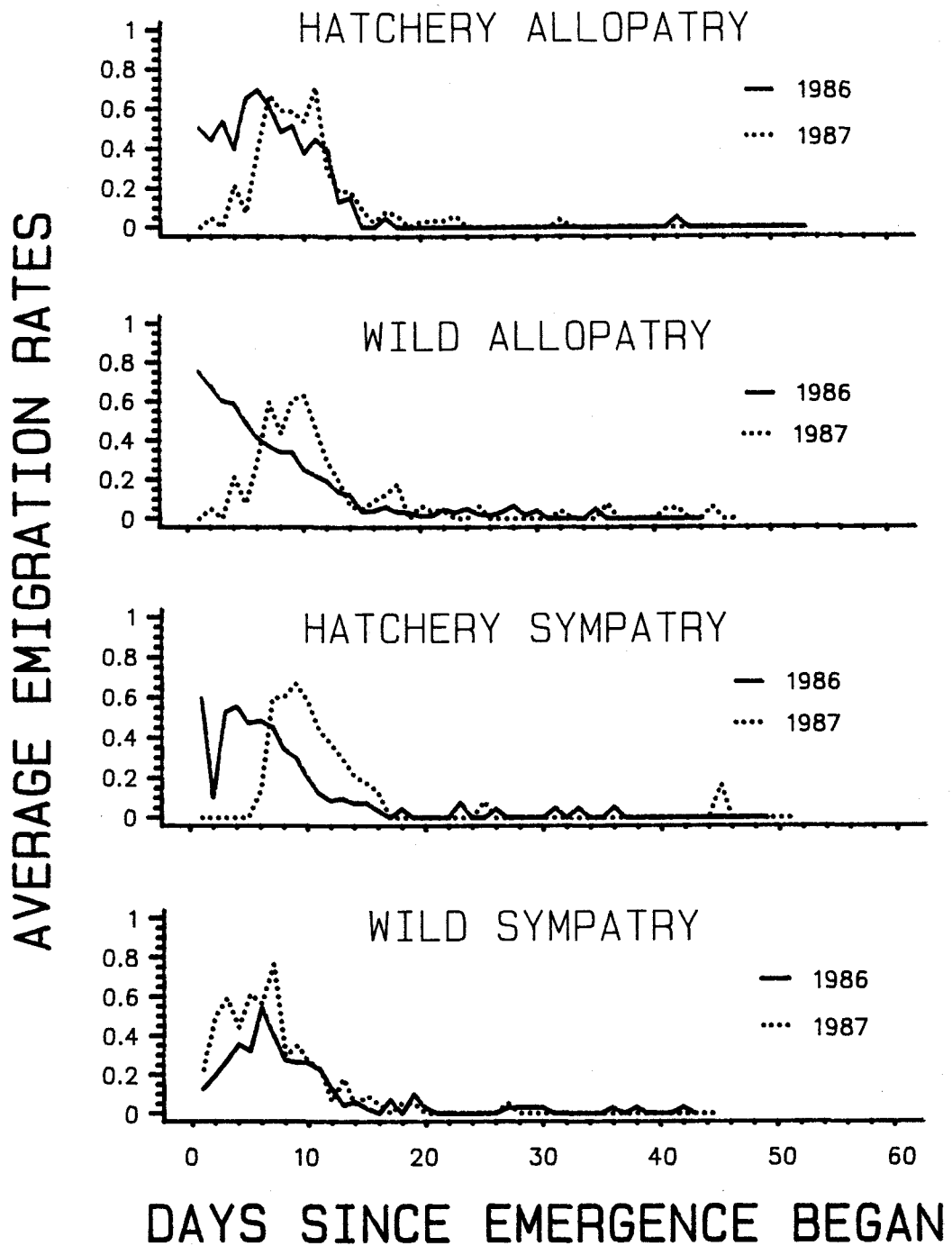


Figure 3. Average emigration rates through time for wild and hatchery fry in allopatry and sympatry, 1986 and 1987.

Table 2. Spearman rank correlations showing effects of time and density on emigration rates for each test section, 1986 and 1987. In sympatry, H = effects of hatchery fry density and W = effects of wild fry density; I = replicate 1 and II = replicate 2 within each year.

| Influence on emigration rate of: | Coefficient ^a | | | |
|--|--------------------------|-------|--------------------|--------|
| | Density | | Time | |
| | 1986 | 1987 | 1986 | 1987 |
| Allopatry: | | | | |
| Hatchery fry | | | | |
| I | 0.513 | 0.716 | -0.761 | -0.586 |
| II | 0.659 | 0.715 | -0.729 | -0.751 |
| Wild fry | | | | |
| I | 0.727 | 0.588 | -0.854 | -0.353 |
| II | 0.501 | 0.816 | -0.881 | -0.748 |
| Sympatry: | | | | |
| | H | W | H | W |
| Hatchery fry | | | | |
| I | 0.656 | 0.602 | 0.655 | 0.581 |
| II | 0.805 | 0.657 | 0.645 | 0.552 |
| Wild fry | | | | |
| I | 0.706 | 0.719 | 0.658 | 0.688 |
| II | 0.557 | 0.687 | 0.243 ^b | 0.826 |

^a +1.00 = perfect positive correlation; -1.00 = perfect negative correlation; P<.01 except where noted.

^b P > 0.1

densities and the emigration rates of hatchery fry. Similarly, emigration rates of wild fry more strongly correlated to the densities of wild fry than to the densities of hatchery fry.

Density

Survival to emergence from artificial redds was high, ranging from 91 to 100% in test sections in both years. The period of highest density in each section coincided with peak emigration and decreased precipitously once emergence ceased. Densities stabilized by the end of the third week after the onset of emergence for both fry types in each test section (Table 1). Using realized densities as fry/m², the only significant difference in densities occurred between hatchery and wild fry in allopatry; wild fry had larger densities than hatchery fry ($P < .02$ both years). Although there was no discernible difference in pooled realized densities between allopatric and sympatric sections for either wild fry ($P < .08$) or hatchery fry ($P < .55$), wild fry in sympatric sections appeared to hold at lower densities than wild fry in allopatry (Table 1).

Results from data on densities suggested that (1) carrying capacity in allopatric sections was higher for wild fry than for hatchery fry, (2) there was no significant difference in realized densities for either hatchery or wild fry when living alone or together, and (3) although not significant, wild fry held at lower densities when living sympatrically with hatchery fry than when living alone.

Spatial Distribution

Spacing

During the first week after emergence, emigration was high and fry were in small, loose groups. By the third week, the hatchery fry began to establish focal points that were stable in respect to the frequency of a fry at the same location, and many fry regularly patrolled space around those points (focal areas). Focal areas developed first and most dramatically among hatchery fry in allopatry. The wild fry did not show this behavior until early in the fourth week after emergence.

By the fifth week, focal points and areas had been established by most fry in all test sections. Fry that did not establish stable focal points ("nomads") remained close to the bottom or within substrate interstices and moved often. These fry either emigrated or remained nomads to the end of the study. A few fry that maintained small focal areas with poorly defined boundaries (i.e. boundaries were not actively defended but regularly patrolled) in each section switched to nomadic status as time progressed. Comparisons of the proportion of nomadic fry in each section during the fifth week (when densities had stabilized and focal points and areas were well established in all sections) revealed that hatchery fry in sympatry had significantly fewer nomadic fry than wild fry in both treatments ($P < .01$ in both years for all comparisons) (Table 3). There was a potential tendency among wild fry in sympatry to have fewer nomadic fry than wild fry in allopatry.

Through time, variances of average distances to nearest neighbor for both fry types in each treatment ranged widely about their means. Since variance between years was greater than within years, I approach interpretation of results with caution. Generally, there was no discernible difference in distances between fry types or between treatments for each fry type (Figure 4). Although tests with 1986 data suggested that hatchery fry in allopatry maintained significantly greater distances to their nearest neighbors through time than did any other fry, results were not significant in 1987.

Consistent in both years of the study, hatchery fry, regardless of treatment, maintained significantly larger focal areas than wild fry in sympatry ($P < .03$ for all tests in both years) (Figure 5). Although tests on data from 1986 revealed that hatchery fry in both treatments maintained significantly larger focal areas than wild fry in allopatry ($P < .01$ for hatchery fry in both treatments), no discernible differences were found in 1987. In 1987, wild fry in sympatry maintained significantly smaller focal areas than wild fry in allopatry ($P < .03$); average size of focal areas between treatments for wild fry were not significant in 1986 ($P < .1$). It is difficult to explain the differences observed between years. Realized densities among wild fry in allopatric

Table 3. The number and proportion of total density of nomadic fry in each test section at the beginning of the fifth week following emergence when densities had stabilized and focal points and areas were established in each section, 1986 and 1987. I is replicate 1 and II is replicate 2 in each year of study.

| Fry type, treatment, and section | 1986 | | | 1987 | | |
|---|---------|--------|-------------------|---------|--------|-------------------|
| | Density | Nomads | Percent nomads | Density | Nomads | Percent nomads |
| Hatchery in Allopatry | | | | | | |
| I | 7 | 1 | 14.3 | 7 | 3 | 42.9 |
| II | 9 | 1 | 11.1 | 11 | 4 | 36.4 |
| Wild in Allopatry | | | | | | |
| I | 29 | 10 | 34.5 | 12 | 6 | 50.0 |
| II | 17 | 6 | 35.3 | 14 | 5 | 35.7 |
| Hatchery in Sympatry | | | | | | |
| I | 9 | 0 | 0 | 3 | 0 | 0 |
| II | 9 | 0 | 0 | 5 | 1 | 20.0 |
| Wild in Sympatry | | | | | | |
| I | 15 | 6 | 40.0 | 8 | 5 | 62.5 |
| II | 14 | 4 | 28.6 | 8 | 6 | 75.0 |

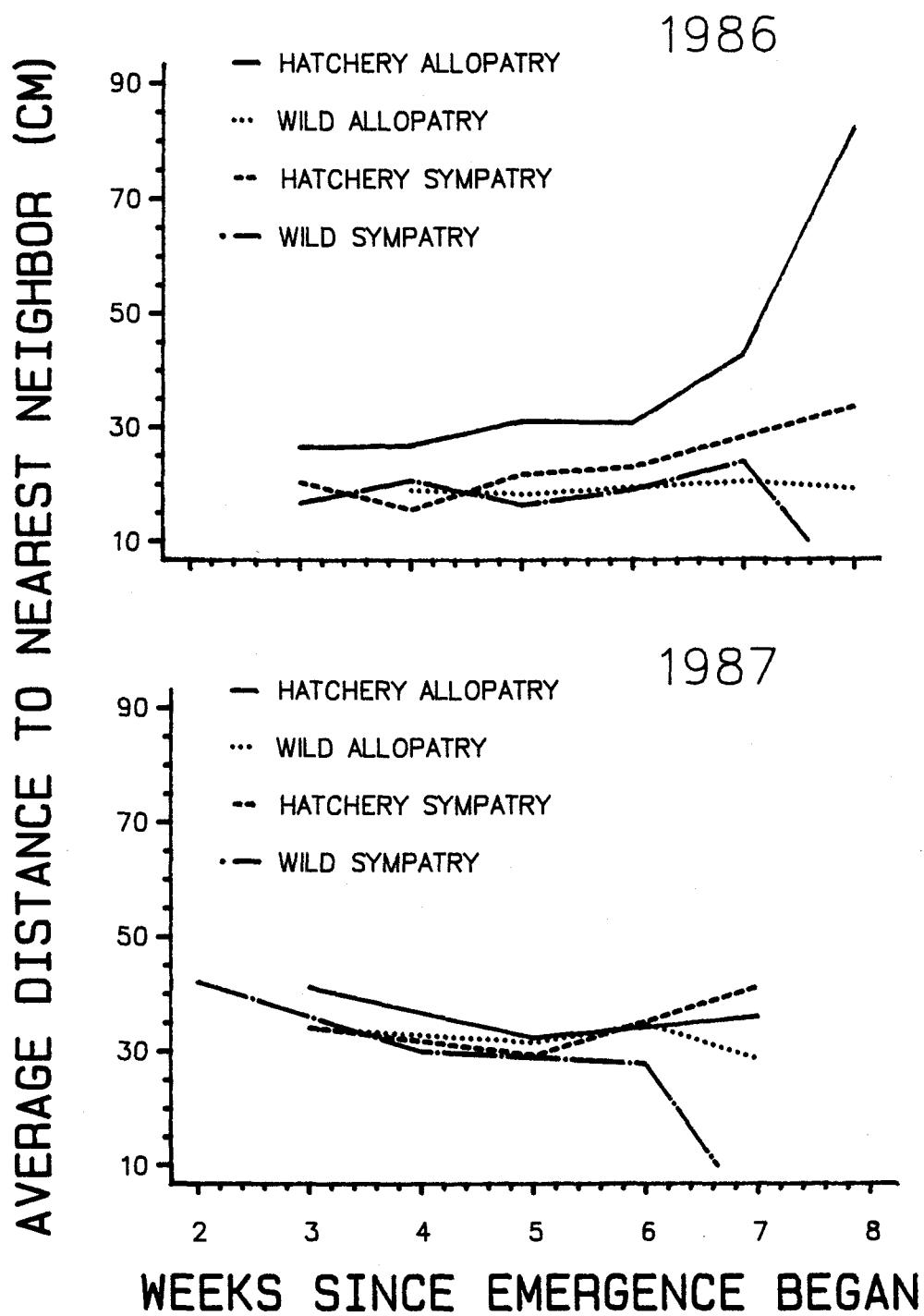


Figure 4. Average distances to nearest neighbor through time for both fry types in each treatment, 1986 and 1987.

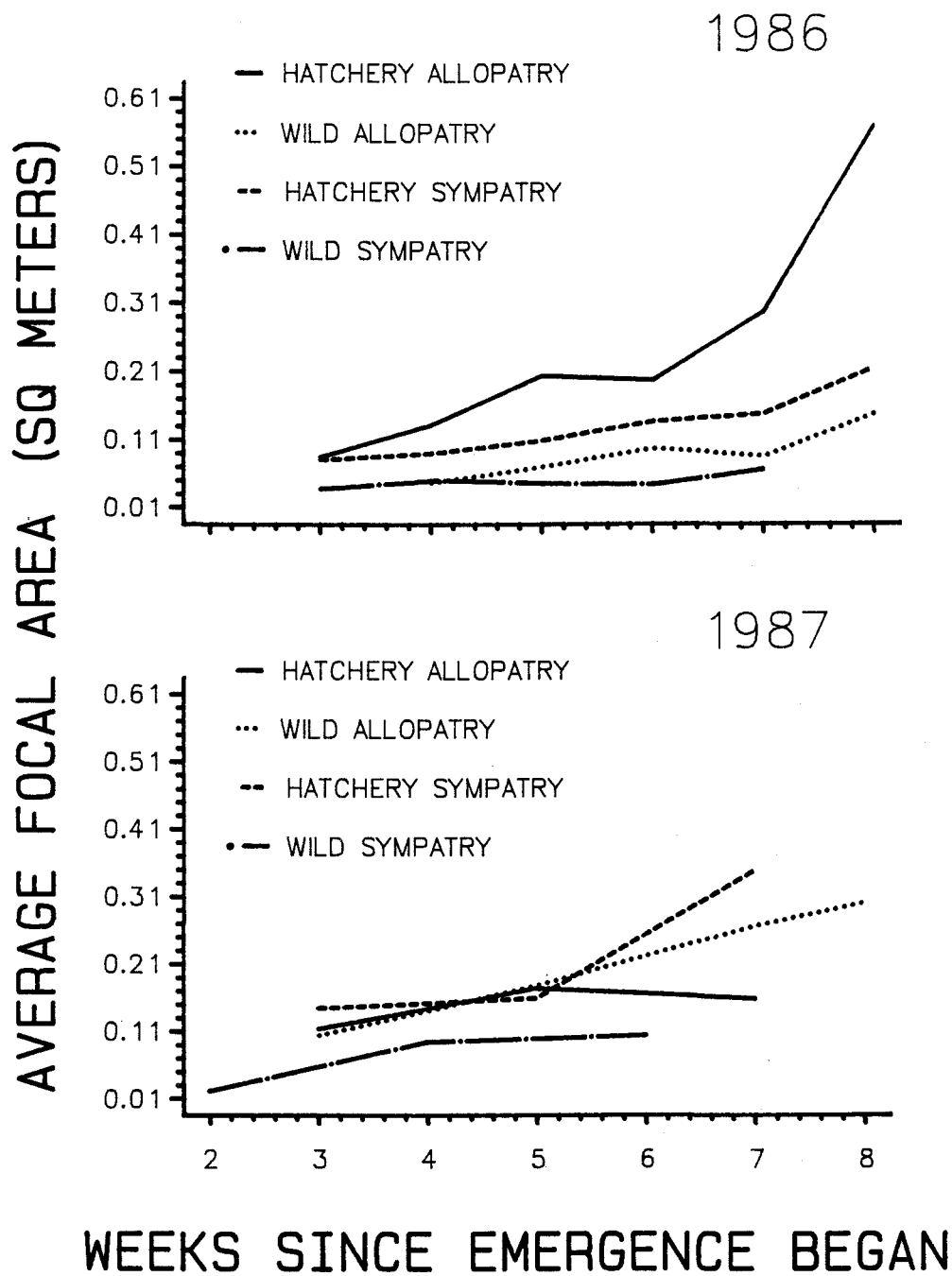


Figure 5. Average size of focal areas through time for fry types in each treatment, 1986 and 1987.

sections were lower and more similar to the densities of hatchery in 1987 than they were in 1986. The availability of more space per fry among wild fry in allopatry in 1987 may have influenced wild fry to maintain larger focal areas. This speculation, however, does not help to explain the differences in results recorded between years for wild fry in the 2 treatments. Although realized densities among wild fry in sympatry decreased in 1987 from those recorded in 1986, the average size of focal areas did not increase substantially in size over those recorded in 1986.

In summary, results on spacing revealed: (1) hatchery fry established focal points and areas more readily after emergence than did wild fry, (2) hatchery and wild fry maintained similar distances to their nearest neighbors regardless of treatment, (3) hatchery fry in sympatry maintained significantly fewer nomadic fry than wild fry in both treatments, (4) wild fry in sympatry generally maintained fewer nomadic fry than did wild fry in allopatry, and (5) although not significant at the .05 level in 1986 for wild fry in the 2 treatments, there was a tendency among wild fry in sympatry to maintain smaller focal areas than any other fry group.

Use of Habitat

Information was gathered on use of depth, substrate, and habitat types. There was no difference in use of depth between fry types or treatments. Fry remained near the surface immediately upon emergence but were not observed at this depth after the first 10 d following emergence. In ensuing weeks, fry used mid-water and near bottom depths interchangeably.

The relative preference of substrate types was similar among fry (Table 4). Gravels and fines were least preferred by all fry both before and after focal points and areas were established in all sections. However, only wild fry in allopatry used gravels and fines significantly less often than the other substrate types during weeks 5 through 8. Through time, hatchery fry in allopatry preferred rubble the most while all other fry showed the highest preference for cobble. Cobble was preferred significantly more often than any other substrate

Table 4. Relative preference and results from comparison tests among substrate types (RUB=rubble, COB=cobble, and GRF=gravels and fines) for each fry type in both treatments. Averages are given for weeks 1-4 and 5-8.

| Fry type, treatment, and week | Relative Preference | | | Results of H_0^a | Differences ^b |
|-------------------------------------|---------------------|------|-------|----------------------------|---------------------------|
| | RUB | COB | GRF | | |
| HATCHERY in ALLOPATRY: | | | | | |
| Weeks 1-4 | most | | least | do not reject $P > .05$ | <u>RUB</u> <u>COB</u> GRF |
| Weeks 5-8 | most | | least | reject $P < .01$ | <u>RUB</u> <u>COB</u> GRF |
| WILD in ALLOPATRY: | | | | | |
| Weeks 1-4 | | most | least | do not reject $P > .05$ | <u>RUB</u> <u>COB</u> GRF |
| Weeks 5-8 | | most | least | reject $P < .01$ | <u>RUB</u> <u>COB</u> GRF |
| HATCHERY in SYMPATRY: | | | | | |
| Weeks 1-4 | | most | least | reject $P < .05$ | COB <u>RUB</u> GRF |
| Weeks 5-8 | | most | least | reject $P < .01$ | COB <u>RUB</u> GRF |
| WILD in SYMPATRY: | | | | | |
| Weeks 1-4 | | most | least | do not reject $P > .05$ | <u>COB</u> <u>RUB</u> GRF |
| Weeks 5-8 | | most | least | reject $P < .01$ | COB <u>RUB</u> GRF |

^a Tests were run on the null hypothesis: all substrate types are equally preferred. Results were the same in both years.

^b Substrate types underscored by the same line are not significantly different ($P > .05$); lack of a common underscore indicates substrate types differ significantly ($P < .05$) (Johnson 1980).

type by both fry types in sympatry during weeks 5 through 8. On the other hand, there were no significant differences in preference for rubble and cobble among hatchery and wild fry in allopatry.

Relative preference for pools with overhead cover was similar for all fry; it was the most preferred habitat type both before and after the establishment of relatively stable focal points and areas (Table 5). In all weeks of the study, hatchery fry in both treatments preferred pools with overhead cover significantly more than any other habitat type. Among wild fry in sympatry, however, differences in preference were not significant between covered and uncovered pools nor between uncovered pools and run areas. Although wild fry in allopatry showed a significant preference for pools with overhead cover before focal points and areas were established, differences in preference were not significant among habitat types for these fry after the establishment of relatively stable focal points. Run areas were the least preferred habitat type among all fry after focal points and areas were established.

In summary, results from observations on habitat use suggest: 1) hatchery and wild fry maintained focal points at similar depths, 2) both fry types in both treatments showed the least preference for gravel and fines and run areas, 3) pools with overhead cover were preferred most by all fry and this preference was significant among hatchery fry in both treatments, and 4) once focal points and areas were established, cobble was the most preferred substrate type for wild fry and hatchery fry in sympatry while rubble was most preferred by hatchery fry in allopatry.

Growth

Hatchery and wild fry emerged at similar average lengths and weights in both years. The size advantage obtained by earlier emergence among hatchery fry was retained to the end of the study in both years (Table 6). At the end of the study, tests revealed no significant difference in average lengths, weights, and relative condition (Q), and overall instantaneous growth rates (G) between treatments for each fry

Table 5. Relative preference and results from comparison tests among habitat types (COVP=pool with overhead cover, NCOVP=pool without overhead cover, and RUN=a run area) for each fry type in both treatments. Averages are given for weeks 1-4 and 5-8.

| Fry type, treatment, and week | <u>Relative Preference</u> | | | Results of H_0^a | Differences ^b | | |
|-------------------------------------|----------------------------|-------|-------|-----------------------------|--------------------------|--------------|------------|
| | COVP | RUN | NCOVP | | | | |
| HATCHERY in ALLOPATRY: | | | | | | | |
| Weeks 1-4 | most | | least | reject P < .01 | COVP | NCOVP | RUN |
| Weeks 5-8 | most | least | | reject P < .01 | COVP | <u>NCOVP</u> | <u>RUN</u> |
| WILD in ALLOPATRY: | | | | | | | |
| Weeks 1-4 | most | | least | reject P < .01 | COVP | <u>NCOVP</u> | <u>RUN</u> |
| Weeks 5-8 | most | least | | do not reject P > .05 | <u>COVP</u> | <u>NCOVP</u> | <u>RUN</u> |
| HATCHERY in SYMPATRY: | | | | | | | |
| Weeks 1-4 | most | least | | reject P < .01 | COVP | <u>NCOVP</u> | <u>RUN</u> |
| Weeks 5-8 | most | least | | reject P < .01 | COVP | <u>NCOVP</u> | <u>RUN</u> |
| WILD in SYMPATRY: | | | | | | | |
| Weeks 1-4 | most | | least | reject P < .05 | <u>COVP</u> | <u>NCOVP</u> | RUN |
| Weeks 5-8 | most | least | | do not reject P > .05 | <u>COVP</u> | <u>NCOVP</u> | <u>RUN</u> |

^a Tests were run on the null hypothesis: all habitat types are equally preferred. Results were the same in both years.

^b Habitat types underscored by the same line are not significantly different ($P > .05$); lack of a common underscore indicates habitat types differ significantly ($P < .05$) (Johnson 1980).

Table 6. Average lengths, weights, and condition factors (Q), and overall instantaneous growth rates (G) for each treatment and fry type in both years using data from the first week following emergence (Week 1) and the end of the study (End) and combining data from replicate sections within years. In parentheses are sample size (n) and standard deviation (s) for averages.

| Fry type, treatment & year | Length (mm) | | Weight (g) | | Q | | G |
|-------------------------------|-------------|------------------|------------|-----------|-----------|-----------|-------|
| | Week 1 | End ^a | Week 1 | End | Week 1 | End | |
| Hatchery in Allopatry | | | | | | | |
| 1986 | 29.6 | 60.7 | 0.19 | 2.54 | 0.72 | 1.14 | 0.051 |
| (n,s) | (30,1.07) | (7,2.29) | (30,0.02) | (7,0.33) | (30,0.08) | (7,0.16) | |
| 1987 | 25.7 | 47.9 | 0.16 | 1.73 | 0.94 | 1.49 | 0.049 |
| (n,s) | (59,1.71) | (18,6.99) | (59,0.03) | (18,0.71) | (59,0.19) | (18,0.10) | |
| Wild in Allopatry | | | | | | | |
| 1986 | 28.9 | 45.8 | 0.16 | 1.13 | 0.67 | 1.13 | 0.045 |
| (n,s) | (20,0.97) | (37,5.39) | (20,0.02) | (37,0.41) | (20,0.07) | (37,0.14) | |
| 1987 | 26.1 | 44.4 | 0.16 | 1.29 | 0.94 | 1.42 | 0.048 |
| (n,s) | (40,1.04) | (24,6.05) | (40,0.01) | (24,0.45) | (40,0.14) | (24,0.14) | |
| Hatchery in Sympatry | | | | | | | |
| 1986 | 30.7 | 58.5 | 0.19 | 2.37 | 0.64 | 1.18 | 0.052 |
| (n,s) | (20,0.93) | (6,3.51) | (20,0.02) | (6,0.45) | (20,0.06) | (6,0.22) | |
| 1987 | 26.1 | 54.4 | 0.16 | 2.41 | 0.94 | 1.48 | 0.054 |
| (n,s) | (30,1.41) | (7,1.72) | (30,0.02) | (7,0.35) | (30,0.19) | (7,0.08) | |
| Wild in Sympatry | | | | | | | |
| 1986 | 29.1 | 47.0 | 0.17 | 1.14 | 0.68 | 1.06 | 0.046 |
| (n,s) | (15,1.10) | (26,4.82) | (15,0.03) | (26,0.37) | (15,0.08) | (26,0.11) | |
| 1987 | 25.4 | 44.9 | 0.17 | 1.27 | 1.04 | 1.37 | 0.049 |
| (n,s) | (52,1.33) | (16,4.36) | (52,0.02) | (16,0.37) | (52,0.22) | (16,0.09) | |

^aEnd = end of study; hatchery fry were in their 8th week since onset of emergence; wild fry were in their 7th week since their emergence began.

type in both years when fry of the same age (weeks since emergence began) were compared. Although not significant in both years, the average condition of wild fry in sympatry appeared to be poorer than the average condition of other fry. At the end of the study, there was a discernible difference between fry types in sympatry; the Q of hatchery fry was significantly greater than that of wild fry (1986: $P < 0.04$; 1987: $P < 0.006$).

In summary, results on growth revealed that: 1) hatchery and wild fry were similar in size and condition upon emergence, 2) hatchery fry maintained larger size due to earlier emergence throughout the study in both years, 3) at the end of the study in both years, hatchery fry in sympatry had significantly greater condition than wild fry in sympatry, and 4) there was a potential for wild fry in sympatry to have poorer condition than other fry groups.

DISCUSSION

Hatchery and wild steelhead fry living separately during the first few weeks after emergence showed striking similarities in emigration, growth, spacing, and habitat use. Upon emergence, they emigrated at similar rates, established relatively stable numbers within equivalent time periods, used comparable space, grew at similar rates, and used many habitat characteristics similarly. The close similarities between hatchery and wild steelhead fry may induce competition for food and space when unfed hatchery fry are released into streams containing wild fry and resources become limited. If hatchery fry emerge a few days before wild fry, they can have a competitive advantage conferred by larger size and first arrival at quality rearing sites. Such an advantage could negatively influence the behavior, distribution, and growth of the local wild population.

It did not appear from this study that the presence of earlier emerging hatchery fry influenced the actual rate of emigration or the time taken to achieve stable numbers among wild fry. When these 2 fry types lived together, however, there was potential for later emerging wild fry to have lower densities and condition, to maintain smaller

focal areas, and to have a larger proportion of nomadic individuals than when no larger hatchery fry were present. There was also potential for hatchery fry to adopt a nomadic existence less frequently than if they lived alone.

Nickelson et al. (1986) reported significantly lower average densities among newly emerged wild fry of coho salmon (Oncorhynchus kisutch) in streams stocked with slightly larger hatchery fry than in unstocked streams. They attributed this decrease to displacement as a result of competition between the 2 fry types. In my study, hatchery fry in allopatry maintained lower densities than wild fry. If hatchery fry can displace later arriving wild fry from quality rearing habitat and hatchery fry maintain lower densities, the overall stream population of juvenile steelhead could be reduced and not increased when hatchery fry are supplemented into streams containing wild fry.

In Idaho, Chandler and Bjornn (1988), who used oval channels similar to those in my study and steelhead fry, also observed lower densities and depressed growth among later emerging fry (late hatchery fry) when in the presence of earlier emerging fry (early hatchery fry) than in their absence. Unlike these authors, I did not observe a smaller percentage of wild fry (late fry) than hatchery fry (early fry) when densities stabilized in sympatric sections. This difference in results between the 2 studies could be attributed to dissimilarities in study design. All fry in the Idaho oval channels were planted in test sections several days after emergence, and their early fry were in channel sections 2 weeks before late fry were introduced. This prior introduction of early fry into Idaho test sections could have influenced the emigration and resulting densities of late fry in sympatric sections. Late fry would have been introduced into test sections after early fry had been given sufficient time to acquire stable densities at carrying capacity and establish a well-developed social structure and fixed focal points and areas in desirable habitats. In my study, all fry emerged in test sections, participated in the development of the social structure, and contributed toward the carrying capacity of study sections.

The presence of earlier emerging, and subsequently larger, hatchery fry could contribute toward lower densities and condition among later emerging wild fry if the hatchery fry occupy quality or preferred habitat that might otherwise be available to wild fry or actively displace wild fry through behavioral interactions. Fausch (1984) suggested that salmonids choose stream positions with respect to food supply, flow, and dominance hierarchy. In his study, the dominant or highest ranking fish maintained the areas with the highest resource levels. Dominant status among salmonids is regularly associated with larger size and often prior residence. This has been reported for juvenile steelhead (Bieber 1977, Abbott et al. 1985), brown trout, Salmo trutta, and rainbow trout (Jenkins 1969), coho salmon (Chapman 1962, Mason 1966, Carline 1968, Nickelson et al. 1986), and brook trout, Salvelinus fontinalis, (Newman 1956, Noakes 1980). Hatchery fry in the sympatric section of this study could have gained dominant status due to their slightly larger size and subsequently maintained positions in areas that provided the most or preferred resources. Wild fry may have been forced into less preferred or resource-poor areas or induced to leave the system entirely to seek better areas. I noted that in sympatric sections larger focal areas were maintained (more of the available resource was commanded) by hatchery fry than by wild fry. I also noted that wild fry in sympatric sections more frequently assumed a nomadic existence, suggesting a lower, less aggressive social status, than they did when living alone.

A major factor that appeared to influence results in this study was the larger size of hatchery fry relative to wild fry. Any influences that could have been attributed to inherent differences between stock origins were probably masked by size differences between fry types. This study would have been more complete if I had included sympatric test sections where wild fry emerged first and where fry types emerged simultaneously. This is not to say that genetic differences are unimportant. On the contrary, variation in the production between wild and hatchery steelhead trout have been attributed to genetic differences (Reisenbichler and McIntyre 1977). Genetic differences may account for

the significantly higher carrying capacities that were realized by wild fry than by hatchery fry in allopatric test sections during both years. Differences in learning experience during the early life stages were unlikely because both groups were reared from eyed eggs in similar environments. I suspect that hatchery fish preferably use more space than wild fish, based on my 1986 findings on size of focal areas and the low densities maintained by hatchery fry in both treatments during both years of study.

Similarly, the differences in results between years for fry in similar test sections could be attributed to genetic variation. Although care was taken to collect spawn from wild and hatchery adults during the same portion of the spawning run each year, only a few individuals of each stock were used to produce fry for this study. In both years, wild fry were produced from the matings of only 5 female and 5 male wild spawners. Theoretically, the progeny produced from a small sample of spawning adults would represent only a very limited number of potential genotypes in a population. Since steelhead express an array of life history strategies and mature at several different ages, the genotypes represented by fry of each stock in this study could have been very different each year. As a result, the influences of hatchery fry on wild fry could have been more pronounced in 1 year and less in the other. Likewise, results may have differed between years for wild fry in similar treatments due to differences each year in genotypic frequency. This may explain why tests that compared the size of focal areas of wild fry in both treatments differed significantly in 1986 and not in 1987.

Although this study falls short of demonstrating all scenarios that can occur when unfed hatchery fry are used for supplementation, it does simulate a realistic practice. Unfed hatchery fry are planted in streams containing wild steelhead populations, and plantings regularly occur before wild fry emerge. The results from this study support suspicions that such introductions can negatively influence the densities, spatial distribution, growth, and behavior of wild juveniles in localized stream populations, especially when carrying capacity is

approached. Supplementation is a useful tool in fishery management and may have positive effects in stabilizing declining wild populations. However, this study, the studies of Reisenbichler and McIntyre (1977), Nickelson et al. (1986), and Chandler and Bjornn (1989) suggest that this practice be used with a great deal of caution.

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CHAPTER III

VARYING INFLUENCES OF EARLIER EMERGING STEELHEAD FRY OF HATCHERY ORIGIN ON THE SOCIAL STRUCTURE OF WILD STEELHEAD FRY

ABSTRACT

The influence of earlier emerging steelhead fry, (Oncorhynchus mykiss), of hatchery origin on the social structure of wild steelhead fry was observed in laboratory stream channels and in natural streams. Fry of both origins in lab channels were raised in 2 treatments: living alone (allopatry) and living together (sympatry). In lab sections, fry of hatchery origin emerged 7-10 d prior to wild fry and remained larger in size during the 8 weeks of study both years. After 7 to 8 weeks from emergence in test sections, wild fry in sympatry were inclined toward maintaining smaller focal areas, greater proportions of nomadic individuals, poorer condition, and later establishment of social hierarchies than wild fry in allopatric sections. They generally were the recipients of aggressive acts perpetrated by hatchery fry, directed agonistic interactions toward each other, and assumed subordinate positions within the social dominance hierarchy. The larger size maintained by hatchery fry throughout the study gave them a competitive advantage. The social behavior observed in allopatric lab sections was compared with observations made on hatchery and wild fry in natural streams. Although distances to nearest neighbor were greater for fry in natural streams, the average size of focal areas and types of agonistic acts used were similar in lab sections and natural stream reaches. Agonistic interactions, however, occurred more frequently in lab sections than in natural stream reaches. Although wild fry in allopatric lab sections were more socially active than hatchery fry, the reverse was observed in natural stream reaches. Earlier emerging hatchery fry can assume dominant positions in local dominance hierarchies which allows them to command more of the available resources in rearing areas. Through overt aggression, the more dominant hatchery

fry could displace wild fry into less preferred or resource-poor rearing habitat, thereby lowering the potential for survival among the wild fry. In this way, the social structure among coexisting hatchery and wild fry can greatly influence the potential success of supplementation efforts.

INTRODUCTION

A growing practice in fishery resource management is the use of unfed fry of hatchery origin to supplement declining natural or wild steelhead (Oncorhynchus mykiss) populations. The practice grows in popularity. It decreases rearing costs at hatcheries and provides a means for public involvement in fishery programs through the use of easily maintained streamside incubators. In view of continuing budgetary constraints, increasing public interest and participation in fishery management decisions, and escalating demands on fishery resources, the use of unfed fry in supplementation programs may appear to be an effective alternative. The practice, however, can influence a decline rather than a stimulation in wild steelhead production.

A regular but fading practice among hatcheries is to select broodstock from adults arriving early to hatchery racks. This selection ensures egg quotas will likely be filled at a hatchery. Unfortunately, it has developed hatchery stocks that emerge as "swim-up" (unfed, newly emerged) fry earlier than wild progeny in prospective recipient streams (Lieder et al. 1986). When used in streamside hatch boxes or other supplementation efforts, the earlier hatchery emergents may have a competitive advantage conferred by larger size and first arrival at rearing sites and may actively displace wild juveniles from quality rearing habitat (Chapman 1962, Solazzi et al. 1983, Nickelson et al. 1986).

The competitive advantage maintained by earlier emerging hatchery fry can disrupt the social organization among localized populations of wild steelhead fry. Juvenile steelhead form relatively stable linear or "peck-dominance" hierarchies early in their life history and express individual territoriality (Bieber 1977, Abbott et al. 1985). The social status held by a juvenile salmonid can influence its potential for survival. Those juveniles that obtain the more dominant positions within a population have shown superior growth rates (Brown 1946, Chapman 1962, Yamagishi 1962, Carline and Hall 1973, Li and Brocksen 1977, Abbott and Dill 1989), defended larger territories for feeding and resting (Keenleyside and Yamamoto 1962), were more aggressive

(Keenleyside and Yamamoto 1962, Abbott et al. 1985, Abbott and Dill 1989), and may have had greater relative fitness (Ejike and Schreck 1980). Dominance among juvenile salmonids is usually positively correlated with size and/or prior residence (Stinger and Hoar 1955, Kalleberg 1958, Chapman 1962, Mason 1966, Carline 1968, Jenkins 1969, Noakes 1980, Jobling and Wandsvik 1983). When wild populations are supplemented with earlier emerging hatchery fry, the hatchery fry have a greater potential to occupy more dominant positions within the localized social hierarchy due to their larger size and first arrival at rearing areas. This dominant status gives the hatchery fry the potential to gain command over available resources.

The purpose of this study was to determine what influence early emerging, and subsequently larger, hatchery fry can have on the social structure of newly emerged wild fry.

METHODS

Conditions of the Experiment

The study was conducted in 2 environments: artificial laboratory channels and natural streams. Tests in lab channels were the major focus of the study. In the lab channels, environmental variables could be controlled to promote similarity of treatments for all fry. The natural stream reaches used in this study served as checks to corroborate lab findings.

Laboratory Channels

Observations on social behavior among steelhead fry of hatchery and wild origins were conducted during June-August in 1986 and 1987 in 2 identical, oval artificial stream channels. The study environment and fry used for this study were the same as those described in Chapter II. The maps, also described in Chapter II, were used to record the points of fry interactions and focal area boundaries.

Social interactions were monitored every other day both before (pre-feeding) and after (post-feeding) feeding periods. The focal animal sampling technique was used to record agonistic acts for individual fry (Altmann 1974). During an observation session, 2

individuals in each section were observed. Each fry selected for observation was observed for 1, 5 minute period. In sympatric sections, 1 wild fry and 1 hatchery fry were sampled each session. Agonistic acts recorded were nip, threat nip, chase, frontal and lateral displays, intention movements, flee, and submit, as described by Kalleberg (1958), Keenleyside and Yamamoto (1962), and Jenkins (1969).

Social hierarchies were calculated for fry in each lab section. Hierarchical ranks of fry were determined by recording all agonistic interactions expressed by individual fry within a subsection (pool or run area) during a 30 minute period. Hierarchic matrices were constructed from these data using a technique by Marler (1955). Using this technique, individuals are ranked according to the number of encounters each wins or loses. The aggressor in an encounter is a "winner" (given a "win" point) while the individual toward which the agonistic act was directed is the "loser" (given a "lose" point). Aggressive acts recorded as wins were nips, threat nips, chases, intention movements, and displays. Initial matrices were created once densities had become stable at the end of the third week following emergence of each fry types in the study sections. Initial hierarchies were reevaluated 10 and 20 d later and again at the close of the experiment. Fry were categorized as "dominants" and "subordinates". Subordinate fry were placed into 2 subcategories: "subdominants" (fry that maintained focal points and focal areas) and "nomads" (fry that did not maintain stable focal points nor focal areas, moved location frequently, and were often observed in hiding).

Natural Streams

During June-August of 1987, observations were made on aspects of social behavior among newly emerged steelhead fry in natural streams for comparison with lab results. Whereas densities in lab sections were believed to be at carrying capacity, the status of densities in natural stream reaches were unknown but were assumed to be at less than carrying capacity, especially among reaches containing only wild fry where densities appeared to be very low. Results from lab sections,

therefore, could represent possible scenarios of social behavior among fry in natural streams when carrying capacity is approached.

All streams included in field studies were within the Santiam River basin, Oregon, and contained fry from the same winter steelhead stock as those used in laboratory channels (Figure 6). A total of 6 reaches, each in a different stream, were monitored weekly. Three reaches contained only wild steelhead fry, and the other 3 contained only fry of hatchery origin. Wild fry emerged from natural redds, and hatchery fry were planted in stream reaches as swim-up fry. The 3 reaches containing only wild fry were in the upper portion of mainstem Calapooia River, the North Fork of the Calapooia River, and Moose Creek in the South Santiam River basin. Each stream reach containing only wild fry was located immediately downstream of at least 3 active, natural redds.

Criteria for selection of streams to provide study reaches for observations on hatchery fry were: 1) absence of steelhead in the watershed or above a migration barrier, 2) location within the Santiam River basin, 3) watershed characteristics similar to those of streams selected for wild fry observations, 4) accessibility, 5) minimal human visitation, and 6) permission from ODFW to plant unfed fry from a Santiam River hatchery into the stream. The 3 streams that met these criteria were the upper mainstem South Santiam River, and Sheep and Soda Fork Creeks in the South Santiam River basin (Table 7).

Fry in sympatry were not represented in the field study since 1) I could not obtain a sufficient quantity of eyed eggs from wild steelhead adults to supply both the experimental reaches in natural streams and lab channels, 2) I found no technique of capturing, handling, and marking newly emerged fry that could not be associated with high mortality or potential alterations in behavior, 3) size difference could not be used as an indicator of origin since emergence of wild fry was protracted from March to July and wild fry could immigrate into streams reaches, and 4) without a reliable, easily recognizable means of identifying fry origin, results would be meaningless.

On June 30, 8,000 hatchery fry were released as swim-up fry in each

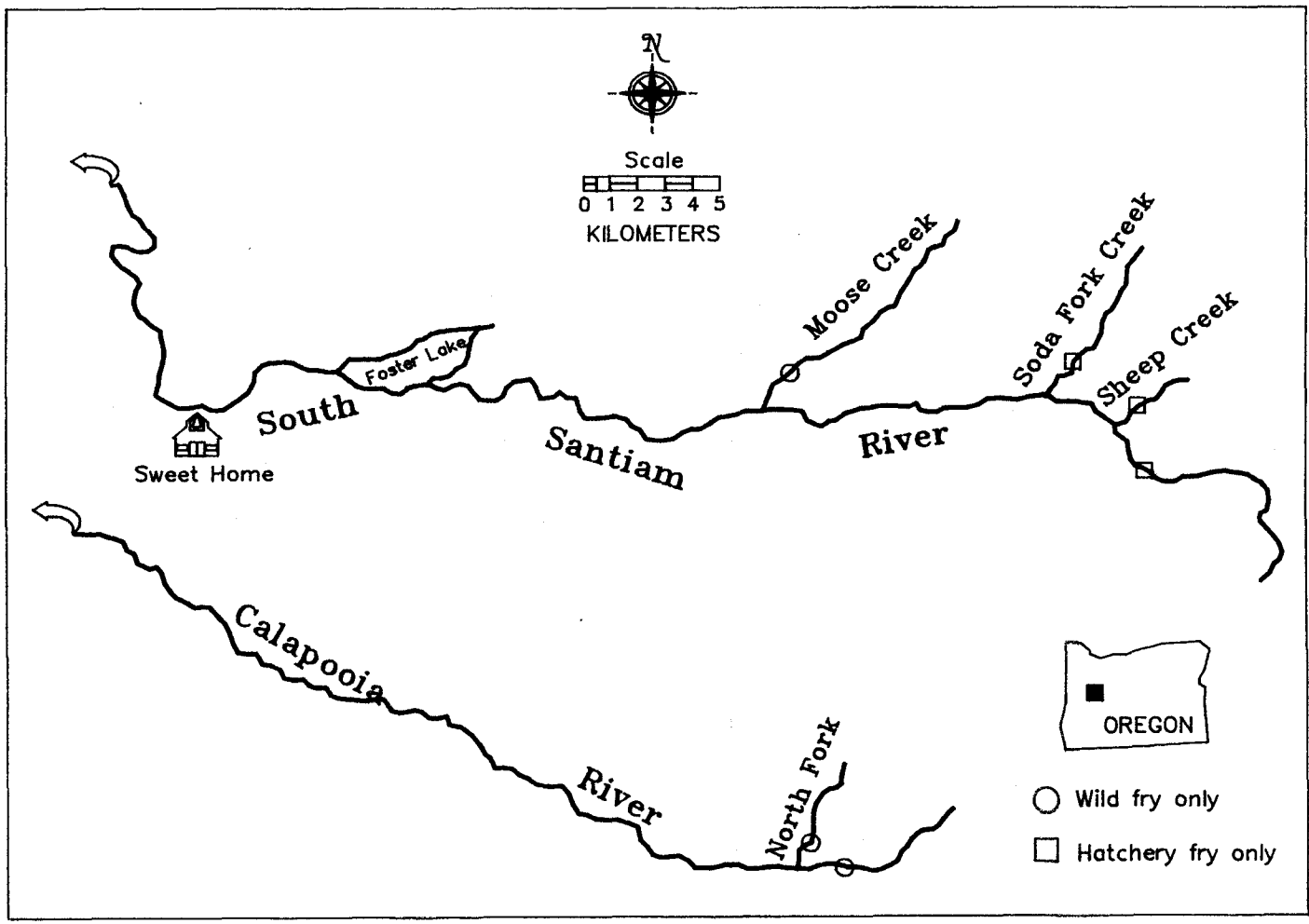


Figure 6. Map of natural streams used in study during 1987.

Table 7. Watershed and reach characteristics of streams used in the field studies, 1987.

| Characteristic | Wild only streams | | | Hatchery only streams | | |
|---|---|----------------|------------------------|--|-----------------------|----------------|
| | Upper ^{a)} Calapooia River | Moose Creek | North Fork Creek | Upper ^{a)} South Santiam River | Soda Fork Creek | Sheep Creek |
| Watershed: | | | | | | |
| Drainage area (km ²) | 47.9 | 52.2 | 15.7 | 80.8 | 41.2 | 15.7 |
| Perimeter (km) | 37.7 | 39.3 | 18.6 | 39.7 | 29.9 | 21.1 |
| Orientation | W | SW | SSW | NW | SW | SW |
| Mean elevation (m) | 889 | 750 | 875 | 891 | 926 | 1851 |
| Drainage density (km/km ²) | 0.99 | 1.56 | 0.84 | 0.81 | 1.69 | 2.46 |
| Mean slope (%) | 55.9 | 54.2 | 31.4 | 28.5 | 38.7 | 39.2 |
| Mainstem fall (m/km) | 56.4 | 60.4 | 88.6 | 62.4 | 73.8 | 96.9 |
| Compactness coefficient | 1.50 | 1.52 | 1.30 | 1.24 | 1.30 | 1.30 |
| Stream length of mainstem (km) | 12.6 | 15.6 | 7.0 | 12.9 | 10.7 | 9.1 |
| Reach (taken May 26-29): | | | | | | |
| Mean width (m) | 11.7 | 14.3 | 6.5 | 13.2 | 5.7 | 5.6 |
| Bankfull width (m) | 23.3 | 18.4 | 9.7 | 25.3 | 11.2 | 17.7 |
| Length (m) | 68.0 | 51.7 | 53.1 | 63.2 | 58.4 | 51.5 |
| Mean depth (m) | 0.38 | 0.27 | 0.19 | 0.31 | 0.22 | 0.23 |
| % Canopy | 5 | 30 | 78 | 27 | 15 | 50 |
| Drift (g/m ² /15 minutes) ^{b)} | 0.114 | 0.497 | 0.929 | 0.274 | 0.319 | 0.419 |
| Substrate composition (% of total): | | | | | | |
| Bedrock | 0 | 0 | 0 | 0 | 0 | 0 |
| Boulders | 12 | 8 | 26 | 7 | 4 | 20 |
| Cobble | 53 | 36 | 33 | 47 | 31 | 32 |
| Large gravel | 19 | 42 | 17 | 19 | 44 | 35 |
| Small gravel | 8 | 10 | 13 | 20 | 18 | 8 |
| Sand, silt, clay | 8 | 4 | 11 | 7 | 3 | 5 |

a) Watershed characteristics for the upper Calapooia River and the upper South Santiam River are only for that part of the watershed upstream of each study reach.

b) Drift samples were grab samples taken on August 10-13. Three drift nets were set: one at mid channel and the other two equal distances from the left and right banks. Drift was collected for 15 minutes, sorted, dried, and weighed for ash free dry weight.

reach of the 3 selected streams. Release of hatchery fry occurred at relatively the same time emergence was peaking in the wild only reaches. Each reach was visited once per week until fry were at least 8 weeks of age. The same focal animal sampling technique that was used in the lab was applied in field observations. Weekly, 5 individuals in each reach were observed to determine distance to nearest neighbor, size of focal area, and types and frequencies of agonistic behavior used during interactions. Each individual was observed for 5 minutes to record agonistic behavior and an additional 15 minutes to determine location of nearest neighbor and boundaries of focal area. To minimize the resampling of fry, focal points were marked with colored and dated rocks. Most observations were made underwater by divers. During the early weeks of the study, fry were often located in edge habitats that could not be snorkeled without disturbance to fry. For these observations, blinds were used and erected at least an hour before observations to allow fry time to adjust to their presence. In both methods of observation, fry were sampled only when they appeared to be unaware of the observer.

Treatment of Data

Analyses were made using data averaged across individuals within a section or reach for a day or a week period. Weeks were counted from the onset of emergence (week 1) in each section for each fry type. Data could then be tested for similarities between fry types (hatchery vs. wild), treatments for each fry type (allopatry vs. sympatry), social status (dominants vs. subordinates), feedings (pre-feeding vs. post-feeding), and experiment locations (stream reaches vs. lab sections) among fry of the same age. Observations for replicate lab sections within years were often pooled when preliminary tests on data revealed that replicate sections within years were similar. Although care was taken to keep environmental variables similar among lab sections in both years of study, I found that variation between years was greater than within years for data on lengths, condition factors, distances to nearest neighbor, and size of focal areas. Therefore, data from 1986

and 1987 were tested separately and results compared for similar trends. Results from comparison tests are reported as "significant" when probability values were at least at the .05 level of confidence in both years; tests resulting in $P < .05$ in 1 year and $P < .1$ in the other are reported as "potential" differences or trends.

Size information for dominant and subordinate fry at the end of the study in each treatment in both years of study is reported as average fork lengths and Fulton's condition factor (Q). Q was calculated as a means of comparing general "robustness" of fry in each treatment (Ricker 1975). Q was calculated for each fry as:

$$Q = W \times 10^5 / L^3$$

where W = live weight (g) and L = fork length (mm).

Distances to nearest neighbor and size of focal areas were determined using the same methods described in Chapter II. Student's t tests were calculated for comparisons of distances to nearest neighbor and average size of focal areas for fry of different origins and social status within the same and different treatments. Agonistic acts were grouped into 2 categories. "High intensity" acts were those acts that were highly offensive in character and included nips, threat nips, and chases. "Low intensity" acts were less offensive or more defensive in character and included frontal and lateral displays, intention movements, submission postures, and fleeing. The log likelihood ratio test (G-test) was used to determine potential differences in the frequency of social interactions among fry of differing fry types, treatments of fry types, social ranks, and feedings. Since variation was large between years in the social activities among fry, data for each year were tested separately. Results from tests for each year were then compared for similar trends.

RESULTS

Social Hierarchy

Linear dominance hierarchies were firmly established in all lab sections by the fifth week following the onset of emergence by both fry type in each section. Stability in hierarchies appeared first among

hatchery fry in allopatric sections at the end of the third week following emergence and last among wild fry in sympatric sections during the fifth week following emergence. In each section, there was at least 1 dominant individual in the downstream pool area and another in the upstream pool/run interface area. Those individuals that occupied dominant positions during the first ranking session remained in those positions to the end of the study in both years. Hatchery fry occupied 10 out of 11 dominant positions in the 4 sympatric sections during the 2 years of the study. In 1 sympatric section in 1986, a single wild fry and 3 hatchery fry were identified as dominant fry. In sympatric sections, all but 3 hatchery fry in 1 of the 4 sympatric sections held higher social ranks than wild fry. In both years, nomadic fry were significantly more common through time among wild fry in both treatments than hatchery fry in sympatry (Table 8).

Dominant and subordinate fry among all fry groups showed remarkably similar growth. Dominant individuals among wild fry in allopatry and hatchery fry in sympatry were significantly longer in average length than subordinate wild fry ($P < .01$ both fry types, both years) (Table 9). There was a potential tendency, however, for dominant hatchery fry in allopatry to have slightly longer average lengths than the subordinate fry. Calculations for condition factors (Q) were similar for dominants and subordinates among all fry groups in both years (Figure 7). Although not significant in both years, subordinate wild fry in sympatry tended to average poorer condition than subordinate wild fry in allopatry.

In summary: 1) hatchery fry established stable social hierarchies more readily than wild fry, 2) establishment of stable social hierarchies was slower when hatchery and wild fry coexisted than when they lived separately, 3) once a fry achieved a dominant position, it retained that position through time, 4) in sympatric sections, hatchery fry usually occupied the dominant positions, 5) wild fry in sympatric sections usually maintained the lowest ranks in linear dominance hierarchies, 6) wild fry more frequently adopted a nomadic existence than hatchery fry, 7) dominant fry in allopatric sections were longer

Table 8. Total number of nomads for each fry type and treatment through time in lab sections during 1986 and 1987.

| | | 1986 | | | | | | | 1987 | | | | | | | |
|---------------|----|------------------------------|----|----|----|----|----|---|------|----|----|----|----|---|---|--|
| | | Week from start of emergence | | | | | | | | | | | | | | |
| | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| WILD FRY: | | | | | | | | | | | | | | | | |
| Allopatry | a) | | 16 | 16 | 20 | 28 | 3 | | 18 | | 11 | 11 | 11 | | | |
| Sympatry | | 5 | 7 | 10 | 12 | 12 | 21 | | 11 | 11 | 7 | | | | | |
| HATCHERY FRY: | | | | | | | | | | | | | | | | |
| Allopatry | | | 2 | 2 | 3 | 5 | 4 | 7 | | 7 | | 4 | | | | |
| Sympatry | | 2 | 1 | 0 | 1 | 0 | 0 | 3 | | 1 | | 1 | | | | |

a) Dominance status not determined for fry when blank cells are shown.

Table 9. Average fork length (mm), sample size (n), standard error (se), and results from tests for significant differences (* = significant at the .05 level; ns = not significant) for dominant and subordinate fry of each fry type and treatment in lab sections, 1986 and 1987.

| | 1986 | | 1987 | |
|----------------------|-----------------------|-------------|----------|-------------|
| | Dominant | Subordinate | Dominant | Subordinate |
| WILD FRY: | | | | |
| Allopatry | 50.6 * | 45.8 | 49.8 * | 43.3 |
| n | 12 | 37 | 4 | 20 |
| se | 0.87 | 0.89 | 3.2 | 1.24 |
| Sympatry | 51.0 ^{a)} ns | 47.0 | b) | 44.9 |
| n | 1 | 26 | | 16 |
| se | 0 | 0.95 | | 1.09 |
| HATCHERY FRY: | | | | |
| Allopatry | 60.7 ns | 59.4 | 54.5 * | 46.0 |
| n | 7 | 8 | 4 | 14 |
| se | 0.87 | 1.50 | 2.63 | 1.70 |
| Sympatry | 58.5 ns | 57.2 | 55.0 ns | 53.7 |
| n | 6 | 11 | 4 | 3 |
| se | 1.43 | 1.29 | 1.08 | 0.33 |

a) This is not an average since there was only one dominant wild fry in sympatric sections in 1986.

b) There were no dominant wild fry in sympatric sections in 1987.

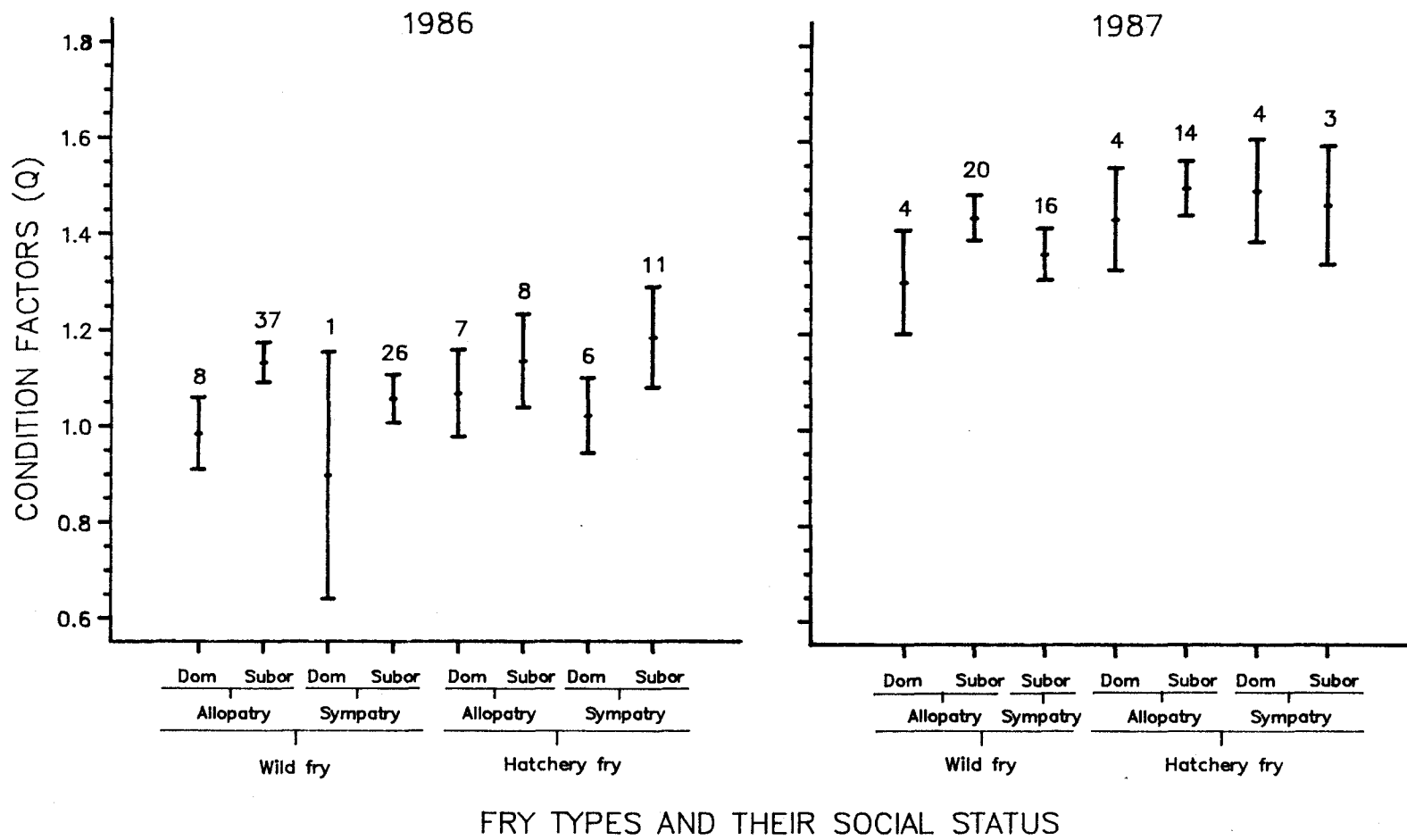


Figure 7. Mean condition factors and their 95% confidence intervals for dominant (Dom) and subordinate (Subor) fry in allopatry and sympatry in lab sections. Numbers above 95% CI bars are the sample size in each category at the end of the study each year.

in length than the subordinate fry, 8) subordinate wild fry in sympatric sections had poorer average condition than subordinate wild fry living alone, and 9) dominant hatchery fry were longer in length than subordinate wild fry.

Distance to Nearest Neighbor and Size of Focal Area

Average distances were significantly different between allopatric sections in the lab and reaches in natural streams for both fry types (1986 and 1987: $P < .001$ for both fry types in both years). Both hatchery and wild fry in stream reaches had greater average distances to nearest neighbor than fry in allopatric lab sections. In stream reaches, wild fry had significantly greater average distance to nearest neighbor than hatchery fry ($P < .05$).

Unlike in natural stream reaches, there was no discernible difference in average distances to nearest neighbor between wild and hatchery fry in allopatric lab sections. Average distances to nearest neighbor were remarkably similar among dominant and subdominant fry of both fry types and fry types in both treatments. The only tests that revealed discernible differences in both years were those involving nomadic wild fry. Average distances to nearest neighbor were significantly greater for nomadic wild fry in both treatments than for dominant and subdominant wild fry and for all hatchery fry.

Unlike results from tests involving distances to nearest neighbor, there was no discernible difference in average size of focal areas through time between fry in natural stream reaches and fry in allopatric lab sections (Table 10).

Although the 1986 data for allopatric sections suggested that hatchery fry had significantly larger areas than wild fry, tests on similar data from 1987 were not significant (Table 10). In both years, dominant fry in sympatric sections (all but 1 were hatchery fry) and allopatric hatchery sections had significantly larger focal areas than subdominant fry ($P < .01$ both years, both treatments) (Figure 8). Dominant wild fry in allopatric sections potentially maintained larger average focal areas than did the subdominant fry.

Table 10. Average size (m^2), sample size (n), and standard error (se) of focal areas through time for both fry types in allopatric lab sections and natural stream reaches.

| | | Weeks since start of emergence | | | | | |
|--------------|-------|--------------------------------|------|------|------|------|------|
| | | 3 | 4 | 5 | 6 | 7 | 8 |
| LAB | | | | | | | |
| Wild fry | | | | | | | |
| 1986 | m^2 | a) | 0.47 | 0.70 | 0.97 | 0.85 | 1.49 |
| | n | | 36 | 30 | 23 | 29 | 16 |
| | se | | 0.04 | 0.11 | 0.23 | 0.18 | 0.54 |
| 1987 | m^2 | 1.04 | | 1.79 | 2.66 | 3.02 | |
| | n | 9 | | 15 | 10 | 9 | |
| | se | 0.35 | | 0.29 | 0.69 | 0.65 | |
| Hatchery fry | | | | | | | |
| 1986 | m^2 | 0.84 | 1.32 | 2.04 | 1.96 | 2.97 | 5.70 |
| | n | 17 | 13 | 14 | 13 | 6 | 6 |
| | se | 0.16 | 0.27 | 0.56 | 0.61 | 1.18 | 0.77 |
| 1987 | m^2 | 1.13 | | 1.82 | | 1.58 | |
| | n | 13 | | 10 | | 13 | |
| | se | 0.20 | | 0.39 | | 0.24 | |
| FIELD - 1987 | | | | | | | |
| Wild fry | | | | | | | |
| | m^2 | | | 1.28 | 2.70 | 5.82 | 3.13 |
| | n | | | 5 | 7 | 4 | 10 |
| | se | | | 0.85 | 1.28 | 2.31 | 1.03 |
| Hatchery fry | | | | | | | |
| | m^2 | 1.77 | 2.89 | 1.75 | 1.37 | 2.91 | 1.94 |
| | n | 10 | 10 | 13 | 10 | 14 | 14 |
| | se | 0.32 | 0.79 | 0.36 | 0.47 | 1.04 | 0.36 |

a) Data not recorded for those weeks with blank cells.

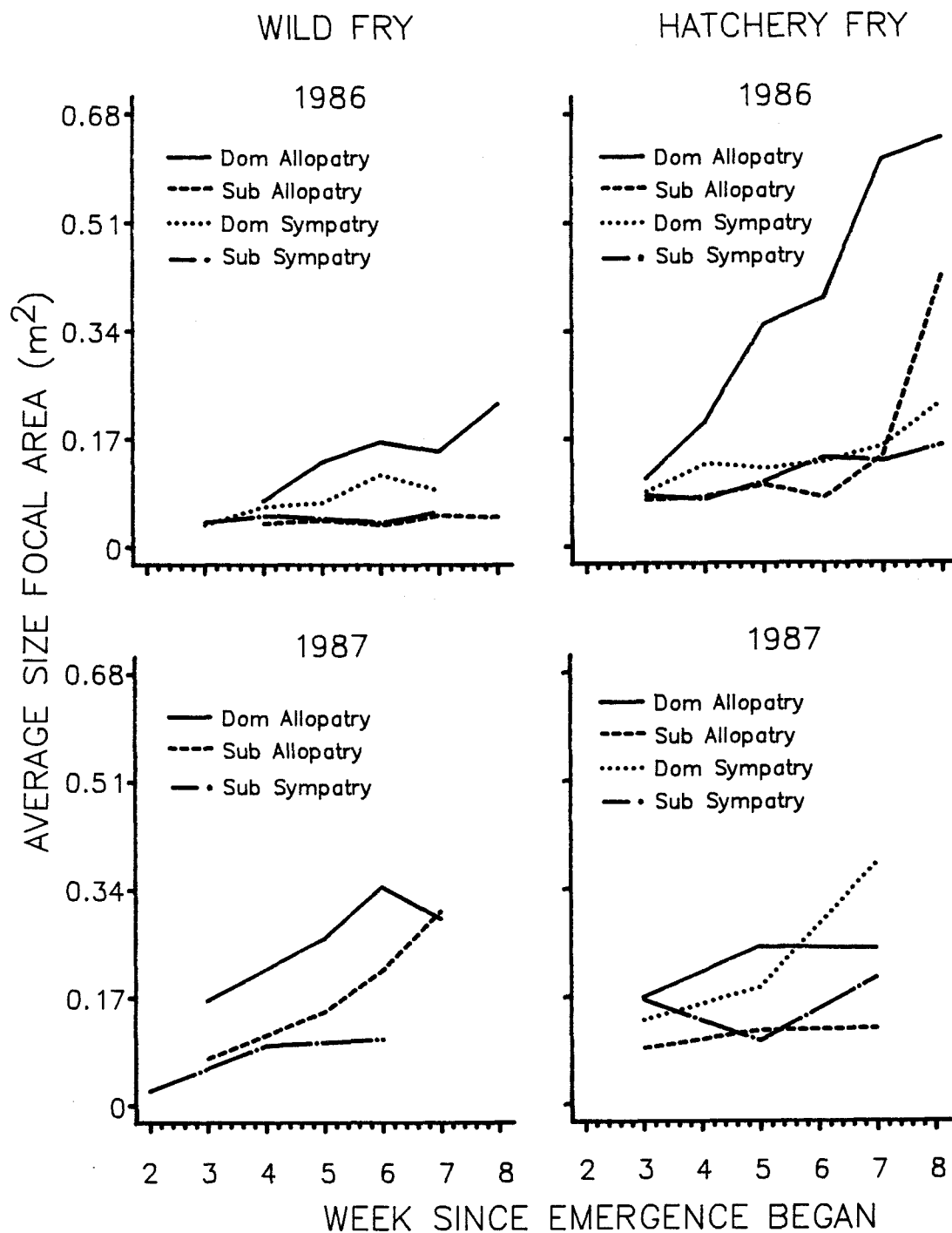


Figure 8. Average size of focal areas through time for dominant (Dom) and subdominant (Sub) fry in allopatry and sympatry in lab sections, 1986 and 1987.

In summary, results on distances to nearest neighbor and size of focal areas revealed: 1) in lab sections, distances to nearest neighbor were similar for fry in all social classes except nomadic wild fry who averaged significantly greater distances, 2) both fry types had significantly greater average distances to nearest neighbor in natural stream reaches than in lab sections, 3) dominant hatchery fry in both treatments maintained larger focal areas than subdominant fry, and 4) the average size of focal areas in lab sections and natural stream reaches were similar for both fry types.

Social Interactions

Overall Results

Since variances within tested groups of data were usually large, tests of significance revealed very few differences between fry types, treatments for each fry type, and lab and field data in the number of agonistic acts delivered of high and low intensities. Test results often differed between years of the study.

Allopatric lab sections vs. natural stream reaches. Although wild fry in allopatric lab sections in 1986 initiated significantly more high and low intensity acts than hatchery fry in allopatry ($P < .01$ for both intensity types), tests on similar data from 1987 were not significant. As in allopatric lab sections in 1987, there was no significant difference between wild and hatchery fry in natural stream reaches in the average number of high intensity acts delivered. Hatchery fry, however, delivered significantly more low intensity acts than did wild fry in the field ($P < .01$).

Comparison tests did not reveal any differences that were significant in both years in the average number of high and low intensity acts delivered by fry in allopatric lab sections and natural stream reaches (Figure 9). One potential difference, however, was found; agonistic interactions were more common among fry in allopatric lab sections than among fry in natural stream reaches, especially among the wild fry. In lab sections, wild fry generally initiated acts more frequently than hatchery fry. This was opposite from what was observed

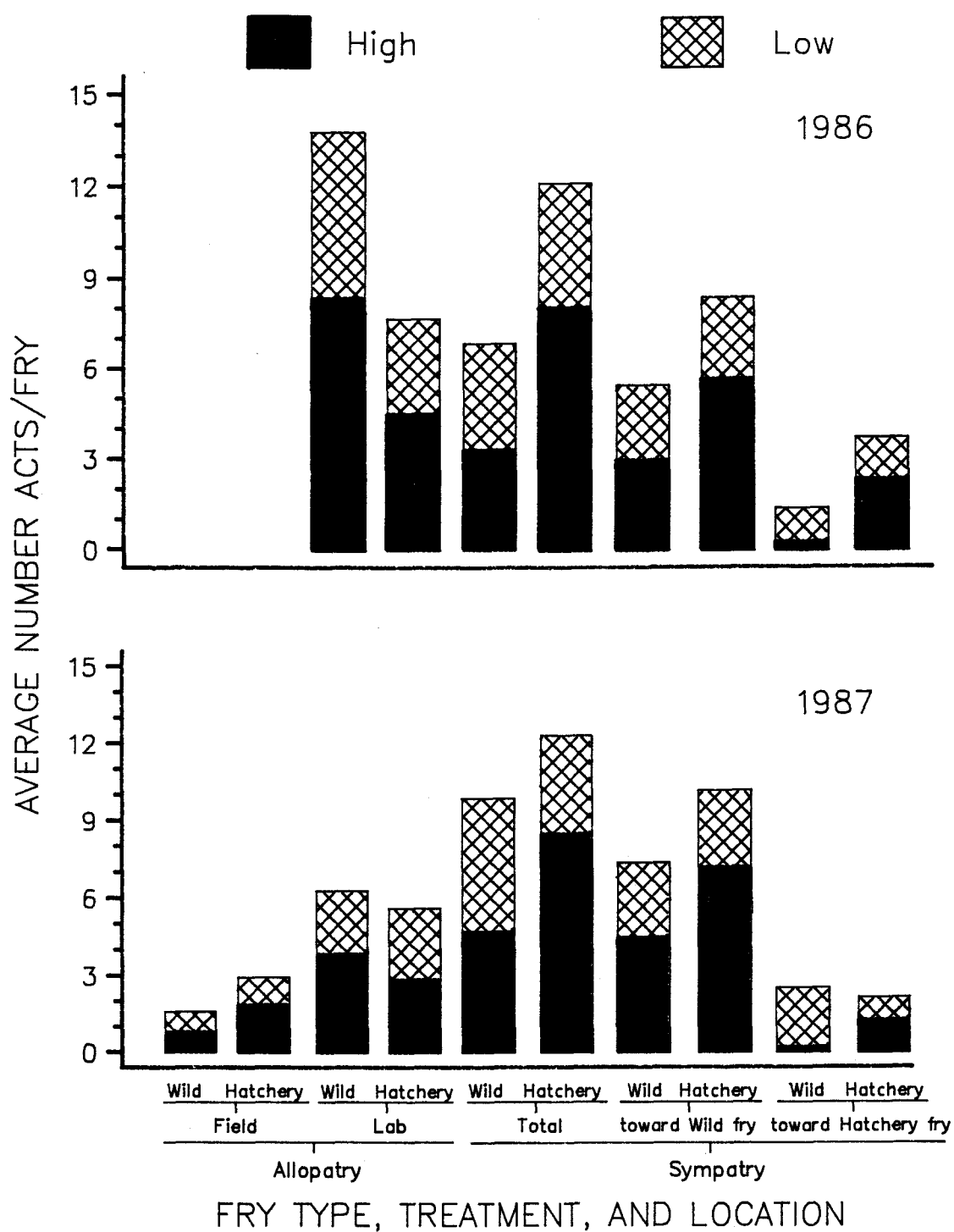


Figure 9. Average high and low intensity acts for both fry types in allopatric and sympatric lab sections (in sympatry, fry type that an act was directed toward is shown), and the field reaches.

in natural streams where hatchery fry used high intensity acts more frequently than wild fry. In both test environments, the same types of aggressive acts were used. Potential trends of agonistic interactions could also be observed through time (Figure 10). Both fry types in allopatric lab sections increased their use of low intensity acts while decreasing or maintaining their use of high intensity acts in the later weeks of the study in both years. This suggests a change toward less offensive, overt aggression. A similar change was not apparent among fry in natural stream reaches.

Allopatric vs. sympatric lab sections. When comparisons were made in the delivery of high and low intensity acts between fry in allopatric and sympatric sections, no significant differences were found among wild fry. In both years, however, hatchery fry in sympatry delivered significantly more high and low intensity acts than did hatchery fry in allopatry ($P < .03$ both intensities, both years) (Figure 9).

Hatchery vs. wild fry in sympatric sections. Since there were 2 fry types in sympatric sections, I recorded the fry type that each agonistic act was directed towards. One trend was consistent throughout the data in both years of study: wild fry were most frequently the recipients of agonistic acts initiated by both hatchery and wild fry in sympatric sections (Figure 9). Hatchery fry engaged in social interactions more often than wild fry. They used high intensity acts significantly more frequently than the wild fry (1986 and 1987: $P < .02$) and directed significantly more of these acts toward wild fry than each other (1986: $P < .001$; 1987: $P < .05$). Conversely, wild fry used low intensity acts significantly more often than the hatchery fry (1986 and 1987: $P < .01$). While wild fry directed high intensity acts more frequently toward each other, they generally used low intensity acts when interacting with hatchery fry (Figure 9).

Effects of Feeding

Comparison tests were run on the number of agonistic acts of each intensity delivered by fry before and after feeding periods. There were no significant differences in the number of high and low intensity acts initiated before and after feedings by any fry group. Although in

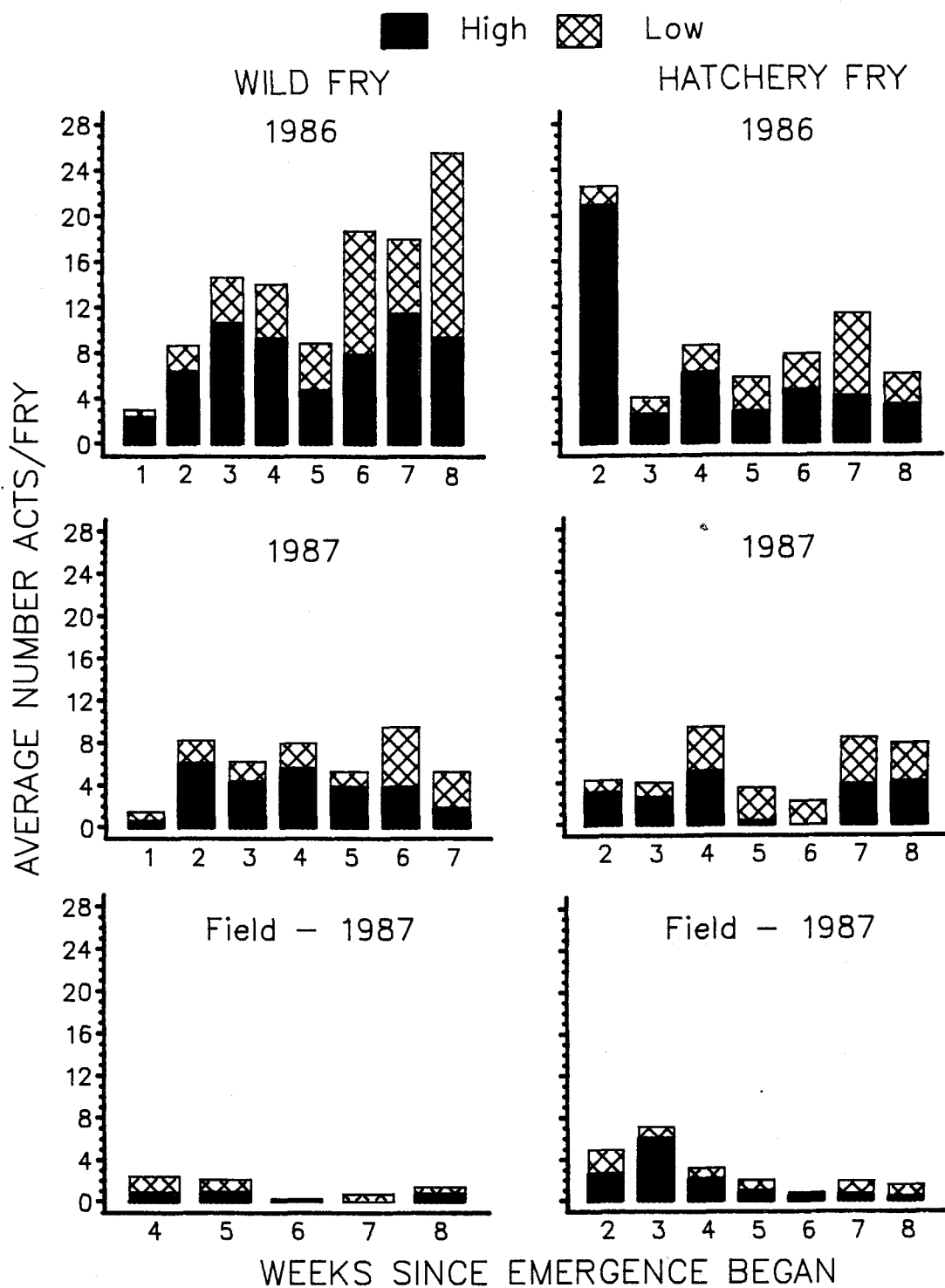


Figure 10. Average high and low intensity acts through time for fry in allopatric lab sections and field reaches.

1986 there were significantly greater number of high and low intensity acts delivered by both fry types in allopatry and hatchery fry in sympatry during pre-feeding periods than in post-feeding periods, tests on similar data from 1987 were not significant (Figure 11). In sympatric sections, wild fry were generally the recipients of high intensity acts initiated by both wild and hatchery fry before and after feeding periods.

Social Status

Tests for significance were run on data for social interaction among fry of different social status (dominants, subdominants, and nomads) within a fry type and among fry of the same fry type and social status but in different treatments. Due to high variance within groups, no tests were significant in both years. There were, however, several potential trends that were apparent when social interactions were considered in terms of fry social status. Generally, dominant fry, regardless of fry type or treatment, delivered more high intensity acts than fry of any other social status (Figure 12). In both years, hatchery fry in sympatry in each social status delivered more high intensity acts than hatchery fry in allopatry; this was not observed among wild fry. Among fry in sympatry, subdominant and nomadic wild fry were more likely to direct high intensity acts toward other wild fry and low intensity acts toward hatchery fry. Trends were similar among dominant and subdominant hatchery fry in sympatry; more high than low intensity acts were directed toward wild fry and less often toward hatchery fry.

In summary, data on social interactions revealed: 1) agonistic acts were more frequent among fry in allopatric lab sections than among fry in natural streams, but types of aggressive acts used were the same, 2) although in allopatric lab sections wild fry engaged in social interactions more frequently than hatchery fry, the opposite was observed in natural streams, 3) hatchery fry in sympatry generally engaged in social interactions more frequently than hatchery fry in allopatric lab and field sections, and this was significant in the use of both types of intensity acts, 4) in sympatry, hatchery fry averaged

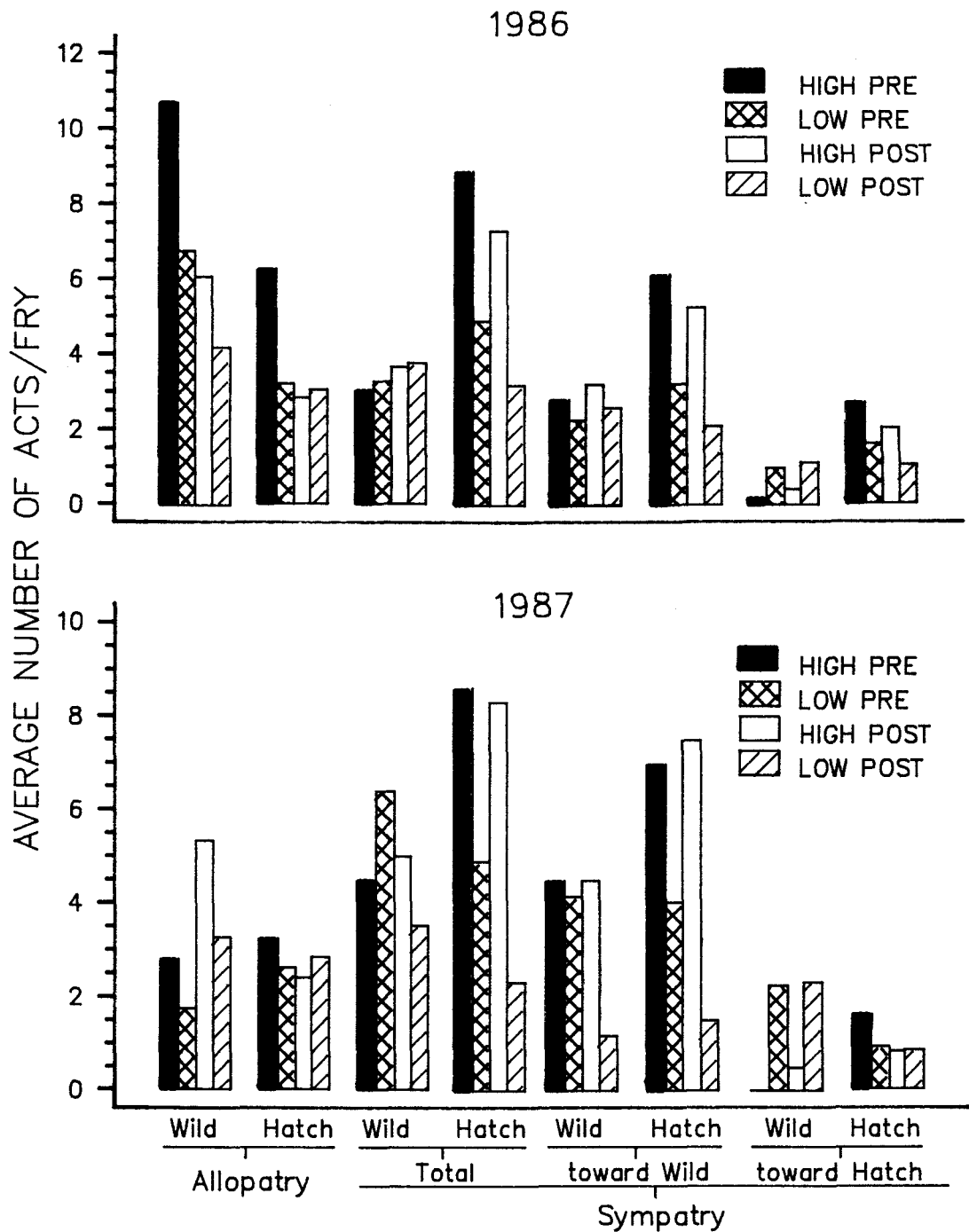
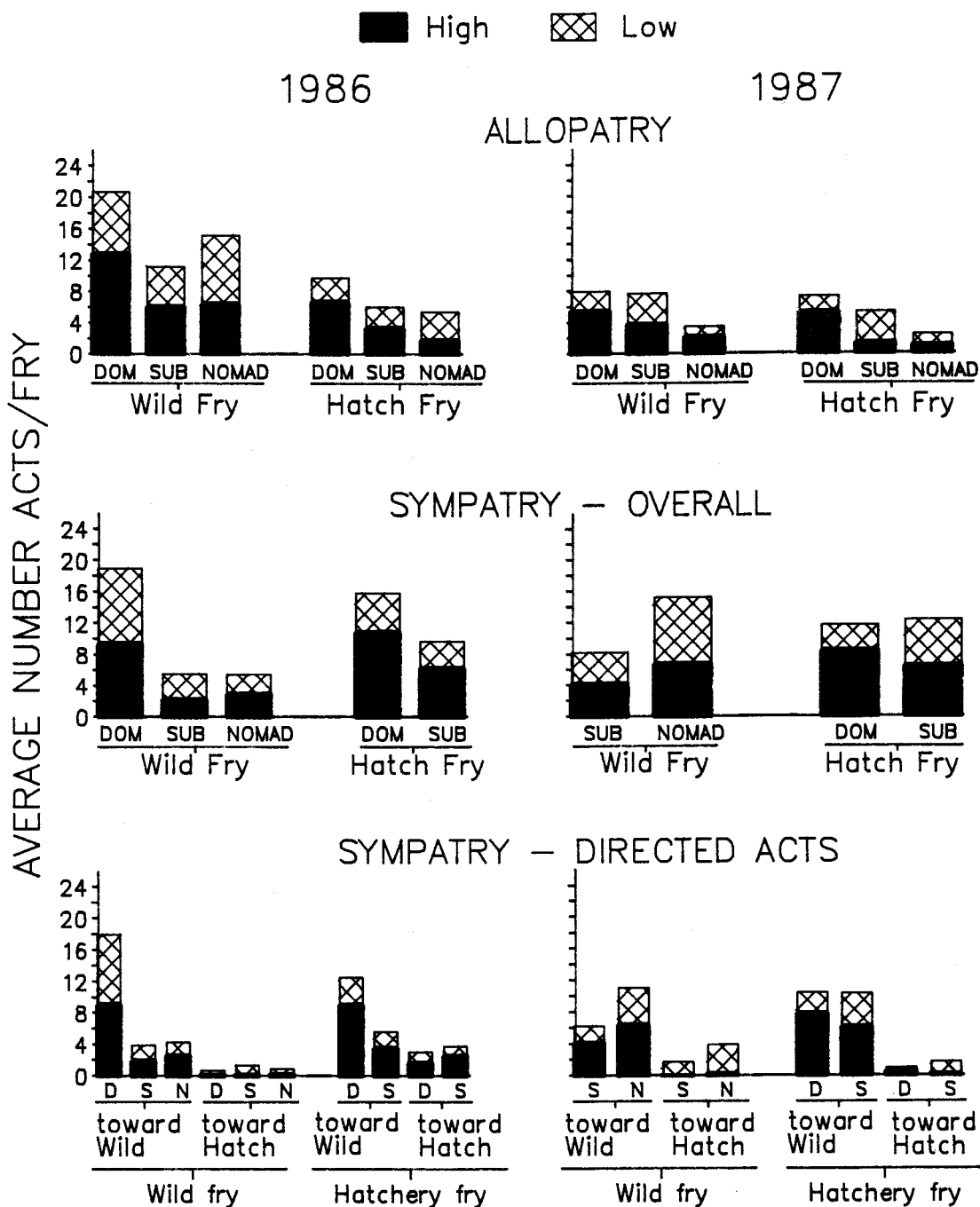


Figure 11. Average number of high and low intensity acts delivered by each fry type (Wild = wild fry, Hatch = hatchery fry) in allopatry and sympatry in lab sections before (Pre) and after (Post) feeding periods.



FRY TYPE AND TREATMENT

Figure 12. Average high and low intensity acts for both fry types in both treatments in the lab by social status (D or Dom = dominant fry, S or Sub = subdominant fry, and N or Nomad = nomadic fry). In sympatry, fry type toward which act was directed is shown (Wild = wild fry, Hatch = hatchery fry).

significantly more high intensity acts per fry while wild fry averaged significantly more low intensity acts per fry, 5) hatchery fry in sympatry used high intensity acts significantly more frequently than wild fry and these were usually directed toward wild fry, 6) wild fry in sympatry generally directed high intensity acts toward each other and used low intensity acts when interacting with hatchery fry, 7) the average number of aggressive acts was similar before and after feedings among all fry groups, and 8) dominant fry, regardless of fry type or treatment, generally used high intensity acts more often than fry of any other social status.

DISCUSSION

In lab sections, the social structure among wild fry differed in the presence of earlier emerging hatchery fry than in their absence. In sympatry, wild fry rarely assumed a dominant position, established stable social hierarchies later, and maintained smaller focal areas than wild fry living in allopatry. Wild fry in sympatry were not only the most frequent recipients of aggressive acts from other wild fry but also received the majority of aggressive acts perpetrated by hatchery fry in those sections. Also, in 3 of the 4 sympatric sections during the 2 years of study, all hatchery fry maintained higher social ranks than wild fry.

From these results, it would appear that wild fry coexisting with earlier emerging, and subsequently larger, hatchery fry could have a lower potential for survival than wild fry living alone. Among social, territorial animals, such as juvenile steelhead, the hierarchical position held by an individual is intricately linked to its potential for survival. Ejike and Schreck (1980) reported an inverse relationship between stress and social rank among yearling coho salmon. They went on to state that dominance could be an indicator of greater relative fitness if levels of chronic stress are maladaptive. Also, since several authors have found that dominance is associated with faster growth (Chapman 1962, Li and Brocksen 1977, Abbott and Dill 1989) and vulnerability to predation increases with smaller size (Werner and

Gilliam 1984), those individuals in dominant and higher ranking positions could have greater potential for survival than individuals in lower ranking positions. Since in my study wild fry in sympatry rarely occupied dominant positions and usually maintained the lowest social ranks in dominance hierarchies, it would follow that their potential for survival may be lower when coexisting with earlier emerging hatchery fry.

The size of focal areas and the frequency and intensity of agonistic encounters also differed among wild fry in different treatments. Both these socially influenced variables, coupled with the dominance hierarchy, could influence the localized distribution and ultimate survival of juvenile salmonids. Jenkins (1971) found that agonistic behavior was largely responsible for the spatial distribution of yearling rainbow trout within a limited stream area. In 1969, he reported that dominant individuals greatly influenced the position choice of subordinates and that when dominants were removed from their territories, subordinates appeared to prefer vacated positions. He also noted that dominants had the highest mean value of drift organisms in their gut, suggesting that their positions enabled them to acquire more food. Territories held by juvenile salmonids are often recognized as feeding territories (Kalleberg 1962, Slaney and Northcote 1974). Fry in dominant and higher ranking social position would potentially select and maintain the most profitable positions in relation to food abundance and energy expended on food acquisition (Fausch 1984, Fausch and White 1986). As in my study, other researchers have noted the high level of aggression expressed by juvenile salmonids of hatchery origin and their ability to maintain dominant positions (Fenderson et al. 1968, Bieber 1977). The more dominant and higher ranking hatchery fry in sympatric sections in my study influenced the size and, potentially, the location of focal areas of wild fry through their intense and highly aggressive interactions. Similar interactions among hatchery and wild fry in natural streams could force wild fry into lower quality habitats or more resource-poor focal areas thereby lowering their potential for survival. Such a scenario is highly probable in view of the higher level of

aggressive behavior observed among hatchery fry than among wild fry in sympatric lab sections in this study.

In lab sections, the earlier emergence and subsequent larger size of hatchery fry in sympatric sections apparently gave them a competitive advantage over the wild fry. Earlier emergence allowed hatchery fry to select positions without competition from wild fry; in this way they had "prior residence" at preferred rearing sites. Their larger size enabled them to obtain and maintain dominant and higher ranking positions in the social dominance hierarchy. Although Jenkins (1971) found prior residence to be an important factor in determining position ownership, he and other authors have stressed the importance of body size in determining social status, and location and size of territories (Kalleberg 1958, Chapman 1962, Mason 1966, Bieber 1977, Abbott et al. 1985, Nickelson et al. 1986). Werner and Gilliam (1984) claim body size governs energetics, resource exploitation, and susceptibility to enemies. When earlier emerging hatchery fry are supplemented into streams prior to wild fry emergence, hatchery fry may be given a potent competitive advantage. This advantage is most effective among localized populations in close proximity to release sites since the majority of outplanted hatchery fry tend to remain close to release sites for several months up to 2 years after release (Bjornn and Mallet 1964, Hume and Parkinson 1988). In my study, hatchery fry tended to remain close to release sites in the natural stream reaches.

Any inherent differences between stocks in this study are masked by the overwhelming influence of the larger size and prior residence of hatchery fry relative to wild fry. This study would have been more complete if I had included sympatric reaches in natural streams and sympatric lab sections where wild fry emerged first and, also, simultaneously with hatchery fry.

Another factor that may have had a strong influence on study results is genetic variability among fry used in the study each year. The differences in results between years for fry in similar lab sections could be attributed to genetic variation. Although care was taken to collect spawn from wild and hatchery adults during the same portion of

the spawning run each year, only a few individuals of wild stock were used to produce fry for this study. While hatchery fry were progeny from a moderate number of spawners returning to the hatchery during the later part of the spawning run, wild fry were produced from the matings of only 5 female and 5 male wild spawners each year. Theoretically, the progeny produced from a small sample of spawning adults would represent only a very limited number of the potential genotypes in a population. Since steelhead express an array of life history strategies and mature at several different ages, the genotypes represented by fry of each stock in this study could have been very different each year. As a result, the influences of hatchery fry on wild fry in lab sections could have been more pronounced in 1 year and less in the other. Likewise, results may have differed between years for wild fry in similar lab treatments due to differences between years in genotypic frequency. Genetic variation may explain why several comparisons of tests on social interactions for fry in similar lab treatments were significant in 1 year and not in the other. Genetic variation may also explain the greater number of differences in results observed between wild fry than between hatchery fry in allopatric lab sections and natural stream reaches. While hatchery fry observed in the lab and the field were progeny from the same stock of spawners received at the hatchery, wild fry used in lab sections were progeny from only a very limited number of wild adults ascending the South Santiam River. The genotypic variation would be very limited among wild fry in the lab in comparison with wild fry observed from several natural redds in the stream reaches. This could explain why differences in size of focal areas and number of agonistic interactions per fry were more pronounced between wild fry in the lab and the field and less prominent between hatchery fry in the 2 environments.

Although this study falls short of demonstrating all scenarios that can occur when supplementation efforts use unfed fry, it does simulate a realistic practice. Study results support suspicions that introductions of hatchery fry of larger size and earlier emergence in streams containing wild stocks can disrupt the social structure of local

wild fry populations. This disruption could negatively influence survival among the wild fry. The use of unfed fry in supplementation efforts can potentially be a useful tool in fishery management. Its effects on the recipient wild population, however, must be understood and incorporated into management plans. Fishery managers need to consider all aspects of steelhead behavior prior to supplementation. This especially includes the important role of social structure in the distribution and subsequent survival of juvenile steelhead.

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CHAPTER IV

GENERAL SUMMARY

Supplementation of wild steelhead populations with juvenile steelhead of hatchery origin continues to be an integral part of mitigation and restoration programs in fishery management. Although in recent years these programs have become common in most major watersheds, the success of supplementation remains uncertain. Success has varied between watersheds and between years within the same watershed. This has given rise to differing opinions among fishery managers as to current supplementation practices and to an increase in studies addressing interactions and differences between hatchery and wild stocks. The use of unfed fry of hatchery origin in supplementation efforts is controversial. Since in these efforts juveniles steelhead of both origins coexist in streams from 1 to 3 years, the potential for competitive interactions between hatchery and wild fry is certainly high. This study addressed a single concern in the hatchery vs. wild stock controversy: potential impacts on wild juvenile steelhead when unfed steelhead fry of hatchery origin are planted in streams prior to wild fry emergence, as commonly occurs in supplementation efforts. This early period in the life history of steelhead was chosen for study since it is a critical time when survival can be heavily influenced by resulting dominance hierarchies established during the first few weeks following emergence.

Observations in laboratory channels in this study suggested that during the first few weeks after emergence hatchery and wild fry emigrate at similar rates, establish relatively stable numbers within equivalent time periods, grow at similar rates, use many habitat variables similarly, establish linear social dominance hierarchies, and use the same types of aggressive acts when interacting. These close similarities could induce competition for food and space when unfed hatchery steelhead fry are released into streams containing wild steelhead populations and resources become limited. The wild fry may

be at a competitive disadvantage when hatchery fry, released prior to wild fry emergence from gravels, maintain larger size and arrive first at rearing areas.

In this study, hatchery fry remained larger in size to the end of the study even though they emerged only 7 to 10 d prior to the wild fry. In sympatric lab sections, hatchery fry maintained significantly larger focal areas and better condition, were more aggressive and occupied more dominant positions than the wild fry in those sections, and directed highly aggressive acts more frequently toward wild fry than each other. Other researchers have associated dispersal and spatial distribution of juvenile salmonids with agonistic interactions (Chapman 1962, Jenkins 1969). By definition, dominant or higher ranking individuals are the "winners" in most agonistic encounters. This enables them to acquire and remain in preferred positions in regard to available resources (Fausch 1984). Dominance among juvenile salmonids is regularly associated with larger size and often prior residence (Newman 1956, Chapman 1962, Mason 1966, Carline 1968, Jenkins 1969, Bieber 1977, Noakes 1980, Abbott et al. 1985, Nickelson et al. 1986). If, as in this study, earlier emerging, and subsequently larger, hatchery fry occupy the most dominant positions in a local social hierarchy, they could force wild fry into resource-poor rearing areas, thereby lowering the potential for survival among the wild fry.

The overall production in supplemented streams may be reduced when earlier emerging hatchery fry are released into streams prior to wild fry emergence. In this study, hatchery fry appeared to maintain larger focal areas and lower densities than the wild fry when at carrying capacity in lab sections. In another study, significantly lower densities among newly emerged wild fry were reported for streams stocked with slightly larger hatchery fry than in unstocked streams (Nickelson et al. 1986). This was attributed to displacement of wild fry by hatchery fry. If the slightly larger hatchery fry preferably use more space than wild fry and can displace wild fry from quality rearing areas, overall densities in a stream may be reduced as carrying capacity is approached in supplemented streams.

It appears from this study that a competitive advantage is given to hatchery fry when they arrive first at rearing areas and remain slightly larger in size than wild fry. Results from this study suggest that wild fry coexisting with hatchery fry can have lower realized densities, maintain smaller focal areas, have greater proportions of nomadic individuals, have poorer condition, and establish stable dominance hierarchies slower than wild fry living alone. Since the purpose of supplementation is to stimulate smolt production among depressed wild stocks and ultimately increase the number of returning adults that spawn in natural streams, it would be wise to give any potential competitive advantage to the wild fry. This will mean obtaining an understanding of the early social and life history patterns among wild steelhead in potential recipient streams prior to supplementation efforts. Only then can a potential competitive advantage conferred by larger size and prior residence be given to emerging wild fry.

Although this study did not focus on genetic differences between stocks, the importance of genetic considerations in supplementation programs cannot be overemphasized. Variation in production of wild and hatchery steelhead stocks has been attributed to genetic differences (Reisenbichler and McIntyre 1977). In this study, genetic differences between stocks may account for the significantly higher carrying capacities that were realized by wild fry than by hatchery fry. Likewise, variation between years in lab results and between lab and field data may be attributed to differences in genotypic frequencies among fry used in the study each year. Similarly, selection (intentional or not) of broodstock at hatcheries could manipulate genotypic frequencies so that expression of genotypes vary between years. This could ultimately result in variation between watersheds and between years in the same watershed in the degree of success or failure of supplementation efforts. In this way, hatchery fry could have a stronger impact on supplemented wild steelhead in some years and less in others.

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