To the Graduate Council:

I am submitting herewith a dissertation written by Mark Edward Clark entitled "An Individual-Based Modeling Study of Brook Char and Rainbow Trout Competition in Southern Appalachian Streams." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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An Individual-Based Modeling Study Of Brook Char and Rainbow Trout Competition In Southern Appalachian Streams

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Mark Edward Clark

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Abstract

An individual-based model of the population dynamics of sympatric rainbow trout (*Oncorhynchus mykiss*) and brook char (*Salvelinus fontinalis*) is described and analyzed. The model simulates daily growth, mortality, movement, and spawning over the full life cycle of each species for 100 years in a compartmentalized, hypothetical stream configured for the southern Appalachian mountains of the United States. Egg and alevin development is temperature-dependent with mortality having constant, spatial, and temperature-dependent components. Daily growth of fry, juveniles, and adults is based on bioenergetics and consumption of drift prey. Mortality rate of fry through adults decreases with length. Model predictions of densities, growth, age, and size structure were similar to those observed in southern Appalachian streams. Five different conditions were simulated to explore the population dynamics and competition between the two species: (1) sympatric populations (baseline); (2) allopatric brook char; (3) allopatric rainbow trout; (4) and (5) sympatric populations with reduced or increased spawning season durations. Results indicated that density-dependence mainly operated during the fry and juvenile stages, brook char were more affected by interspecific competition than rainbow trout, and crowding of fry negatively affected brook char (with little effect on rainbow trout), whereas low fry density favored brook char.

The individual-based model was used to examine possible explanations for rainbow trout dominance over brook char in southern Appalachian streams. Model simulations were used to quantify the effects of: (1) greater aggressiveness in rainbow trout, (2)

latitudinal differences in stream temperatures, flows, and daylight, (3) year-class failures, (4) lower fecundity of brook char, and (5) reductions in spawning habitat on the competitive dynamics between rainbow trout and brook char. Average densities of each species based on 100 year simulations were compared for several levels of each of the five factors and for sympatric and allopatric conditions. Based on model results and empirical information, it was concluded that more frequent year-class failures and the lower fecundity of brook char were both possible and likely explanations for rainbow trout dominance, warmer temperatures due to latitude and limited spawning habitat were possible but unlikely explanations, and rainbow trout aggressiveness was a highly unlikely explanation. Additional field work should focus on comparative studies of the reproductive success and the early life stage mortalities of brook char and rainbow trout among Appalachian streams with varying rainbow trout dominance.

The brook char - rainbow trout model was applied to evaluate management strategies for enhancing brook char densities in southern Appalachian streams. Management strategies were compared for 100 year simulations under: (1) electrofishing removal of rainbow trout, (2) stocking of brook char, (3) habitat alteration (changing mean pool size), and (4) angler harvest of rainbow trout. Results indicated that realistic levels of electrofishing removal of rainbow trout and stocking of brook char juveniles could produce allopatric brook char densities, but that habitat alteration and rainbow trout fishing would not significantly increase brook char densities. Electrofishing and stocking results were robust as similar predictions were obtained under conditions that favored rainbow trout (invasion of rainbow trout adults, frequent year-class failures, reductions in

spawning habitat). Approximately 10 to 20 years are required for allopatric densities to be achieved. Management strategies that reduce competition in the young-of-the-year life stages offer the most promise for restoring brook char stocks in southern Appalachian streams.

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Part 1

General Introduction

Background

Since the 1930's, populations of native brook char, *Salvelinus fontinalis*, have declined throughout streams in the southern Appalachian mountains. Numerous factors (e.g., logging, fishing, stocking of exotics) have contributed to the decline (King 1937), with much emphasis being placed on competition with exotic rainbow trout, *Oncorhynchus mykiss* (Kelly et al. 1980). Coincident with the decline in brook char populations has been an increase in rainbow trout populations (Kelly et al. 1980; Larson and Moore 1985). Many researchers have hypothesized that competitive exclusion of brook char by rainbow trout is the primary factor causing the demise of brook char in southern Appalachian streams.

The factors influencing competition between brook char and rainbow trout remain poorly understood (Fausch 1988). Diets of juvenile and adult brook char and rainbow trout are similar in southern Appalachian stream populations (Ensign 1988; Ensign et al. 1989). No significant difference in habitat use between the species has been observed (Lohr and West 1992). In classical competition theory, differentiation in either diet or behavior (i.e., niche shift) is expected when competitive exclusion occurs (Roughgarden 1989). Little attention has been given to interactions between young-of-the-year life stages of brook char and rainbow trout. Several investigators have observed that juvenile brook char exhibit greater responses than adults to rainbow trout presence (Moore et al. 1983; Whitworth and Strange 1983; Habera 1987). Hence, factors affecting the growth and survival during young-of-the-year life stages may be the key to understanding rainbow trout dominance over brook char in southern Appalachian streams.

Recent emphasis has been placed on the individual's role in population dynamics (Lomnicki 1988) and on the explicit simulation of the individual in models of populations and communities (DeAngelis and Gross 1992; DeAngelis et al. 1994). Individual-based modeling has been useful in examining density-dependence in smallmouth bass, *Micropterus dolomieu* (DeAngelis et al. 1991) and recruitment in striped bass, *Morone saxatilis* (Cowan et al. 1993; Rose and Cowan 1993; Rose et al. 1993). By simulating individuals, competition for food and space can be relatively easily represented. Because of the importance of competition for food and space among stream salmonids (Chapman 1966; Bachman 1984), an individual-based modeling approach for simulating brook char and rainbow trout interactions is especially appropriate.

Overview of Parts

The contents of this work include the development of an individual-based population model for stream-resident brook char and rainbow trout, and its application to examine factors influencing interspecific competition and assess alternative management actions for enhancing brook char stocks. Each part contains its own abstract, introduction, and discussion. Tables, figures, and literature cited within each section appear at the end of the respective section. Part 5 contains a general summary of all results and some concluding remarks regarding areas for future study.

Part 2 provides a model description and the results of model corroboration. This section begins with a detailed description of the model. Model predictions under baseline conditions (water flow, temperature, prey densities typical of southern Appalachian

streams) are reported and corroborated by comparison with data reported in the literature. The section also includes results from allopatric (single-species) simulations and sympatric simulations under contracted and protracted spawning seasons. Part 2 concludes with a general discussion of the effects of sympatry, allopatry, and spawning season duration on density-dependent and competitive interactions between brook char and rainbow trout.

Part 3 examines five factors (aggression, latitude, year-class failures, brook char fecundity, and spawning habitat) as possible explanations for rainbow trout dominance over brook char. A background introduction reviews the evidence for the effects of each of the five factors on brook char - rainbow trout interactions. A short model description is provided, along with a summary of the baseline simulation results. How each of the five factors are simulated is described and results of simulations are analyzed. The section concludes with an evaluation of the likelihood that each factor causes rainbow trout dominance in southern Appalachian streams based on model results and field-based evidence.

Part 4 describes an application of the model for evaluating the effectiveness of potential management actions (electrofishing removal of rainbow trout, stocking of brook char, habitat alteration, and angler harvest of rainbow trout) for enhancing brook char densities. Management approaches designed to enhance brook char populations are reviewed. This is followed by a short model description and a summary of baseline simulation results. How each management action was simulated and the results of simulations are then described. The robustness and response times of successful management actions are determined. This section concludes with a discussion that

combines model results and field observations reported in the literature to determine viable management actions for restoring southern Appalachian brook char populations.

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Part 2

An Individual-Based Model of Stream-Resident Rainbow Trout and Brook Char: Model Description, Corroboration, and Effects of Sympatry and Spawning Season Duration

Abstract

An individual-based model of the population dynamics of sympatric rainbow trout (*Oncorhynchus mykiss*) and brook char (*Salvelinus fontinalis*) is described and analyzed. The model simulates daily growth, mortality, movement, and spawning over the full life cycle of each species for 100 years in a compartmentalized, hypothetical stream configured for the southern Appalachian mountains of the United States. Egg and alevin development is temperature-dependent with mortality having constant, spatial, and temperature-dependent components. Daily growth of fry, juveniles, and adults is based on bioenergetics and consumption of drift prey. Mortality rate of fry through adults decreases with length. Model predictions of densities, growth, age, and size structure were similar to those observed in southern Appalachian streams. Five different conditions were simulated to explore the population dynamics and competition between the two species: (1) sympatric populations (baseline); (2) allopatric brook char; (3) allopatric rainbow trout; (4) and (5) sympatric populations with reduced or increased spawning season durations. Results indicated that density-dependence mainly operated during the fry and juvenile stages, brook char were more affected by interspecific competition than rainbow trout, and crowding of fry negatively affected brook char (with little effect on rainbow trout), whereas low fry density favored brook char.

Introduction

Interspecific competition for space and prey among stream salmonids is frequently conjectured to be a key force controlling their population dynamics. Native brook char,

Salvelinus fontinalis, and exotic rainbow trout, *Oncorhynchus mykiss*, show strong competition in the Appalachian streams of the southeastern United States (Moore et al. 1983). Large reductions in brook char range have been coupled with the expansion of rainbow trout distribution in streams of the Great Smoky Mountains National Park (Kelly et al. 1980; Larson and Moore 1985). These investigations have provided some understanding of the interactions of sympatric populations of brook char and rainbow trout. However, the processes underlying the competitive interactions and the various other factors affecting brook char - rainbow trout communities have yet to be quantified and compared (Fausch 1988).

Mathematical and computer simulation models have been widely used to explore fish population and community dynamics, and the role of inter-individual variation has recently been emphasized (Lomnicki 1988; DeAngelis and Gross 1992; DeAngelis et al. 1994). Competition and predation occur among individuals, and the variability in traits among individuals can have significant consequences on the dynamics of populations (Huston et al. 1988). Individual-based modeling offers great promise for understanding population dynamics of fish (Van Winkle et al. 1993). An individual-based modeling approach has been used to evaluate density-dependence in smallmouth bass populations (DeAngelis et al. 1991) and to compare factors affecting recruitment in striped bass populations (Cowan et al. 1993; Rose and Cowan 1993). Our approach to analyzing competition between brook char and rainbow trout is to use coupled individual-based population models to evaluate the effects of abiotic and biotic factors on the dynamics and interactions of the two populations.

An individual-based model of brook char and rainbow trout resident in a hypothetical stream representative of small, headwater streams in the southern Appalachians is described in this section. Model objectives were: (1) synthesis of field and laboratory data into a spatially-explicit, full life cycle model of brook char and rainbow trout, (2) determining factors controlling competitive dominance between the species, and (3) examining management strategies for enhancing brook char populations. This section is concerned with the first objective. Field and laboratory information on the biology of each species was obtained from the literature (for southern Appalachian salmonids whenever possible). Model predictions under baseline conditions are compared to data reported in the literature, and are analyzed for density-dependent effects on recruitment. Model predictions under allopatric (single species) conditions, and for reduced and expanded spawning seasons, are used to investigate the degree of interspecific competition. In Part 3 the model is used to examine factors affecting competitive dominance of rainbow trout. An evaluation of management strategies for enhancing brook char populations is presented in Part 4..

Model Overview

The model follows the daily growth, survival, and reproduction of individual brook char and rainbow trout in a stream reach consisting of a linear series of connected cells. Water temperature, flow, and prey density are uniform throughout the reach and temperature and flow vary daily. Water velocity, depth, and stream width are calculated from flow, and vary from cell to cell and over time. The model begins with 200 56 mm

individuals of each species; all individuals are model-generated by year three in the simulation. Mature individuals spawn, and eggs and alevins in individual redds are then followed as a cohort until development of the alevin stage is completed. Individual cohorts of swim-up fry resulting from each redd are tracked until development to the juvenile stage, after which individual fish are followed through the juvenile and adult stages. The daily dynamics are simulated for 100 years, with each 365-day year beginning on January 1. Brook char and rainbow trout are treated identically in the model except for their metabolic rates, fecundities, spawning season, egg and alevin incubation times, and length-weight relationships.

Model Stream

The model stream reach is 600 m long and is divided into pool, run, and riffle cells. The reach is composed (by length) of 50% pools, 40% runs, and 10% riffles. Riley (1986) reported compositions of 51 to 83% pools and 17 to 49% riffles and runs for 24 streams in Great Smoky Mountains National Park. The length of each cell is determined as a random deviate from a triangular distribution (mode = mean length of that cell type, minimum = 0.7 * mean, maximum = 1.3 * mean). Mean lengths used are 2.0 m for pools, 1.6 m for runs, and 0.4 m for riffles.

Slope (vertical drop in meters/horizontal change in meters) is used to calculate stream velocity in each cell. Slopes of individual cells are fractions (α for pools, β for runs, and γ for riffles) of the average stream slope, $\bar{s}$ which is equal to 0.10 (Moore et al. 1983; Larson and Moore 1985; Riley 1986). Parameters α and β are generated for each

cell from uniform distributions ($0 < \alpha \leq 0.01$ and $0.5 \leq \beta \leq 1$). For each stream segment (i.e., consecutive pool, run and riffle), γ is then calculated such that the slope over the three cells equals $\bar{s}$. Determined values of γ varied from 5.0 to 18.0.

Daily water temperatures (T, °C) and stream flows (Q, m^3/sec) are generated as stochastic deviations (see Shuter et al. 1980; Rose and Cowan 1993 for details) from the following regression equations fit to long-term observations:

$$T = 8.72 - 5.36\cos(0.0172 day) - 2.41\sin(0.0172 day) \quad (1)$$

$$Q = 0.302 + 0.092\cos(0.0172 day) + 0.169\sin(0.0172 day) \quad (2)$$

where day is calendar day (1 to 365) and the arguments of the trigonometric functions are in radians. Long-term means, and a typical simulated year, of daily temperatures and flows are shown in Figures 1 and 2. Equations (1) and (2) were determined from adjusted daily measurements from 1977 to 1982 in the Little River in Blount County, Tennessee (United States Geological Survey Station 03497300). Little River is a fifth order stream with a drainage area of 27,454 ha at this station. Temperatures used in the simulation (Equation 1) at the Little River station were reduced from observed values by multiplying by 0.7, based on a pattern of decreasing temperature with increasing elevation observed in streams of Great Smoky Mountains National Park (Powers 1929). Daily flows used in the baseline simulation (Equation 2) were reduced from observed values by multiplying by 1,088/27,454, where 1,088 is the drainage area of Sams Creek which is a second order tributary of the Little River with populations of rainbow trout and brook char (Ensign 1988).

Daylight hours are calculated following the methods outlined in Brock (1981) for a latitude of 35°N. The Sams Creek watershed is located at approximately this latitude. The minimum number of daylight hours is 9.6 on December 21 (day 355) and the maximum number of daylight hours is 14.5 on June 22 (day 173).

Water velocity, depth, and width of each cell are calculated from stream flow (Q) and slope of the cell. First, the cross sectional area of the stream is computed from a width to depth relationship. Using channel characteristics for 24 streams in Great Smoky Mountains National Park with sympatric populations of rainbow trout and brook char (Riley 1986), width (w) in meters can be related to depth (d) in meters as a power function (Richards 1976; $R^2 = 0.71$):

$$w = 13.29d^{0.638} \tag{3}$$

Note that d (and thus w) varies from cell to cell in the model using Riley's between-stream data for within-stream variability. Cross sectional area of a cell (A, m^2) depends on depth

$$A = \int_0^d 13.29y^{0.638}dy = 8.11d^{1.638} \tag{4}$$

Manning's equation is then used to determine velocity (v, m/sec) in a cell from the slope, depth, and assumed roughness, n (= 0.045 for streams with gravel beds; Chow 1959):

$$v = \frac{1}{n}d^{\frac{2}{3}}\sqrt{Ms} \tag{5}$$

where M is α for pools, β for runs and γ for riffles. Flow is equal to the product of

velocity and cross sectional area, which from equations (4) and (5), allows calculation of depth at time t in each cell.

$$d(t) = 0.403 \cdot \left(\frac{Q(t)}{\sqrt{Ms}} \right)^{\frac{3}{6.914}} \qquad (6)$$

Equation (3) can then be used to determine width of the cell from the depth.

To summarize, length and slope vary across cells but are constant across days; flow and temperature vary daily, but are constant throughout all cells on any given day; velocity and stream width vary both among cells and over time; water depth varies among cells, over time, and (from bank to bank) within cells. The shapes and slopes of cells in a representative section of the model stream are shown in Figure 3.

Life Stages and Length-Weight Conversions

The life cycle of trout is represented in the model with 5 life stages: eggs (spawning to hatch); alevins (hatch to swim-up); fry (swim-up to 30 to 40 mm, depending on growth rate); juvenile (30-40 mm to 100 mm); and adult (greater than 100 mm). Eggs, alevins, and fry are associated with their redd; fry, juveniles and adults feed on drift prey. Model trout mature at 100 mm (Konopacky and Estes 1986).

Weight of fry, juveniles, and adults (W, g wet weight) is converted to length (L, mm total length) daily:

$$L = 47.88W^{0.329} \quad for \ brook \ char \tag{7}$$

$$L = 46.37W^{0.337} \quad for \ rainbow \ trout \tag{8}$$

Equations (7) and (8) were fit to reported length-weight data (Harned 1976; Whitworth 1980; Riley 1986; Rose 1986; Habera 1987) for brook char ($R^2 = 0.94$) and for rainbow trout ($R^2 = 0.97$). Weight and length are partially uncoupled. Weight is updated daily based on growth. Length increases if weight equals or exceeds weight predicted by Equation (7) or (8). Maximum allowed daily weight loss is 1.5% of body weight for fry and 1% of body weight for juveniles and adults.

Egg and Alevin Development

Individual redds are followed from spawning until emergence (start of fry stage). Days to hatch (egg stage) and days from hatch to emergence (alevin stage) are temperature-dependent. Hatch date and swim-up date are determined by accumulating daily fractional development rates (1/incubation times) until the cumulative value exceeds one. The fractional development rates are from data reported in Regier et al. (1990) for eggs, in Kamler (1992) for rainbow trout alevins, and in Brown and Buck (1939) for brook char alevins (Figure 4). Alevin regressions were slightly modified to obtain realistic emergence dates in the simulations.

Mortality of eggs and alevins occurs via predation, desiccation (drying), disturbance, and temperature extremes. For predation, a mortality rate of 0.013/day is assumed for brook char and 0.03/day for rainbow trout. Brook char egg and alevin

mortality rates were set lower than the rainbow trout egg and alevin mortality rates to obtain similar survival rates (= $e^{-\text{mortality rate}*\text{duration}}$) for both species. The fraction of a redd exposed to the air is determined on a daily basis, with that fraction of eggs or alevins assumed killed by desiccation. The proportion of any existing redd that overlaps with a subsequently created new redd is used to kill that fraction of eggs or alevins in the existing redd. If the sum of redd areas created on a given day exceeds the area of the cell, the egg numbers in each of the new redds are reduced by the ratio of cumulative redd area to cell area. For days when water temperature is less than 0.1°C (Lennon 1967) or greater than 21°C (Carlander 1977), there is a 50% chance of complete loss of the redd.

Fry Stage

Initial lengths of all fry are 20 mm (Brown and Buck 1939; Scott and Crossman 1973). Fry from each redd are followed as a cohort. Fry are first located in water less than 10 cm deep in the same cell as the redd (Cunjak and Green 1983). Fry may move downstream from their natal cell via active movement (growth rate-based or crowding-induced) or passive movement.

Fry more than two days old may actively move downstream in response to weight loss. If fry growth rate today (g_t, g/g/day) is less than their past average growth rate ($\bar{g}_t$, g/g/day), the cohort is split into remaining and moving subcohorts. The past average growth rate ($\bar{g}_t$) is computed as $0.5*\bar{g}_t+0.5*\bar{g}_{t-1}$. The ratio of today's growth rate to their past average growth rate is the fraction of the cohort that remains. For fry less than 30 mm, moving subcohorts are relocated to the first available downstream fry habitat (water

depth less than 10 cm). For fry greater than 30 mm, moving subcohorts become juveniles and enter the stream habitats utilized by juveniles and adults (water depths greater than 10 cm).

Active movement of fry can also be triggered by crowding. Fry require a territory size (tfry, m^2) based on prey density (Slaney and Northcote 1974):

$$tfry = \min\left(0.004 + \frac{0.0025}{mprey^{0.1}} , 0.04 \right) \quad (9)$$

where mprey is the biomass of prey available (mg dry weight). If the sum of tfry values exceeds the available fry habitat in a cell (defined as the surface area from 10 cm depth to each bank), then fry cohorts move downstream (from smallest to largest in mean length) until the sum of fry habitats in the cell is less than the available habitat.

No active movement is permitted when water temperature is at or below 2°C. Fry may not actively move to downstream cells with slopes greater than 0.6 or velocities greater than 20 body lengths (BL)/sec. A 15% mortality is incurred by all actively moving subcohorts.

Passive downstream transport of fry can occur under extreme flow conditions. Feeding fry experience velocities one-half of water velocities in a cell (0.5*v). If experienced velocity is greater than 10 BL/sec, fry "hunker" on the bottom (where they experience velocities of 0.02*v) and do not feed. If hunkering velocity is greater than 10 BL/sec, a 15% mortality is imposed and the entire cohort is moved downstream until reaching a cell whose velocity permits hunkering or the cohort is washed out of the stream reach (i.e., complete mortality).

Fry feeding is based on a territorial mosaic (Hartman 1963; Caron and Beaugrand 1988). All prey entering the fry habitat of a cell are evenly divided among the total number of fry in that cell (see **Growth**).

Mortality of fry is weight- and length-dependent. If fry weight is less than 70% of the weight expected from the fry's length (Equations 7 and 8), then the cohort number is reduced by the ratio of predicted to expected weights. Mortality rate based on length (Z, 1/day) is (Figure 5):

$$Z = 0.0021 + 0.0012e^{-\frac{L}{8252}} \qquad (10)$$

The number of fry in each cohort is reduced on a daily basis by multiplying by e^{-Z}.

Juvenile and Adult Stage

Juvenile and adult fish are followed as individuals, each with the attributes of its original fry cohort (e.g., natal cell, hatch date). Sex of each individual is randomly assigned assuming a 50:50 sex ratio. Juveniles and adults do not enter fry habitat.

Feeding

Three types of feeding are represented: stationed, floater, and mover. Stationed feeding is preferred and is determined assuming establishment of partial territories with a length-based linear dominance hierarchy (longer fish successfully defend against shorter fish) (Jenkins 1969; Caron and Beaugrand 1988). Stationed feeding is only permitted in those cells with depths and lengths greater than 10 cm, and slopes less than 0.6 m/m (i.e.,

not in riffles). Fish without a feeding territory on a particular day become floaters (Grant and Noakes 1987). Drifting prey remaining after consumption by stationed feeders are evenly divided among all floaters in a cell. If water flow decreases such that depth of the cell is less than 10 cm, then all fish in the cell become movers and leave the cell.

Feeding territories are represented by imposing a grid of 60 cm x 60 cm squares (Grant et al. 1989) in each cell. Each day the fish in a cell selects (in order of decreasing length) the 60 cm x 60 cm square closest to the upstream boundary of the cell with the highest available drift. Drift entering a cell depends on water velocity in the cell and cross-sectional area at that site, adjusted for any consumption by stationed feeders in directly upstream squares in the cell. Stationed feeders prevent subdominant (shorter) individuals from occupying any of the 60 cm x 60 cm squares adjacent to or upstream within 5 BL of themselves (McNicol and Noakes 1981; Grant et al. 1989).

Movement

Adult and juvenile fish are allowed to move upstream or downstream among cells on a daily basis, and may be passively washed downstream by extreme flows. Active movement is triggered when today's growth rate is less than the past average growth rate or when water depth becomes less than 10 cm. If experienced velocity (0.7*v for stayers, v for floaters) is greater than 10 BL/sec, fish cease feeding and "hunker" on bottom. Passive downstream movement occurs when velocity experienced by hunkering fish (0.05*v) is greater than 10 BL/sec. Fish are washed downstream to the first cell in which 0.7*v is less than 10 BL/sec, or out of the stream.

Selection of a new cell due to active movement depends on direction of movement, the density of larger individuals, and the maximum distance allowed to move. Direction (upstream or downstream) of movement is assumed equally likely (Cargill 1980; Whitworth 1980). Fish located in the end cells of the stream reach must move further into the stream reach. Fish select the cell, within a maximum distance that has a depth and length greater than 10 cm and slope less than 0.6 m/m, with the fewest fish larger than themselves. Maximum distance is 25 m, or until an upstream cell is encountered which has 10% of its velocity greater than 10 BL/sec and a vertical drop greater than the depth of the adjacent downstream cell (i.e., a barrier). Metabolic costs are incurred dependent on distance moved (see *Metabolism*).

Spawning

Day of spawning is assigned to each mature female from a normal distribution with mean equal to the midpoint of the spawning season and standard deviation (σ) equal to 10 days. The spawning season for brook char is October 1 to December 31 (McFadden 1961; Harned 1976) and for rainbow trout is January 1 to March 31 (Lennon and Parker 1960). Spawning only occurs on days with water temperatures between 2°C and 12°C. Both mature males and females spawn. Spawning lasts one day, during which increased metabolic costs occur, but no feeding takes place. Fecundity (NE, eggs/female) depends on female length (Scott 1962; Lennon 1967):

$$NE = 0.034L^{1.603} \quad \textit{for brook char} \tag{11}$$

$$NE = 0.077L^{1.63} \quad \textit{for rainbow trout} \tag{12}$$

Rainbow trout produce approximately two times more eggs per mm than female brook char.

Spawners move upstream or downstream to get as close as possible to their natal (birth) cell. The day after spawning, spawners return to the feeding location they left to spawn. Spawner movement is the same as relocation of feeders, except spawners may move a maximum distance of 50 m. Cell selection for redd location occurs in the natal or closest cell with depth greater than 6 cm, slope less than 0.6 m/m, and velocity less than 0.5 m/sec on the day of spawning. The redd is located randomly within the cell with area (AR, cm^2) dependent on female length:

$$AR = 0.0114\pi L^{2.137} \tag{13}$$

Equation (13) is based on data compiled by Crisp and Carling (1989) and Dechant and West (1985) for dimensions and shapes of salmonid redds. Eggs in a redd are assumed to be placed uniformly on a square (10 x 10) matrix of points inscribed in a circle with area equivalent to AR. The redd area is discretized into a matrix of points to permit computation of its overlap with other redds.

Mortality

Mortality of adults and juveniles is length- and weight-dependent. Length-based

mortality is based on the same relationship used for fry (Equation 10, Figure 5). An individual dies if a uniform random deviate is less than the probability of death ($1-e^{-Z}$). Weight-based mortality is triggered if weight falls below one-half their expected weight based on their length.

Growth

Growth in weight (W, g wet weight) is represented using a bioenergetics equation

$$W_{t+1} = W_t + pC_{max}A - M \tag{14}$$

where C_{max} is the maximum daily consumption (g wet weight/day), p is the proportion of C_{max} realized, A is assimilation efficiency, and M is total metabolism (g wet weight/day). Assimilation is assumed to be 0.65 for all fish.

Maximum consumption

C_{max} is a function of weight and temperature:

$$C_{max} = 0.28\left(\frac{8.0+35.57W^{0.64}}{220}\right)\left(3.77^{\frac{T-15}{10}}\right)\left[1+\frac{h}{6}\left(1-e^{-hR}\right)\right] \tag{15}$$

$$R = 0.053e^{0.112T} \tag{16}$$

where T is water temperature (°C), h is the number of feeding hours, and R is the rate of gastric evacuation (Elliott 1972). Equation (15) was determined from data for brown trout (Elliott 1975a; 1975b); the multiplier of 0.28 adjusts predicted growth rates to

reported rates for rainbow trout (Wurtsbaugh and Davis 1977a; 1977b). The 0.28 multiplier is also used with brook char, whose consumption rates are assumed to be similar to rainbow trout. The value of h depends on feeding strategy (see Table 1).

Calculation of p

Parameter p is determined as realized consumption (C_r) divided by C_{max}. C_r depends on the number of each of four prey types eaten,

$$C_r = \sum_{i=1}^{4} B_i PW_i \qquad (17)$$

where B_i is the number of prey type i eaten and PW_i is the weight (g wet weight) per individual of prey type i. The summation over prey types differs based on fish size (Bisson 1978; Allan 1981; Grant and Noakes 1986). Fish less than 30 mm eat the smallest prey type; fish between 30 mm and 50 mm eat the two smallest prey types; fish between 50 mm and 60 mm eat the three smallest prey types; fish between 60 mm and 80 mm eat all prey types; and fish greater than 80 mm eat the three largest prey types (Hill and Grossman 1993). If necessary, prey are removed from the smallest to largest types until C_r is less than C_{max}.

B_i is computed as a deviate from a binomial distribution, with the number of encountered prey of type i (E_i) as the number of trials and the probability of capture (P_c) as the probability of success. The number of encountered prey of each type is computed differently for the different feeding strategies (see Table 1). Probability of capture (P_c;

Figure 6) decreases sharply with increasing water velocity and decreases slightly with decreasing water temperature (Hill and Grossman 1993).

Densities of each of four prey types (1.4/m^3, 0.07/m^3, 0.04/m^3 and 0.008/m^3 from smallest to largest prey) are assumed uniform throughout the stream reach. Weights per individual associated with the four prey types are: 3.6, 9.5, 32.0 and 104.0 mg wet weight. This yields a total prey biomass of 2.7 mg wet weight/m^3, similar to values reported for southern Appalachian trout streams (0.9 to 8.0 mg wet weight/m^3 - Ensign 1988; 0.3 to 5.5 mg wet weight/m^3 - O'Hop and Wallace 1983) with the smallest prey dominating numerically in the drift (see Waters 1961; Hill and Grossman 1993).

Metabolism

M (g wet weight/day) is the sum of routine and active metabolism:

$$M = 0.19\left((24-H)\left(\frac{6.2+2.5W^{0.92}}{10^4}\right)\left(2.1^{\frac{T-9}{10}}\right)+0.0028HWe^{-D_0+D_1 v_{sw}}\right) \quad \textit{for brook char} \quad (18)$$

$$M = 0.19\left((24-H)\left(\frac{6.2+3.2W^{0.92}}{10^4}\right)\left(1.9^{\frac{T-11}{10}}\right)+0.0028HWe^{-D_0+D_1 v_{sw}}\right) \quad \textit{for rainbow trout} \quad (19)$$

where D_0= 0.57, 0.67, 0.67, and 1.06 and D_1= 0.05, 0.07, 0.08, and 0.08 (for spring, summer, fall, and winter, respectively), H is the number of hours of activity during the day (distinct from h, the number of feeding hours; Table 1), and v_{sw} is the cell water velocity expressed as BL/sec. Routine metabolism terms are derived from laboratory data (brook char: Beamish 1963, Kamler 1992; rainbow trout: Wieser 1985, Kamler 1992). The

multiplier of 0.19 adjusts predicted growth rates to reported rates for rainbow trout (Wurtsbaugh and Davis 1977a; 1977b). The 0.19 multiplier is also used with brook char, whose metabolic rates are assumed to be similar to rainbow trout. Active metabolism is an exponential function of swimming speed (v_{sw}, BL/sec) whose values of D_0 and D_1 vary seasonally (Facey and Grossman 1990). H and v_{sw} are computed dependent on feeding strategy (Table 1).

Technical Information and Order of Computations

The model computer code was written in FORTRAN 77 computer language and simulations were performed on a DEC Alpha workstation (UNIX operating system). A typical simulation with sympatric populations and 100 year duration required approximately two hours of CPU time.

Previously written, public domain algorithms were used to generate random numbers, binomial deviates, and standard normal deviates. The function RAN1 (Press et al. 1992), which returns pseudorandom numbers between 0 and 1 (given an initial negative integer), was used to create all random numbers required by the model. The function BNLDEV (Press et al. 1992), which returns pseudorandom deviates from a binomial distribution given the number of trials and the probability of success, was used to generate binomial deviates used in determining prey capture success. The function GASDEV (Press et al. 1992), which returns pseudorandom deviates from a standard normal distribution, was used to generate normal deviates used to assign spawning days. Pseudorandom deviates from a gamma distribution, used to create stochastic temperature

and flow, were generated according to an alogrithm using exponential variates developed by Hastings and Peacock (1975).

The first step in the computations is the initialization of the model stream and of the brook char and rainbow trout populations. During initialization of the stream, length and slope of each pool, run, and riffle cell are assigned. These values remain constant throughout the simulation. Each individual of each species in the initial populations is assigned an initial length (random between 55 mm and 57 mm), weight is then determined from the length-weight relationship (Equations 7 and 8), and sex is assigned based on 50:50 sex ratio.

The sequence of computations in the model involves a series of nested loops. The loops consist of an outermost loop over years (from 1 to 100), for each year a loop over days (from 1 to 365), for each day a loop over stream cells (from 1 to 450 for a 600 m stream), a loop over redds, and a loop over fry cohorts, juveniles and adults, and for each cell two loops over fry cohorts and three loops over juvenile and adult fish.

Each year before the loop over days begins, stream flows and stream temperatures for each day of the year are generated and stored. Daily temperatures and flows are the result of deviations from the long term means (Equations 1 and 2). Day-to-day stochasticity is determined from a two parameter gamma distribution. The parameters of the gamma distribution are the ratio of the mean to variance and the ratio of the mean squared to the variance. Parameter estimates were determined from the temperature and flow data records of the actual observations of temperature and flow.

For each cell, depth, width, and water velocity are computed and all fry cohorts

and juvenile and adult individuals in the cell are identified, and their growth, survival, spawning, and movement are evaluated. Depth, width, and water velocity are computed from the daily flow and the slope of the cell. For each cell, initial loops over fry cohorts and juvenile and adult individuals are performed to determine the number of each in the particular cell. These loops also index the fry cohorts, juveniles, and adults in descending order of length and determine if passive movement is occurring. A second loop over the fry cohorts located in the cell determines their prey consumption, growth rates, movement (new cell location) for the next day, and length-based, weight-based, and movement-based mortalities. A second loop over individual juveniles and adults in the cell identifies spawners, stayers, floaters, and movers (active and passive). The spawning cell, redd location, number of eggs spawned, and growth is determined for spawners. Feeding site, prey consumption, growth, weight-based movement for the next day, and total prey consumption is determined for stayers. A third loop over juveniles and adults in the cell determines prey consumption, growth, and weight-based movement for the next day by floaters.

At the end of each day (i.e., after loops over cells, fry cohorts, and juveniles and adults are completed), loops over active and new redds and over fry cohorts, juveniles, and adults are performed. In the loop over redds, location of new redds is determined, and development and mortality of existing redds is updated. In the loop over fry cohorts, juveniles, and adults, new location, prey consumption, and growth of movers, and length-based and weight-based mortalities of juveniles and adults are determined. The loop over fry cohorts, juveniles, and adults also removes dead fish and fry cohorts with no surviving

fry from arrays. After this is completed on the last day (day 365) of the last year (year 100), the simulation ends.

Simulations

Five different conditions were simulated to explore the population dynamics and competition between the two species: (1) sympatric populations (baseline); (2) allopatric brook char; (3) allopatric rainbow trout; (4) and (5) sympatric populations with reduced or increased spawning season durations. Spawning season duration was changed by changing the standard deviation of the normal distribution used to assign day of spawning (σ) from the baseline value of 10 days. A value of $\sigma = 5$ days was used for decreased spawning season duration, and $\sigma = 20$ days was used for increased spawning season duration. Spawning season duration was varied to further investigate the effects of crowding on fry stage dynamics, which the baseline and allopatric simulations indicated as important. The same initial conditions were used for all simulations. Three replicate simulations that differ in their random number sequence were performed for each of the five conditions, but two additional baseline simulations were also performed to compare variation in life stage estimates and densities among replicates. Different random number sequences affect the outcome of stochastic processes, such as stream morphology (lengths and slopes of individual pools, runs, and riffles), prey encounters, mortality, and direction of movement. Stream geometry, temperature, and flow differed between replicates, but were identical for each replicate across the five simulations. Whenever possible, results are reported separately for the three replicates; for simplicity, simulations of replicate 2

only are reported in some instances. For some simulations, major differences in growth and survival were obtained during the first five years of the simulation. During this transition period, the populations were changing rapidly as they approached the more stable levels representative of the remaining 95 years of the simulation. Results are reported in three sections: sympatric simulations under baseline conditions, allopatric results, and results with reduced and increased spawning season durations.

Baseline Results

Densities

Predicted annual post-fry densities of both species were stable over time (Figure 7). Annual densities were computed as the average over all days of the year. Brook char annual densities ranged from 0.04 to 0.16/m^2 and rainbow trout annual densities from 0.05 to 0.16/m^2 across all replicates; average rainbow trout annual density (0.13/m^2) was higher than average brook char annual density (0.10/m^2). Predicted annual densities were similar to reported values for southern Appalachian streams (0.01 to 0.17 trout/m^2 - Habera 1987; 0.06 to 0.34 rainbow trout/m^2 and 0.01 to 0.23 brook char/m^2 - Whitworth 1980; 0.016 to 0.13 rainbow trout/m^2 and 0.007 to 0.06 brook char/m^2 - Ensign et al. 1989). Predicted and observed (from Habera 1987) correlations between annual densities of brook char and rainbow trout were also similar (Figure 8).

Age and Size Structure

In agreement with Whitworth and Strange (1983), the age and size structures of

both species were dominated by recruits (Figures 9 and 10). Lennon (1967) and Larson and Moore (1985) also reported that in contrast to trout populations in other streams, southern Appalachian rainbow trout and brook char populations are dominated by less than age-2 fish. Size and age structure in the model populations were the result of relatively low prey density and high mortality of younger, smaller fish.

Survival and Growth

Survival rates of eggs, fry, juvenile, and age-1 adult brook char were higher than those for rainbow trout, but age-2 and age-3 rates were similar for both species (Table 2). The differences between brook char and rainbow trout egg and juvenile survival rates were small, but consistent for all three replicate simulations. Lower predation mortality offset longer egg and alevin durations in brook char to yield a slightly higher survival of brook char eggs and alevins (13% versus 12% for rainbow trout). Faster growth rates of fry, juvenile, and age-1 brook char accounted for their higher survival rates, because mortality decreases with size.

Predicted growth rates were of similar magnitude to observed rates, were initially higher for brook char, and decreased with age for both species. Predicted average fry growth rates were 0.38 mm/day (0.05/day) for brook char and 0.30 mm/day (0.04/day) for rainbow trout. Rose (1986) reported growth rates of brook char fry of 0.58 mm/day (0.06/day) and of rainbow trout fry of 0.42 mm/day (0.04/day). Predicted growth rates were also similar to rates derived from data reported in Whitworth (1980) -- brook char: 0.016/day versus 0.009/day for age-1, 0.0029/day versus 0.0038/day for age-2, 0.001/day

versus 0.0006/day for age-3; rainbow trout: 0.012/day versus 0.009/day for age-1, 0.0029/day versus 0.0049/day for age-2, 0.001/day versus 0.0002/day for age-3. Model brook char grew faster than rainbow trout because of their lower routine metabolism (Equations 18 and 19). Lohr and West (1992) also observed that age-0 brook char grew faster than age-0 rainbow trout, with little differences between the species for older fish.

Habitat, Movement and Behavior

Pools were utilized the most (> 71% of all brook fry, > 57% of rainbow fry, and > 90% of all juveniles and adults were in pools). Riffles were utilized very little due to high water velocities or shallow water. Annual percentage of juveniles and adults in pools correlated to annual percentage surface area of pools in the stream ($R^2 > 0.30$ for brook char, $R^2 > 0.37$ for rainbow trout), but not for fry ($R^2 < 0.02$), which moved little from their redd location.

Stationed feeding increased with fish size. In all simulations, 47 to 82% of juveniles exhibited stationed feeding with 1 to 28% adopting the floater strategy. For age-1 and older fish, greater than 66% held feeding territories, while less than 7% were floaters. Over 99% of stationed and floater individuals (both species, all replicates) occupied cells with water velocities from 15.0 to 30.0 cm/sec, compared to trout being found in waters with velocities of 5.0 to 25.0 cm/sec (Lohr and West 1992; Hill and Grossman 1993).

Movement of individuals through the stream reach was limited. Average net movement of fry was 4.3 m downstream for brook char and 5.0 m downstream for

rainbow trout. For individuals surviving to age-3, net movement was 4.6 m upstream for brook char and 6.9 m upstream for rainbow trout. Net movement of model fish was limited partially because of cancellation by equally likely upstream or downstream direction of movement, and partially because low variability in adult growth rates seldom triggered a movement response. Whitworth (1980) reported little movement (an average of 13 m upstream for brook char, 24 m upstream for rainbow trout) of sympatric trout in southern Appalachian headwater streams. Whitworth's estimates of movement are higher than our predicted values because his measurement resolution (30 m stream sections) was much coarser than is possible in model simulations. Passive movement and "hunkering" did not occur in the simulations because fish never experienced velocities greater than 10 BL/sec.

Recruitment and Density Dependence

Annual recruitment (survivors to 100 mm) was positively correlated to egg production (Figure 11; $R^2 = 0.66, 0.26, 0.40$ for brook char and $R^2 = 0.33, 0.23, 0.08$ for rainbow trout for the 3 replicate simulations). Average fry growth rate was negatively related to the number of fry for each species (Figure 12; $R^2 = 0.24, 0.05, 0.32$ for brook char and $R^2 = 0.55, 0.64, 0.52$ for rainbow trout). No significant correlations between numbers and growth rates were obtained for juveniles and adults. Fry survival was positively correlated to fry growth rate (Figure 13; $R^2 = 0.56, 0.35, 0.58$ for brook char and $R^2 = 0.59, 0.67, 0.62$ for rainbow trout). Survival was less correlated with growth rate for juveniles ($R^2 < 0.19$ for brook char; $R^2 = 0.32, 0.52, 0.36$ for rainbow trout) and

for adults ($R^2 < 0.06$ for both species, all replicates). Prey are equally divided among the fry in a cell; thus fewer fry resulted in faster growth, and faster growth translated to increased survival.

Fry growth was largely determined by temperature and density of trout, while flow was more important to juvenile and adult growth (Table 3). Multiple regression analysis of daily temperature, daily flow, and total daily biomass of trout (for each replicate) explained about 20 to 50% of the variation in daily growth rate of fry, juveniles, and adults. Brook char and rainbow trout fry growth rates were negatively related to total fry biomass. Rainbow trout fry growth rates were also positively related to temperature. Flow accounted for less than 6% of the variation in fry growth for both species over all replicates. For juveniles and adults, variation explained by flow generally increased with age (i.e., size), while variation explained by temperature and biomass decreased with age. Flow affects prey availability to juveniles and adults. Increasing flow increases prey encounters by increasing velocity (i.e., increased delivery rate) and depth (i.e., increased search area) within a cell.

Variation among Replicates

Predicted probability of survival, growth rates, and densities were very similar among replicates. Based on five replicate baseline simulations, maximum percentage deviations from the grand mean of predicted probability of survival were less than 8%, of predicted growth rates were less than 4%, and of predicted mean densities were less than 11% (Table 4).

Allopatric Results

The major difference between baseline (sympatry) and allopatric conditions was in fry-stage survival, with brook char being more affected than rainbow trout. Brook char densities increased from approximately $0.10/m^2$ under baseline to approximately $0.23/m^2$ when alone, while rainbow trout densities increased from approximately $0.13/m^2$ to approximately $0.17/m^2$ in allopatry (Figure 14). During the transition period (years 1 to 5), allopatric brook char fry survival was higher than in baseline due to reduced movement-related mortality; fry growth rate increased slightly and starvation-related mortality decreased slightly (Figure 15). Rainbow trout fry showed similar, but smaller, responses to allopatry. Fry survival during the transition period increased mostly due to decreased starvation-related mortality. Growth rates and movement mortality changed little from baseline. Juvenile and adult growth and survival rates, and fry rates after the transition period, were similar between allopatric and sympatric conditions with maximum percent changes less than 8% over all replicates for both species.

Spawning Season Duration Results

Increased spawning season duration ($\sigma = 20$) favored brook char, while decreased spawning season duration ($\sigma = 5$) favored rainbow trout (Figure 16). Changed spawning season duration caused more variation in emergence times of brook char than rainbow trout because of the differences in the temperature dependencies of egg and alevin development rates (Figure 4) and temperatures during spawning (Figure 17). Brook char emergence times were greatly spread out in time for $\sigma = 20$ compared to baseline.

Changed spawning season duration affected the degree of fry crowding for both species. Because of reduced fry crowding under increased spawning season duration ($\sigma = 20$), fry survival of both species increased (movement mortality of brook char decreased) during years 6 to 100 (Figure 18). Fry survival of brook char also increased slightly during the transition period (Figure 15). Increased fry survival caused higher juvenile densities that decreased rainbow trout growth rates more than brook char because of brook char's lower routine metabolic rate (Equations 18 and 19). Slower juvenile rainbow trout growth rates significantly decreased their survival (Figure 18) and their mean size at age (102 mm versus 115 mm in baseline for age-1). Smaller size at age resulted in decreased rainbow trout egg production (an average of 64% below baseline) and thus lowered rainbow trout density.

Decreased spawning season duration ($\sigma = 5$) resulted in moderately decreased brook char densities and had little effect on rainbow trout densities (Figure 16). Brook char fry survival was slightly decreased (due to increased movement-related mortality) during the transition period (Figure 15). Growth and survival rates of juvenile and adult brook char, and all stages of rainbow trout, did not consistently differ from their baseline values (Figure 18).

Discussion

A spatially explicit, individual-based model was used to simulate the competition between brook char and rainbow trout in a hypothetical stream representative of a small, high-gradient southern Appalachian stream. Mechanisms for competitive exclusion of

brook char by rainbow trout in southern Appalachian streams remain unclear (Fausch 1988). Model predictions under baseline (sympatric) conditions compared favorably to available information. Model predictions under allopatry, and for increased and reduced spawning season durations, were compared to better understand the factors affecting interspecific competition. Model results indicated that: (1) density-dependence operated mainly during the fry and juvenile stages, (2) brook char were more affected by interspecific competition than rainbow trout, and (3) high fry density negatively affected brook char with little effect on rainbow trout whereas low fry density favored brook char.

Model simulations indicated strong density-dependence in the fry stage, moderate density-dependence during the juvenile stage, and little density-dependence during the adult stage. Recruitment was strongly correlated to egg production (Figure 11). Under baseline conditions, fry survival rate was positively related to fry growth rate (Figure 13), which in turn, was negatively related to fry number (Figure 12). The major difference between sympatric and allopatric conditions, and between reduced and increased spawning season durations, was in fry and juvenile stage growth and survival rates. No differences were found in predicted adult survival and growth rates between sympatric, allopatric, and changed spawning season duration simulations. Elliott (1987) also found limited density-dependence in a stream-resident population of brown trout, which he suggested was due to the low densities typical of populations in marginal habitats. In the model, prey and trout densities were low relative to many trout streams outside of the Appalachian region (see Waters 1961). Others (Habera 1987; Ensign 1988; Ensign et al. 1989; Lohr and West 1992) have suggested that direct competition between adults likely plays a minor

role in determining population dynamics under sympatry.

Brook char were more affected by interspecific competition in model simulations than were rainbow trout. Under allopatric conditions, brook char densities increased 130% compared to a 31% increase in rainbow trout. With increased spawning season duration, fry crowding was reduced, and brook char densities increased 155% while rainbow trout densities decreased 57%. Under decreased spawning season duration, fry crowding and competition were intensified, and brook char densities decreased 56%; rainbow trout densities were only slightly affected (increased by 14%).

Increased crowding of fry had negative effects on brook char but little effect on rainbow trout, whereas lowered fry densities favored brook char. Rose (1986) reported reduced growth of brook char fry upon emergence of rainbow trout fry. Thus, the higher fecundity of rainbow trout and contraction of the spawning seasons could lead to competitive exclusion by emerging rainbow trout fry simply numerically overwhelming brook char fry.

Predicted population level changes occurred as a result of small, subtle changes in growth, movement, and survival in the relatively brief fry stage (20 to 30 mm) and among juveniles (less than 100 mm). A critical assumption of the model is that prey are divided equally among all fry in a cell. Evidence suggests that trout fry competing over a relatively uniform substrate do not exhibit a dominance hierarchy because of their similarities in size, age, and development (Jenkins 1969; Caron and Beaugrand 1988). The validity of the model assumption of equal division of prey among fry deserves further evaluation.

Environmental variability led to coexisting populations of brook char and rainbow trout. In model baseline simulations, rainbow trout fry and age-0 growth rates were more highly correlated to temperature than brook char fry and age-0 growth rates (Table 3). Survival was positively correlated to fry growth rate (Figure 13) and juvenile growth rate (R^2 = 0.32, 0.52, 0.36) in rainbow trout. Rainbow trout recruitment was higher in years with warmer temperatures than in years with colder temperatures. There were an average of 219 rainbow trout recruits in years with average spring temperatures greater than 11.2°C compared to 194 recruits in years with average spring temperatures less than or equal to 11.2°C. Higher rainbow trout recruitment resulted in greater rainbow trout egg production in subsequent years as recruits aged, which decreased brook char fry growth and survival in those years. Brook char post-fry densities were negatively correlated to rainbow trout egg production (R^2 = 0.47, 0.43, 0.21). Therefore, brook char populations declined following years with environmental conditions that caused increased rainbow trout recruitment (warmer temperatures), but brook char increased when conditions were less favorable for rainbow trout recruitment (colder temperatures). Also, infrequent low flow events during egg incubation resulted in high (> 20%) egg losses that drastically reduced fry emergence and effectively reset initial conditions for the populations. Because of the differences in the timing of their spawning seasons, low flow events did not always effect both species the same. Year to year differences in water temperatures and infrequent low flow events during egg incubation created environmental fluctuations that enabled brook char and rainbow trout to coexist. Chesson (1994) also found that environmental stochasticity promoted coexistence of competitors in Lotka-Volterra

population models. Chesson and Warner (1981) explained coexistence in competing coral reef fishes by chance availability of feeding territories that were related to environmental variability.

Predicted dynamics occurred without differences in prey utilization, habitat utilization, or behavior by either species. The differences between brook char and rainbow trout in the model were only in egg and alevin incubation times, metabolic rates, length-weight relationships, fecundities, and timing of spawning. Field studies designed to detect differences in diets, habitat use, or behavior between brook char and rainbow trout adults have been unsuccessful (Ensign et al. 1988; Lohr and West 1992). Our model results suggest that major differences between brook char and rainbow trout adults are not necessary for rainbow trout to outcompete brook char. Focusing on early life stage dynamics may be the key to determining the mechanisms controlling competitive exclusion of brook char in the southern Appalachians.

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Appendix: Tables and Figures

Table 1: Specific values used for the number of feeding hours (h), swimming speed (v_{sw}, BL/sec), area searched (m^2), and the number of active hours (H). These quantities are used to compute the number of prey encountered (E_i), which with the probability of capture (P_c), results in the number of prey eaten (B_i, in Equation 17). T=temperature (°C), v=cell current velocity (m/sec), and L_s (m standard length); L_s is computed as L/(1000·1.15) where L is length (mm total length) and 1.15 converts standard length to total length.

Individual	Number of feeding hours (h)	Swimming speed (v_{sw})	Area searched	Number of prey type i encountered (E_i)	Number of active hours (H)
Stayer	Daylight hours or 1 if T ≤ 2°C	$0.7v/L_s$	The area determined by the stream bed, surface of the water, and the depth 2 BL to each side of the fish	Product of the area searched, v and prey drift density minus prey eaten by stayers *directly upstream* in the cell	h
Floater	Daylight hours or 1 if T ≤ 2°C	v/L_s	The area determined by the stream bed, surface of the water and the 10 cm depth marks	Product of the area searched, v and prey drift density minus prey eaten by all stayers in the cell; prey are divided equally among all floaters in the cell	h
Upstream mover	Sum of time swimming in cells where feeding occurs; calculated as 3 times cell length divided by swimming speed in m/s ($=v_{sw}L_s$)	$2v/L_s$ in cells where feeding occurs; $0.1v/L_s$ in cells where no feeding occurs	$4\pi L$ in cells where feeding occurs; 0 in cells of no feeding	Product of 3 times the cell length, area searched and prey drift density minus prey eaten by all stayers and floaters in the cells	h + sum of time swimming in cells where no feeding occurs; calculated as cell lengths divided by swimming speeds in m/s ($=v_{sw}L_s$)
Downstream mover	0	0	0	0	0
Spawner	0	$2v/L_s$	0	0	1 + sum of time swimming through cells; calculated as cell lengths divided by swimming speeds in m/s ($=v_{sw}L_s$)
Feeding fry	Daylight hours or 1 if T ≤ 2°C	$0.5v/L_s$	The area determined by the stream bed, surface of the water, 10 cm depth marks, and the stream banks	Product of the area searched, v and prey drift density; prey are divided equally among all fry in the cell	h
Hunkered adult	0	$0.05v/L_s$	0	0	Daylight hours
Hunkered fry	0	$0.02v/L_s$	0	0	Daylight hours

Table 2: Life stage-specific mean duration, mortality rate, probability of survival, growth rate, and mean length for years 6 to 100 of the replicate 2 baseline simulation. Age-1 fish have lived 1 year, age-2 fish have lived 2 years, and age-3 fish have lived 3 years.

Stage	Duration (days)	Mortality rate (1/day)	Survival ($=e^{-\text{mortality rate}*\text{duration}}$)	Growth rate (mm/day)	Growth rate (1/day)	Mean length (mm)
Brook char						
eggs and alevins	159	0.014	0.13	-	-	-
fry	33	0.051	0.19	0.38	0.046	31[a]
juveniles (< 100mm)	138	0.0029	0.67	0.52	0.027	100[b]
age-1	252	0.0027	0.51	0.34	0.016	116
age-2	365	0.0023	0.43	0.13	0.0029	164
age-3	365	0.0022	0.45	0.06	0.0010	185
Rainbow trout						
eggs and alevins	70	0.031	0.12	-	-	-
fry	41	0.057	0.10	0.30	0.035	31[a]
juveniles (< 100mm)	173	0.0028	0.62	0.43	0.022	100[b]
age-1	313	0.0026	0.44	0.27	0.012	115
age-2	365	0.0023	0.43	0.13	0.0029	163
age-3	365	0.0022	0.45	0.06	0.0010	186

[a]Length at end of fry stage, [b]Length at maturity

Table 3: Squared partial correlation coefficients (with their sign) from the multiple regression of brook char and rainbow trout growth rates (g/g/day) on daily biomass, temperature and flow for the 3 replicate baseline simulations.

Y (dependent variable)	X (independent variable)	brook char			rainbow trout		
		replicate 1	replicate 2	replicate 3	replciate 1	replicate 2	replicate 3
fry growth rate	total fry biomass	-0.20	-0.21	-0.19	-0.21	-0.24	-0.21
	temperature	NS	NS	NS	+0.34	+0.34	+0.33
	flow	NS	NS	NS	NS	NS	NS
age-0 (juveniles and adults) growth rate	total adult and juvenile biomass	NS	NS	NS	NS	NS	NS
	temperature	+0.23	+0.19	+0.21	+0.47	+0.45	+0.47
	flow	+0.15	+0.10	+0.15	NS	NS	NS
age-1 growth rate	total adult and juvenile biomass	NS	NS	NS	NS	NS	NS
	temperature	+0.14	+0.14	+0.11	+0.11	+0.10	+0.12
	flow	NS	NS	NS	+0.16	+0.15	+0.14
age-2 and older growth rate	total adult and juvenile biomass	NS	NS	NS	NS	NS	NS
	temperature	NS	NS	NS	NS	NS	NS
	flow	+0.19	+0.21	+0.17	+0.15	+0.17	+0.12

NS means partial $R^2 < 0.10$

Table 4: Mean values of life-stage specific estimates of probabilities of survival, growth rates, and post-fry densities based on years 6 to 100 for each of 5 replicate model simulations. Also shown are the grand means over replicates, and the maximum percentage deviations among replicates ($100 \cdot (x_{rep\ i} - \bar{x})/\bar{x}$).

	Replicate					Grand	Maximum
Brook char	1	2	3	4	5	mean, $\bar{x}$	deviation
egg survival	0.13	0.12	0.13	0.13	0.13	0.13	-7.7%
fry survival	0.19	0.19	0.19	0.18	0.18	0.19	-5.3%
juvenile survival	0.68	0.68	0.68	0.68	0.67	0.68	-1.5%
age-1 survival	0.44	0.44	0.43	0.44	0.43	0.43	2.3%
fry growth (mm/day)	0.37	0.38	0.38	0.37	0.38	0.37	2.7%
juvenile growth	0.52	0.52	0.52	0.52	0.52	0.52	0.0%
age-1 growth	0.13	0.13	0.13	0.13	0.13	0.13	0.0%
post-fry density (number/m^2)	0.09	0.10	0.10	0.11	0.11	0.10	-10.0%
Rainbow trout							
egg survival	0.12	0.12	0.12	0.12	0.12	0.12	0.0%
fry survival	0.10	0.10	0.10	0.10	0.10	0.10	0.0%
juvenile survival	0.62	0.63	0.63	0.62	0.62	0.62	1.6%
age-1 survival	0.44	0.44	0.43	0.44	0.43	0.43	2.3%
fry growth	0.29	0.29	0.30	0.30	0.30	0.30	-3.3%
juvenile growth	0.42	0.43	0.43	0.43	0.42	0.42	2.4%
age-1 growth	0.13	0.13	0.13	0.13	0.13	0.13	0.0%
post-fry density (number/m^2)	0.13	0.13	0.13	0.12	0.12	0.13	-7.7%

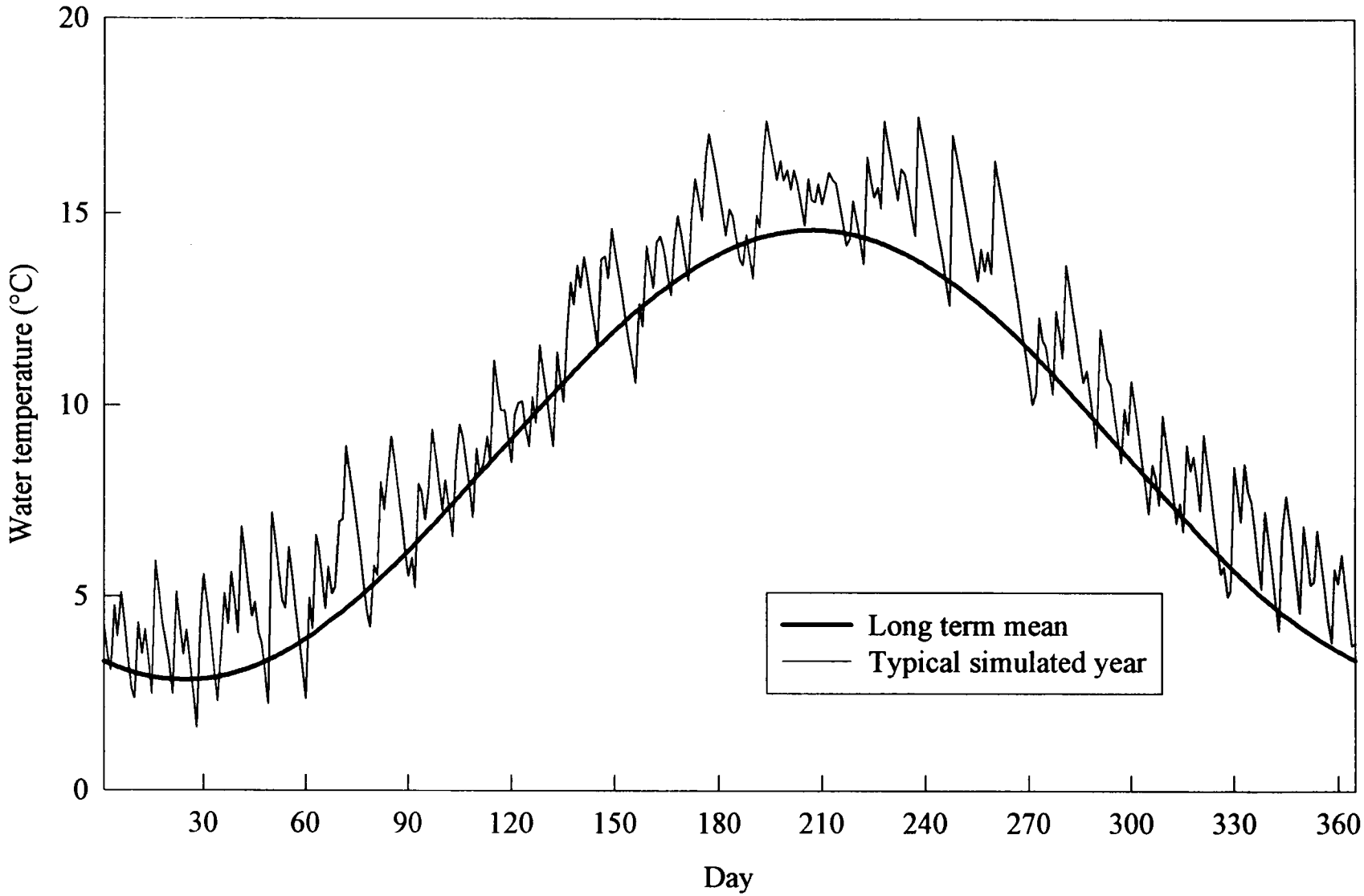

Figure 1: Long term mean and a typical simulated year of daily water temperature in the model stream.

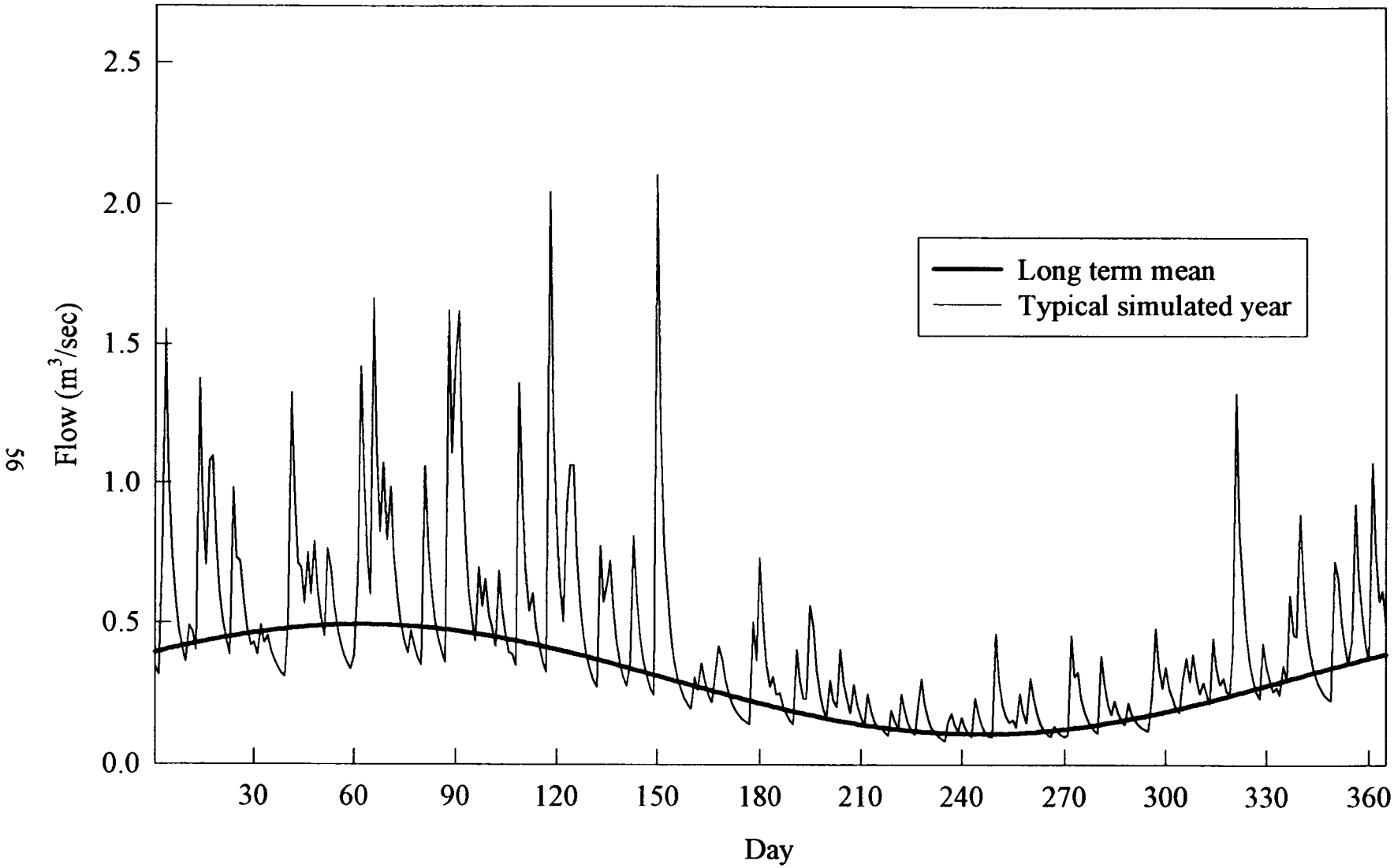

Figure 2: Long term mean and a typical simulated year of daily model stream flow.

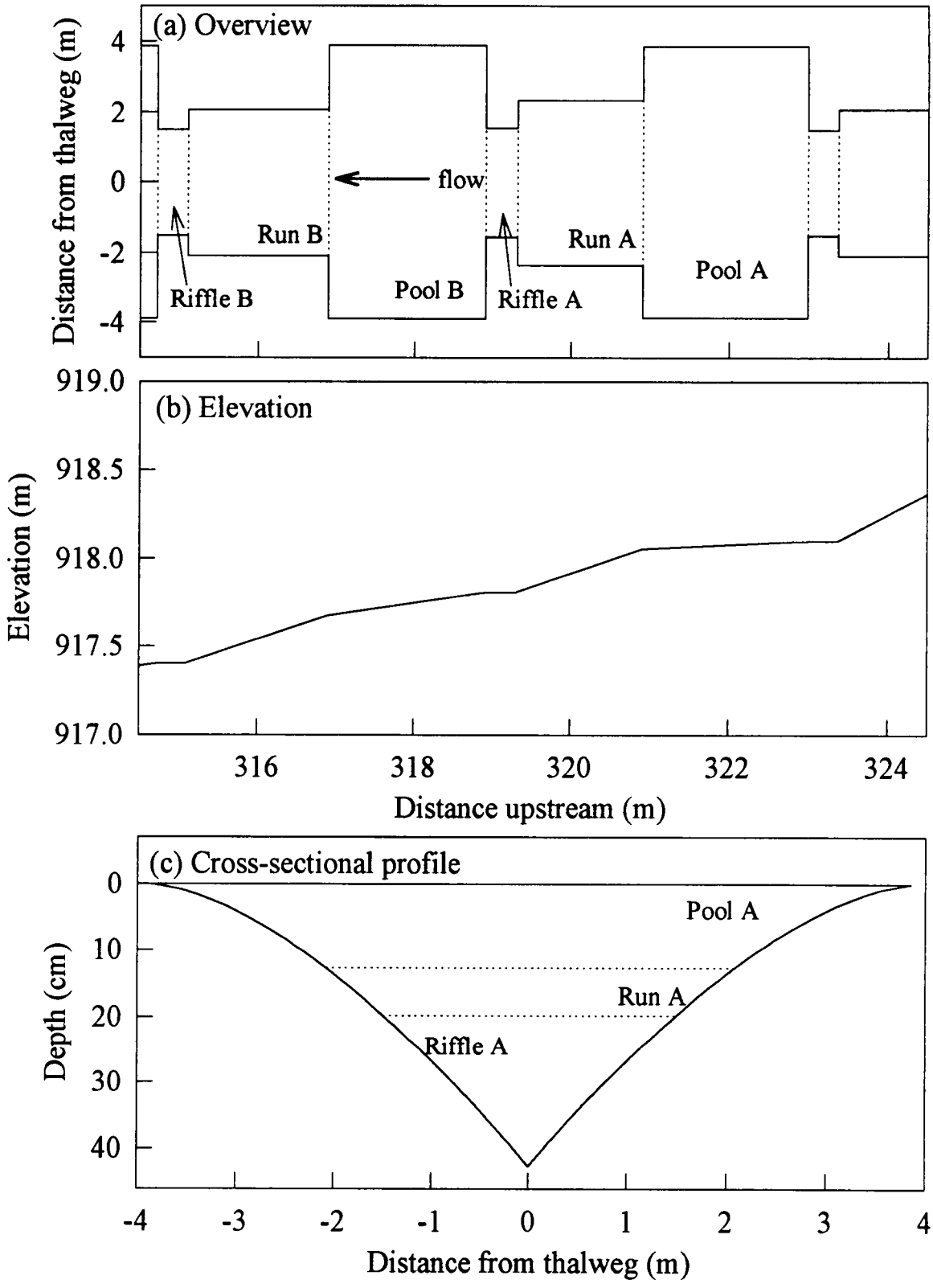

Figure 3: The shapes and slopes of cells in a representative section of the model stream (a) overview (i.e., aerial view), (b) elevation, and (c) cross-sectional profile.

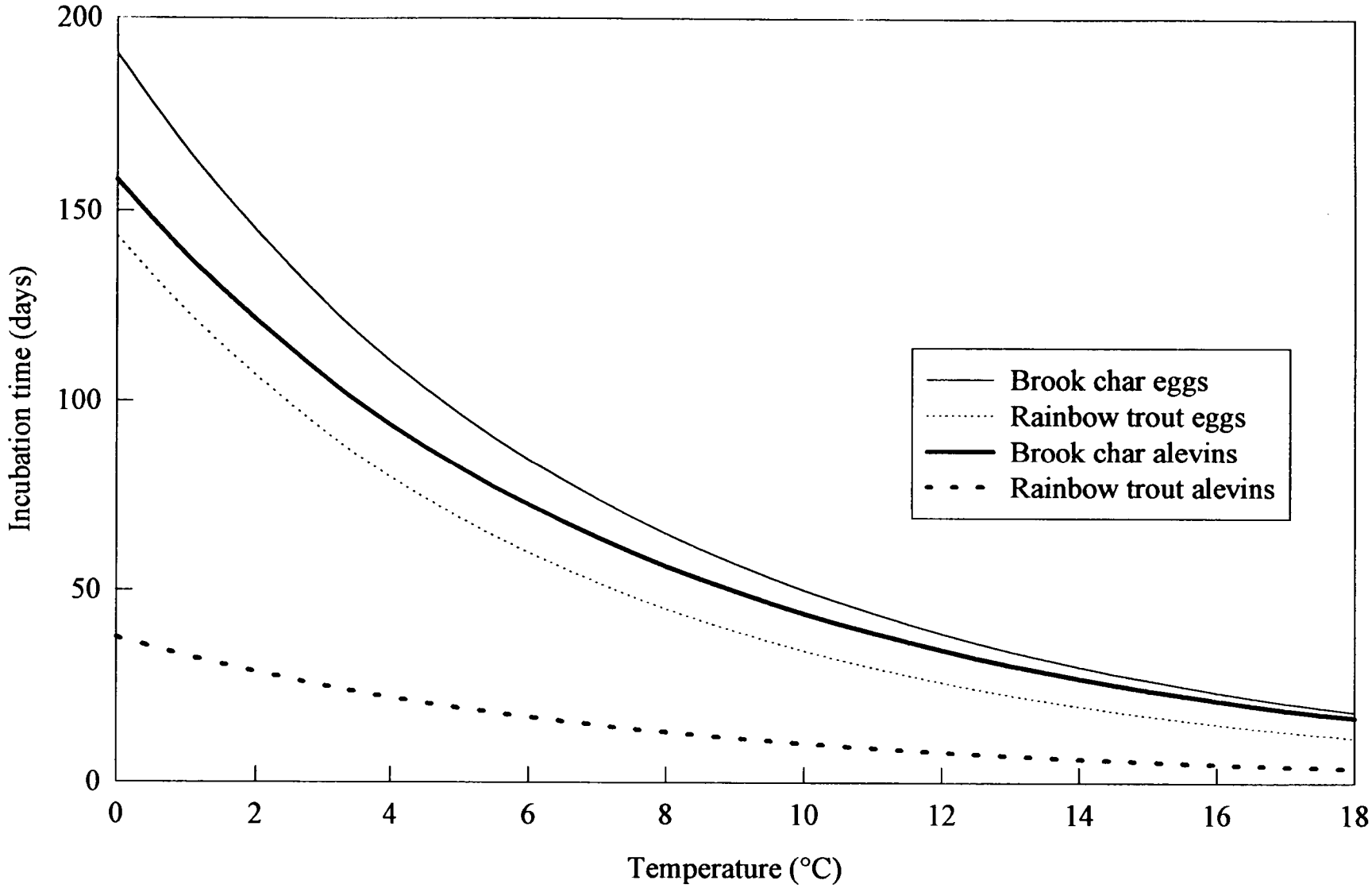

Figure 4: Dependence of brook char and rainbow trout egg and alevin incubation times on temperature.

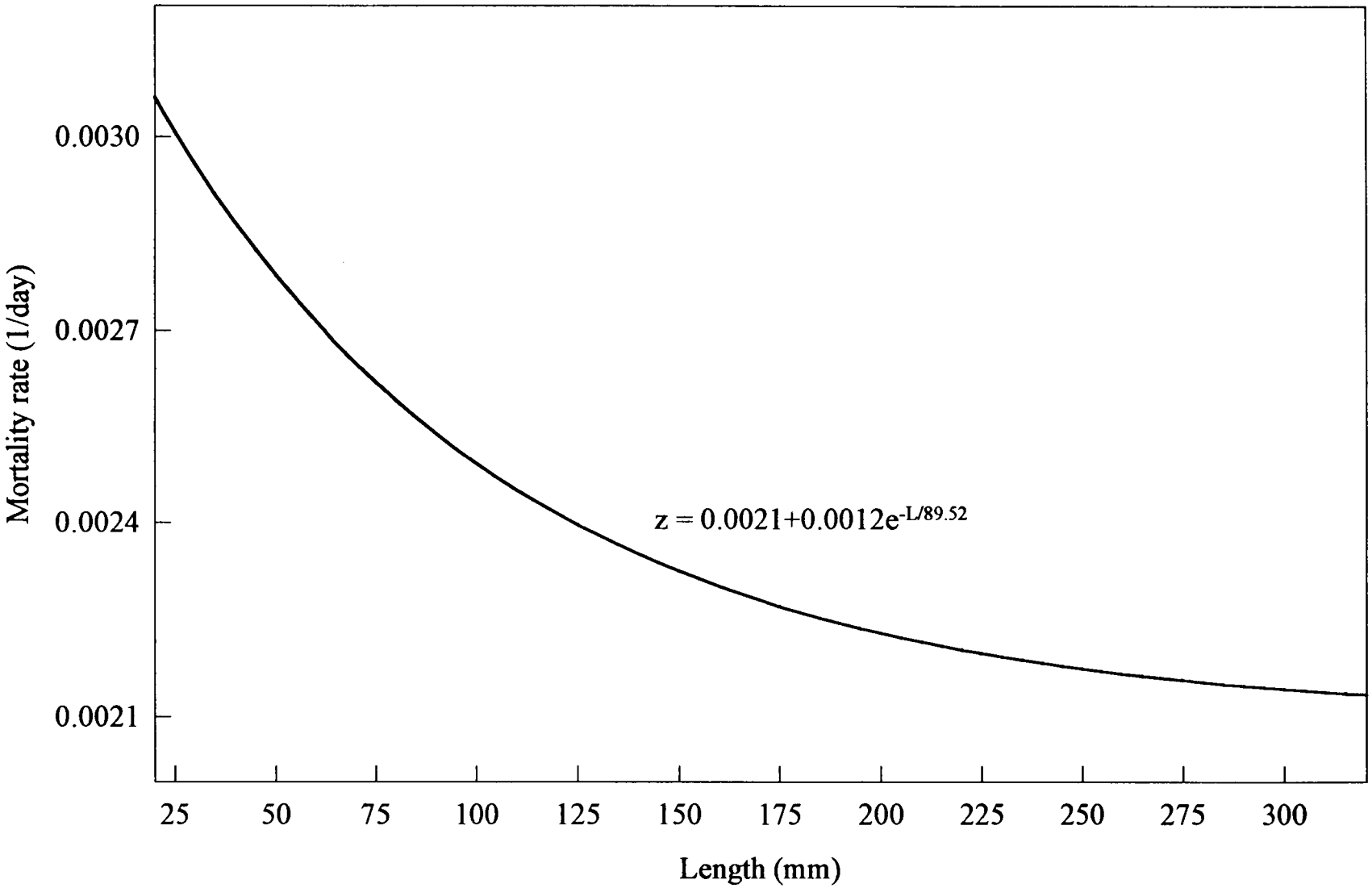

Figure 5: Dependence of fry, juvenile, and adult mortality rate on length.

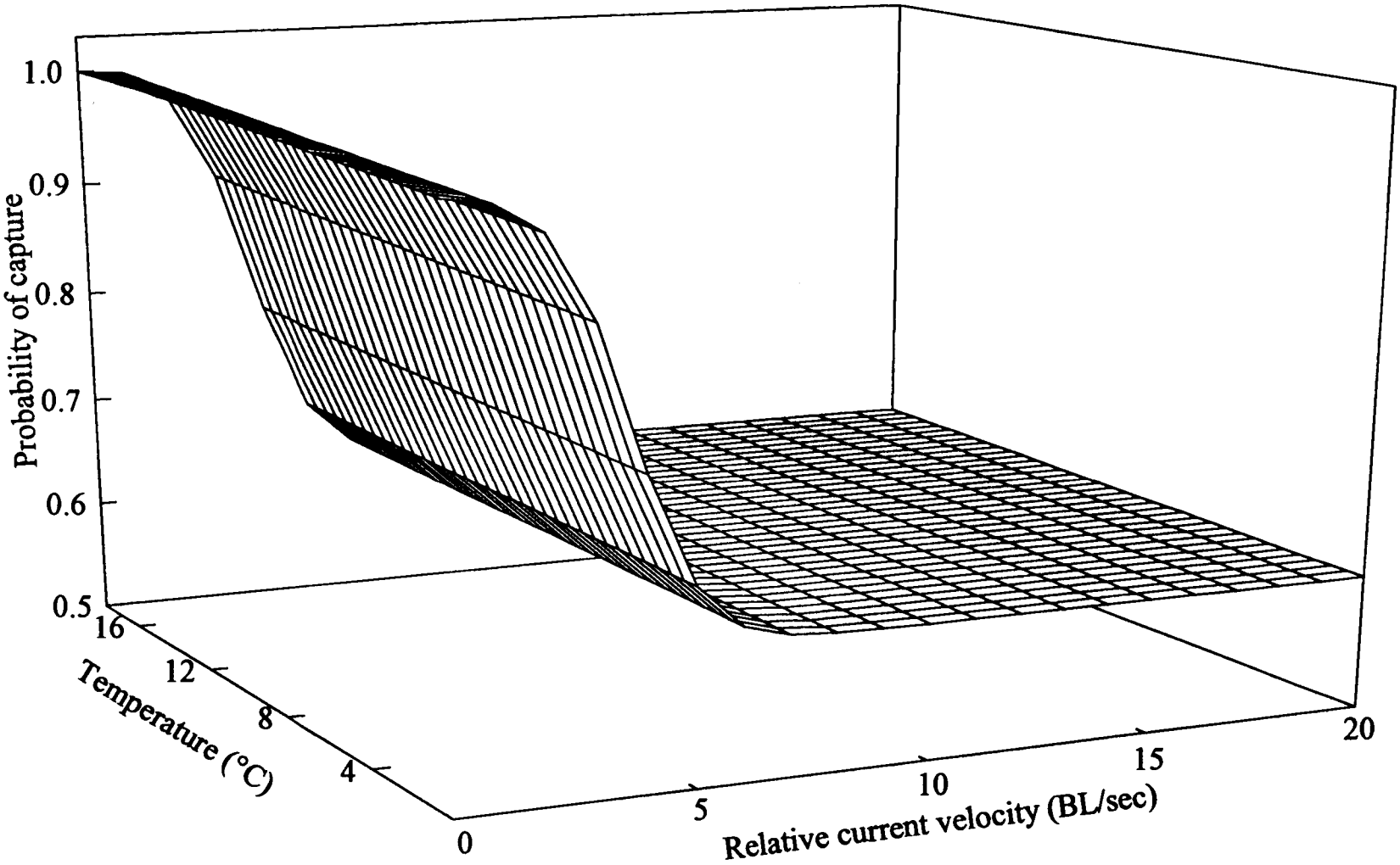

Figure 6: Dependence of probability of prey capture (P_c) on water temperature and relative current velocity (or swimming speed).

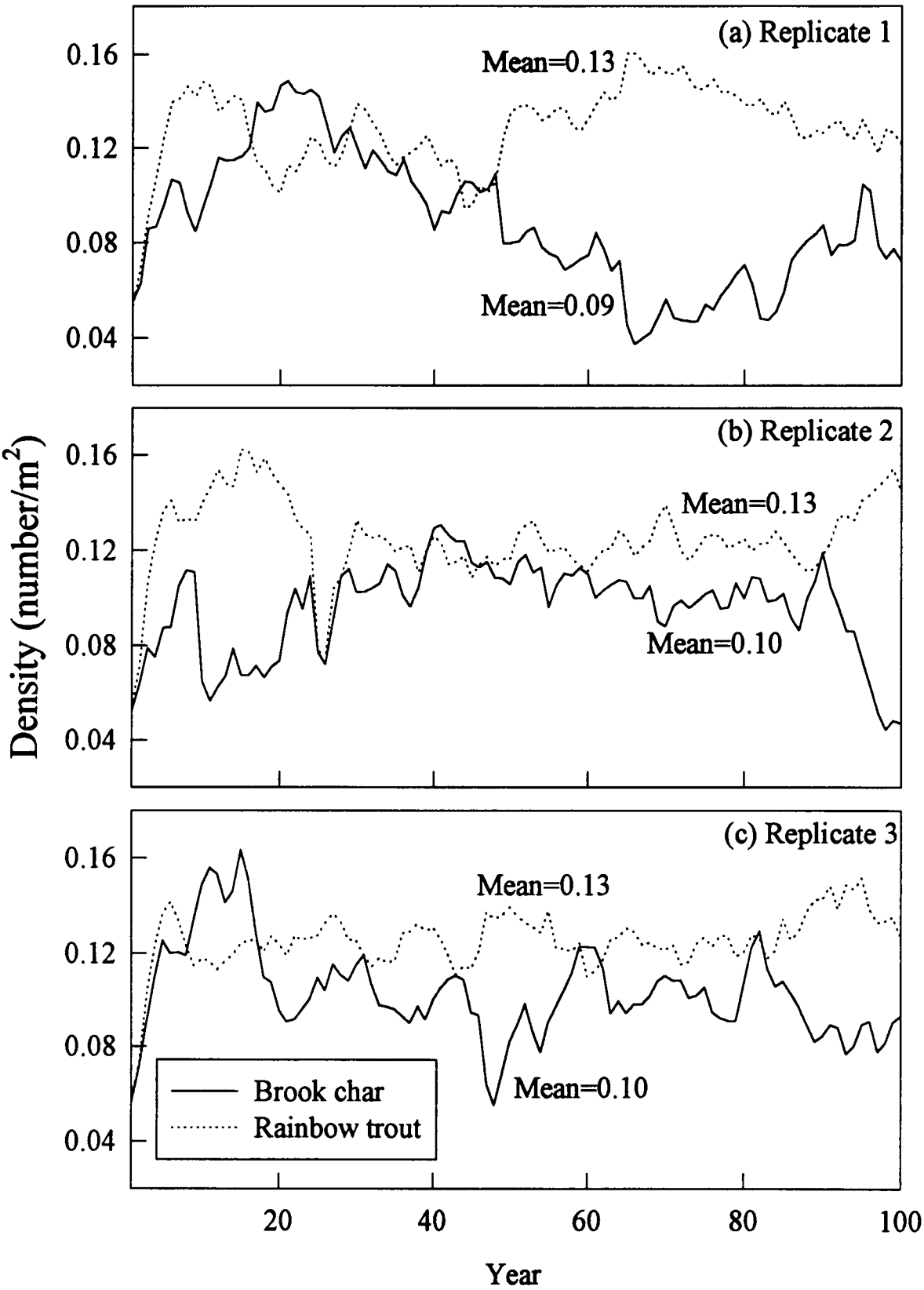

Figure 7: Annual brook char and rainbow trout post-fry densities for the 3 replicate baseline (sympatric) simulations.

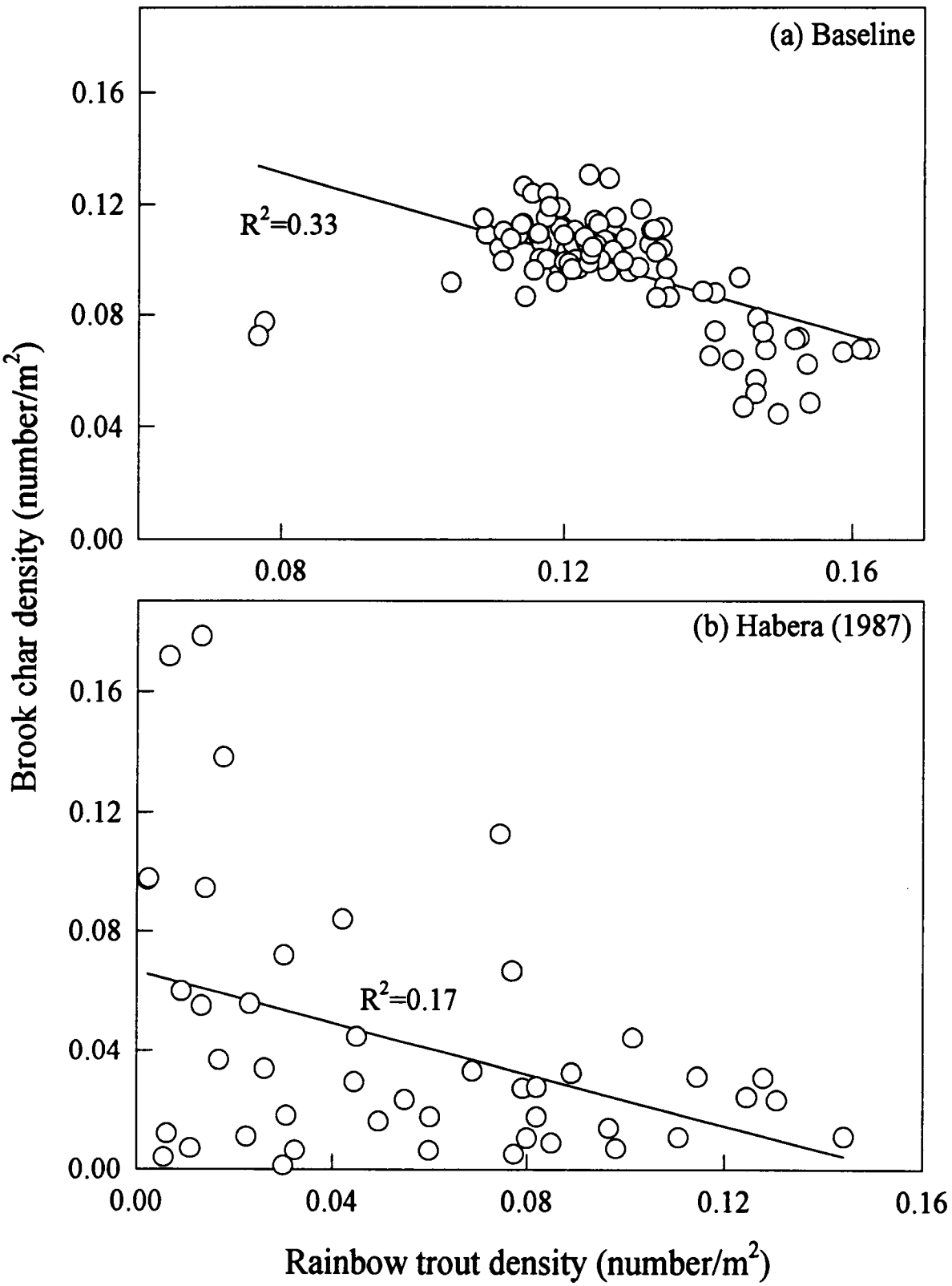

Figure 8: Moderate negative correlation between adult brook char and adult rainbow trout densities in (a) replicate 2 of the baseline simulations (years 6 to 100) and (b) sympatric populations studied by Habera (1987).

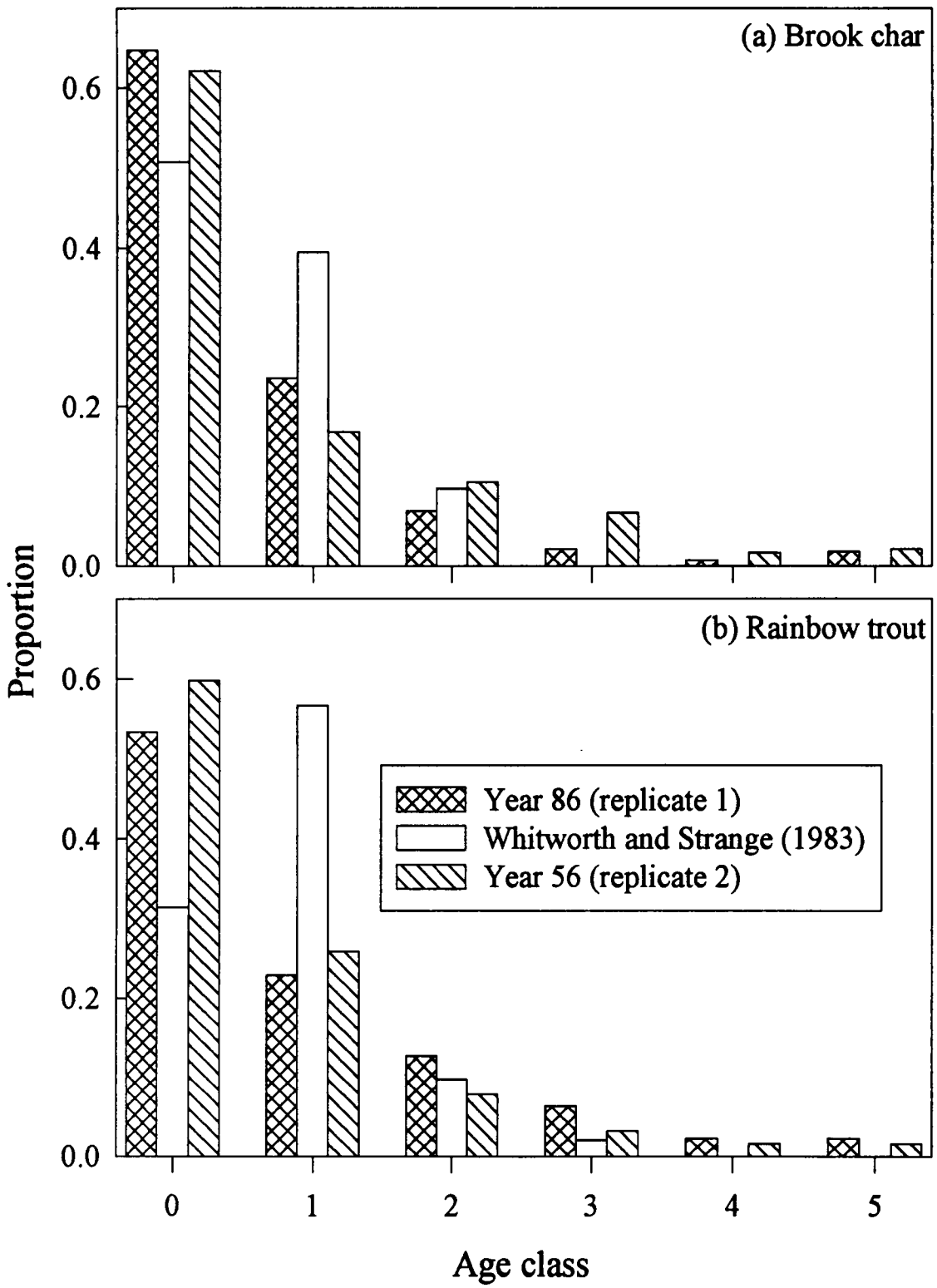

Figure 9: Mid-summer (July 29) age histograms for (a) brook char and (b) rainbow trout for 2 years of the baseline simulations compared with sympatric populations studied by Whitworth and Strange (1983).

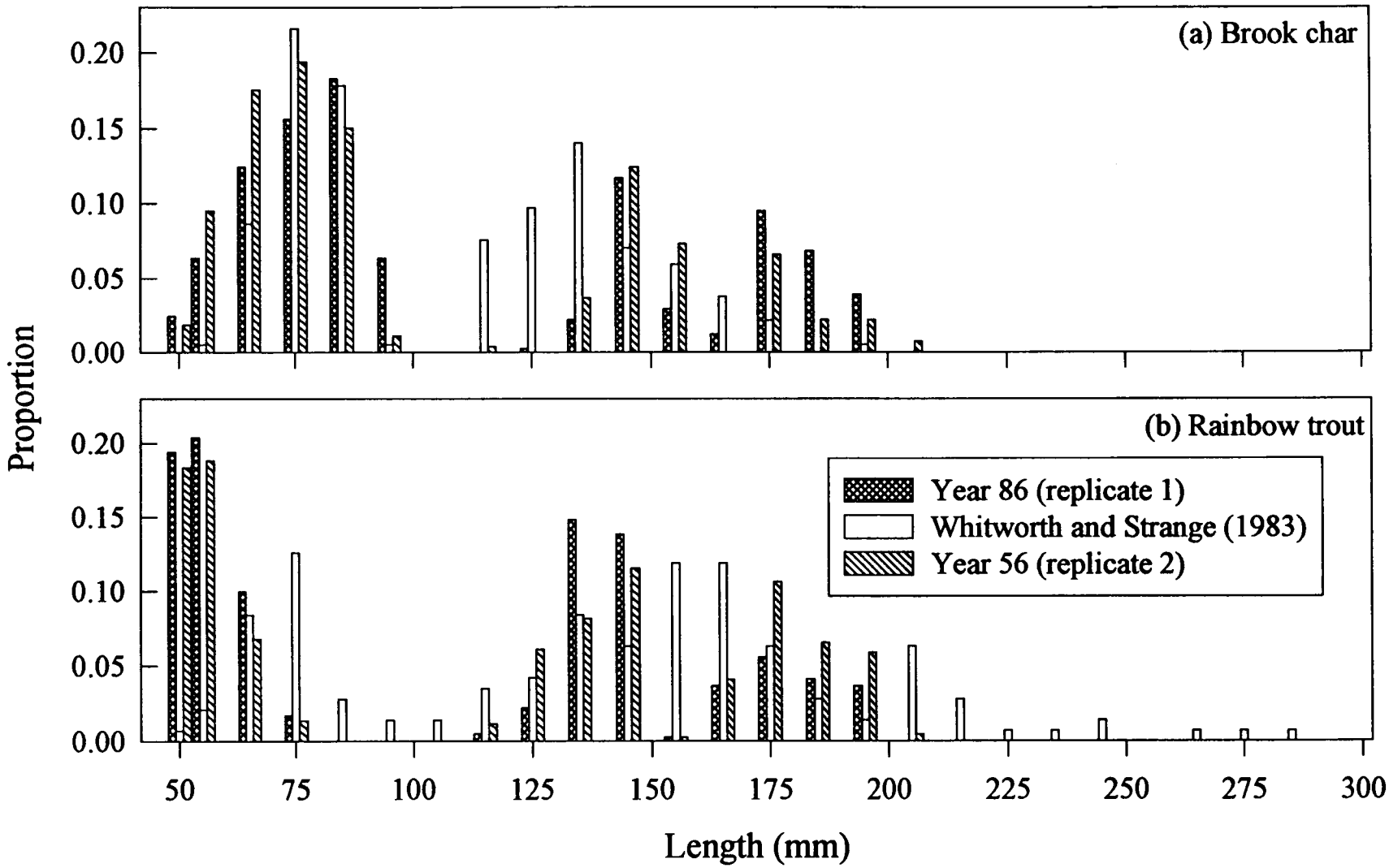

Figure 10: Mid-summer (July 29) length histograms for (a) brook char and (b) rainbow trout for 2 years of the baseline simulations compared with sympatric populations studied by Whitworth and Strange (1983).

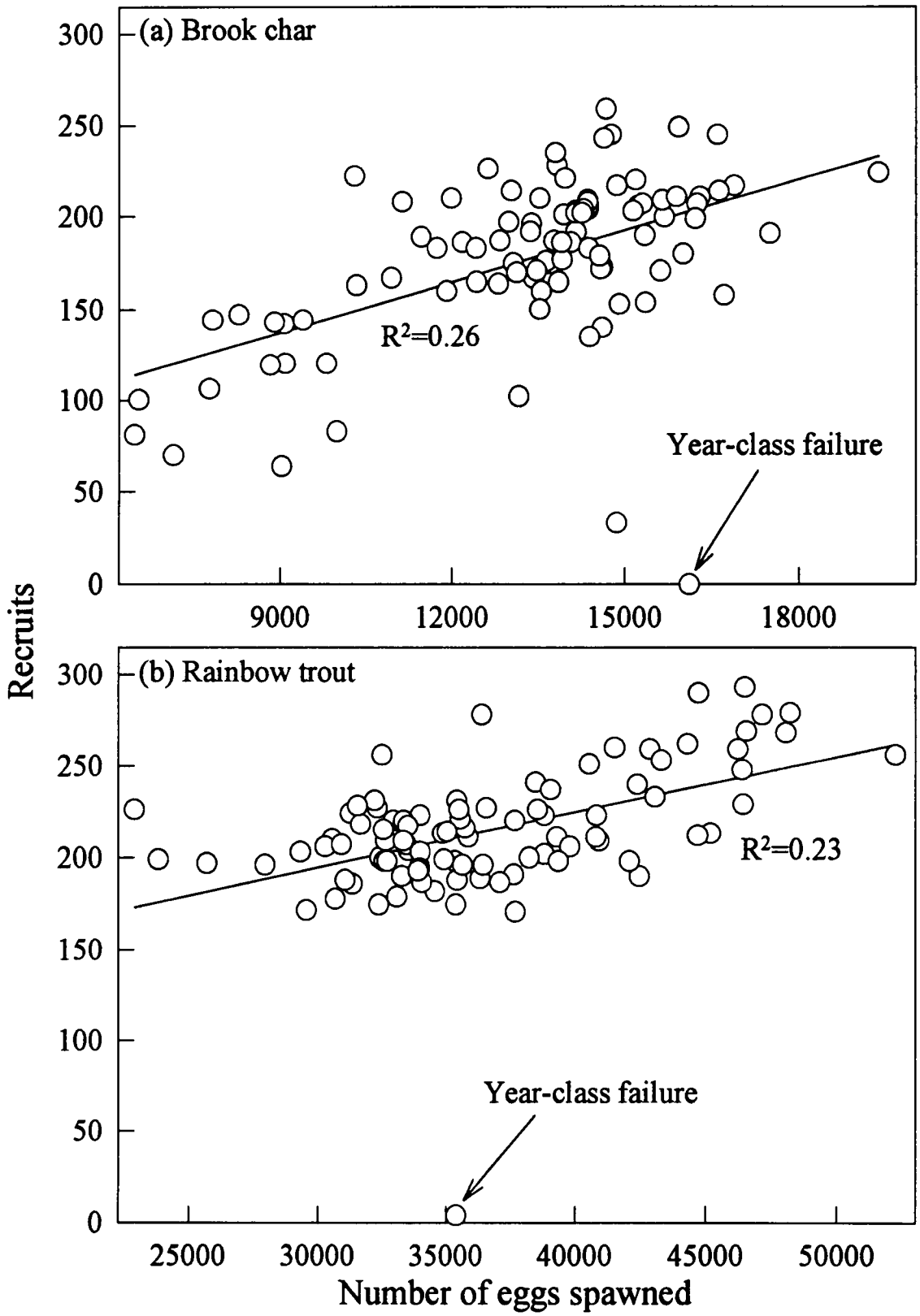

Figure 11: Positive correlation between egg production and recruitment for (a) brook char and (b) rainbow trout for years 6 to 100 of the replicate 2 baseline simulation.

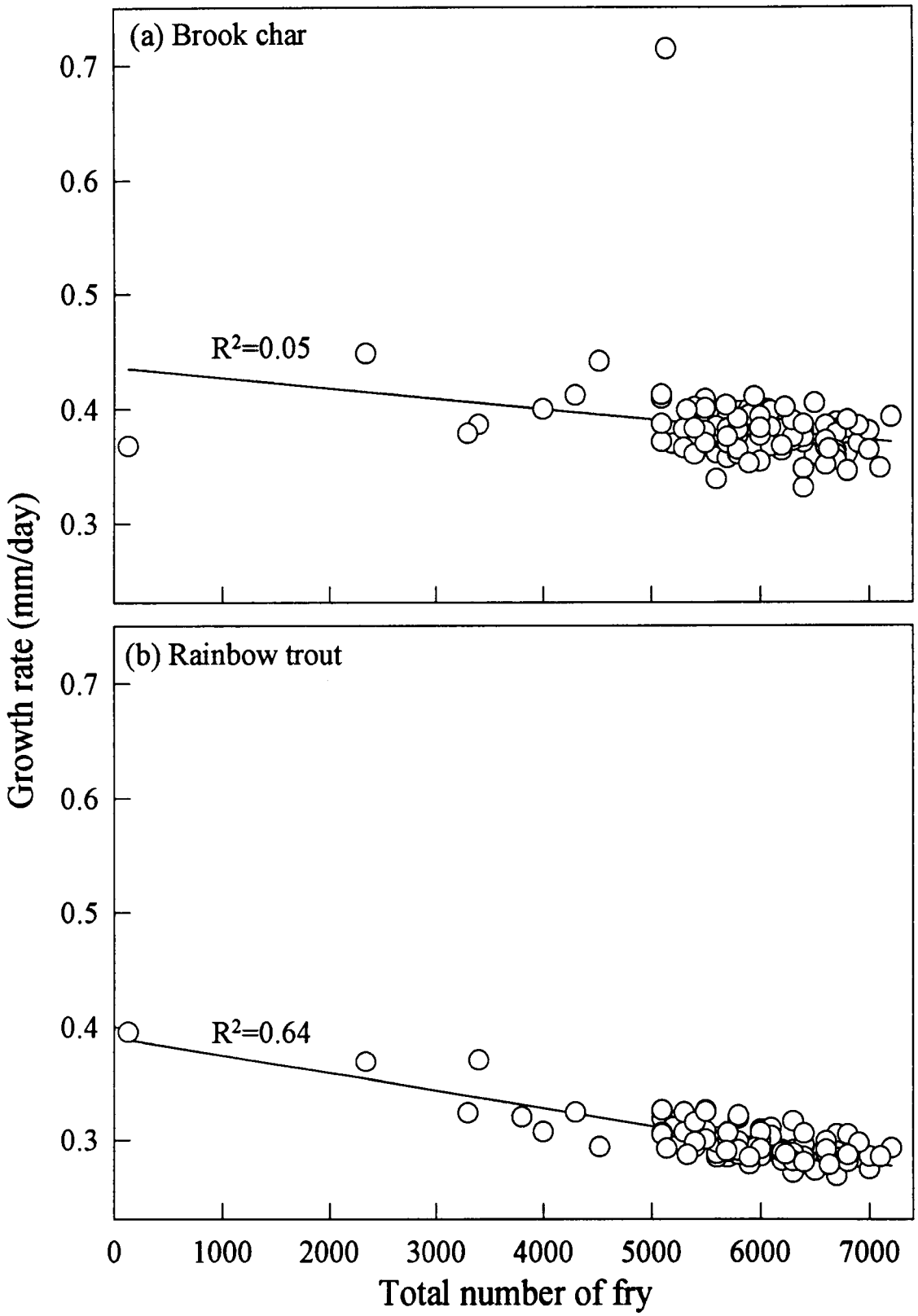

Figure 12: Negative correlation between total number of fry (both species combined) and fry growth rate for (a) brook char and (b) rainbow trout for years 6 to 100 of the replicate 2 baseline simulation.

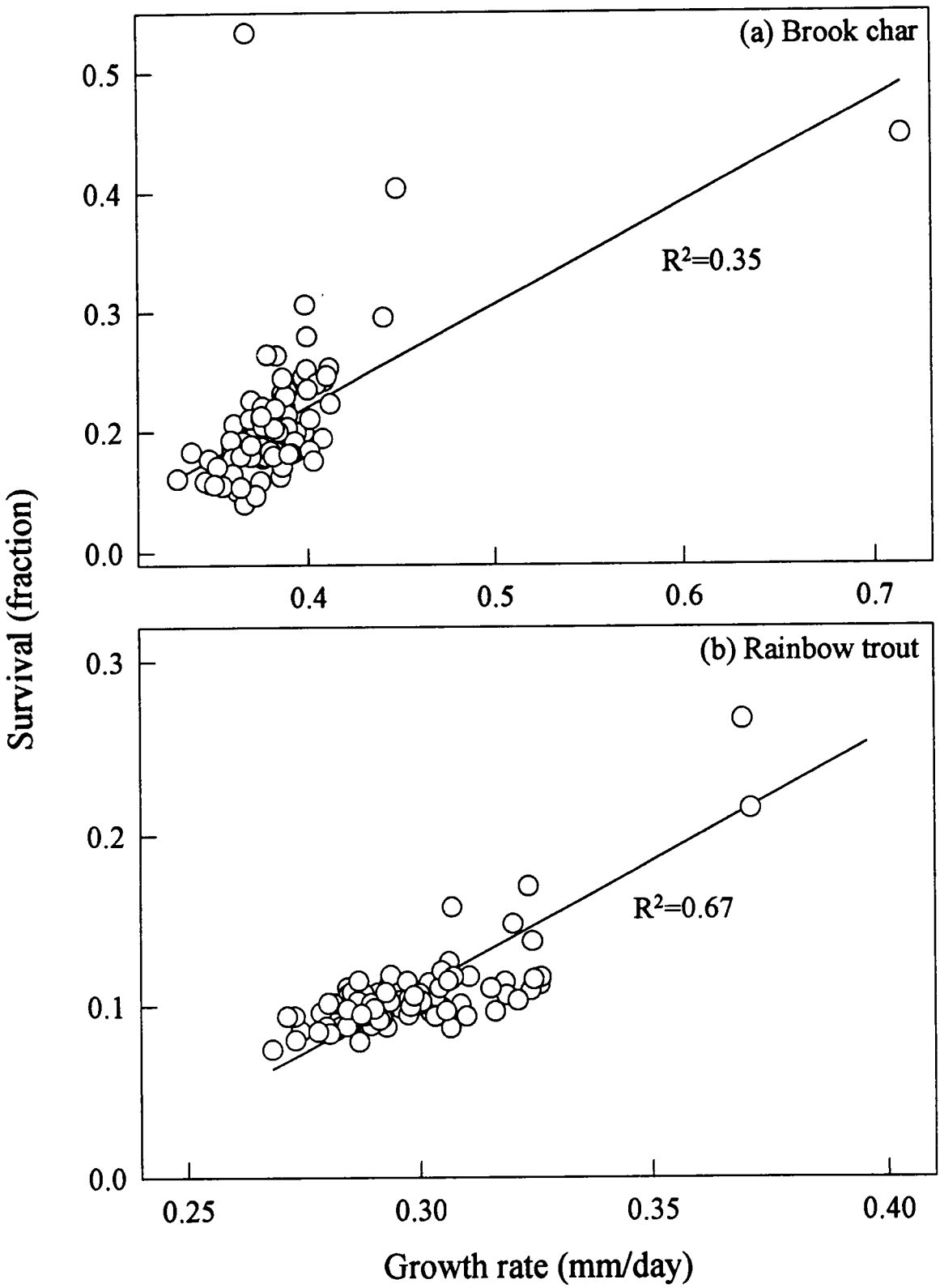

Figure 13: Positive correlation between fry growth rate and survival for (a) brook char and (b) rainbow trout for years 6 to 100 of the replicate 2 baseline simulation.

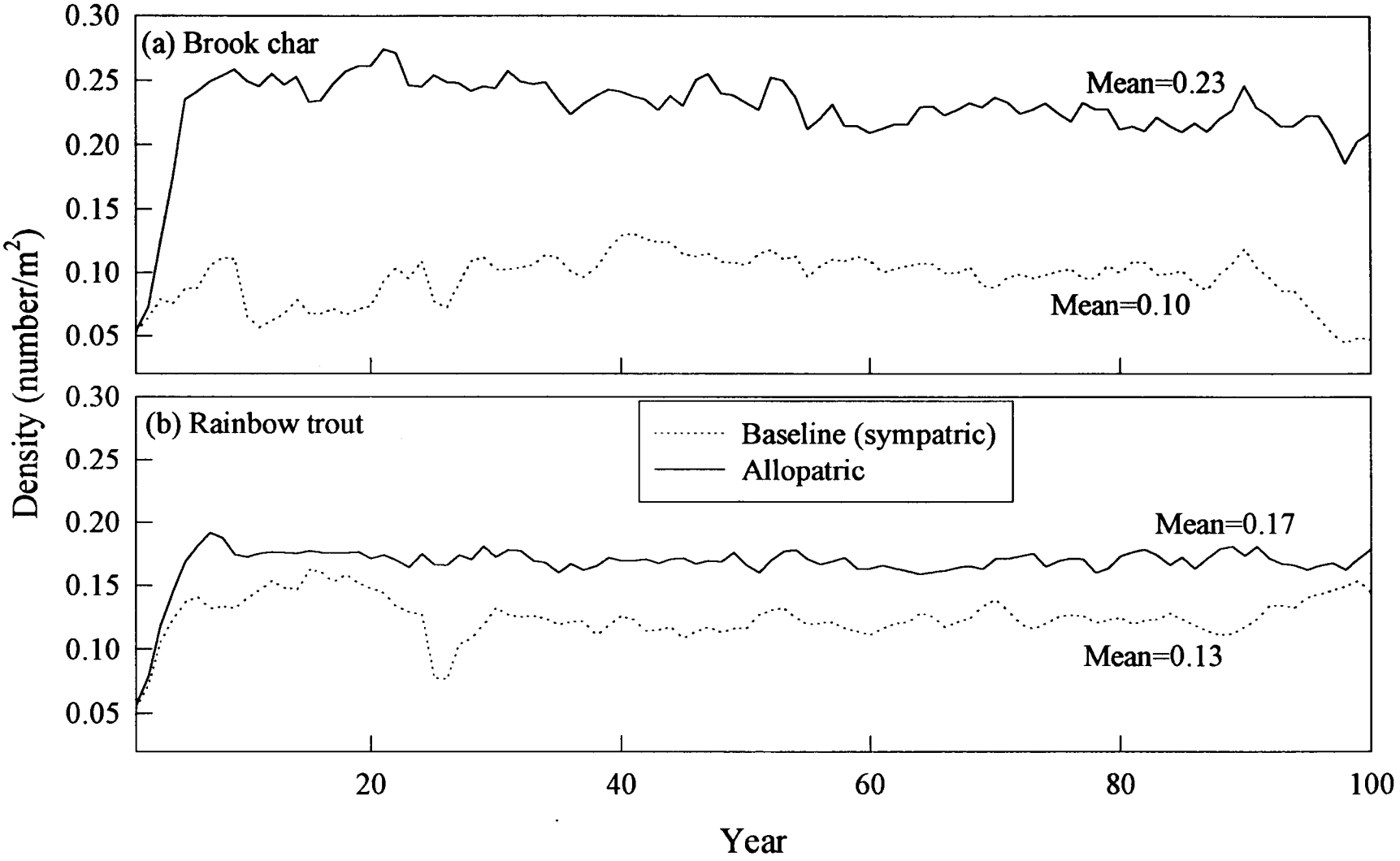

Figure 14: Annual brook char and rainbow trout post-fry densities for the replicate 2 baseline (sympatric) and allopatric simulations.

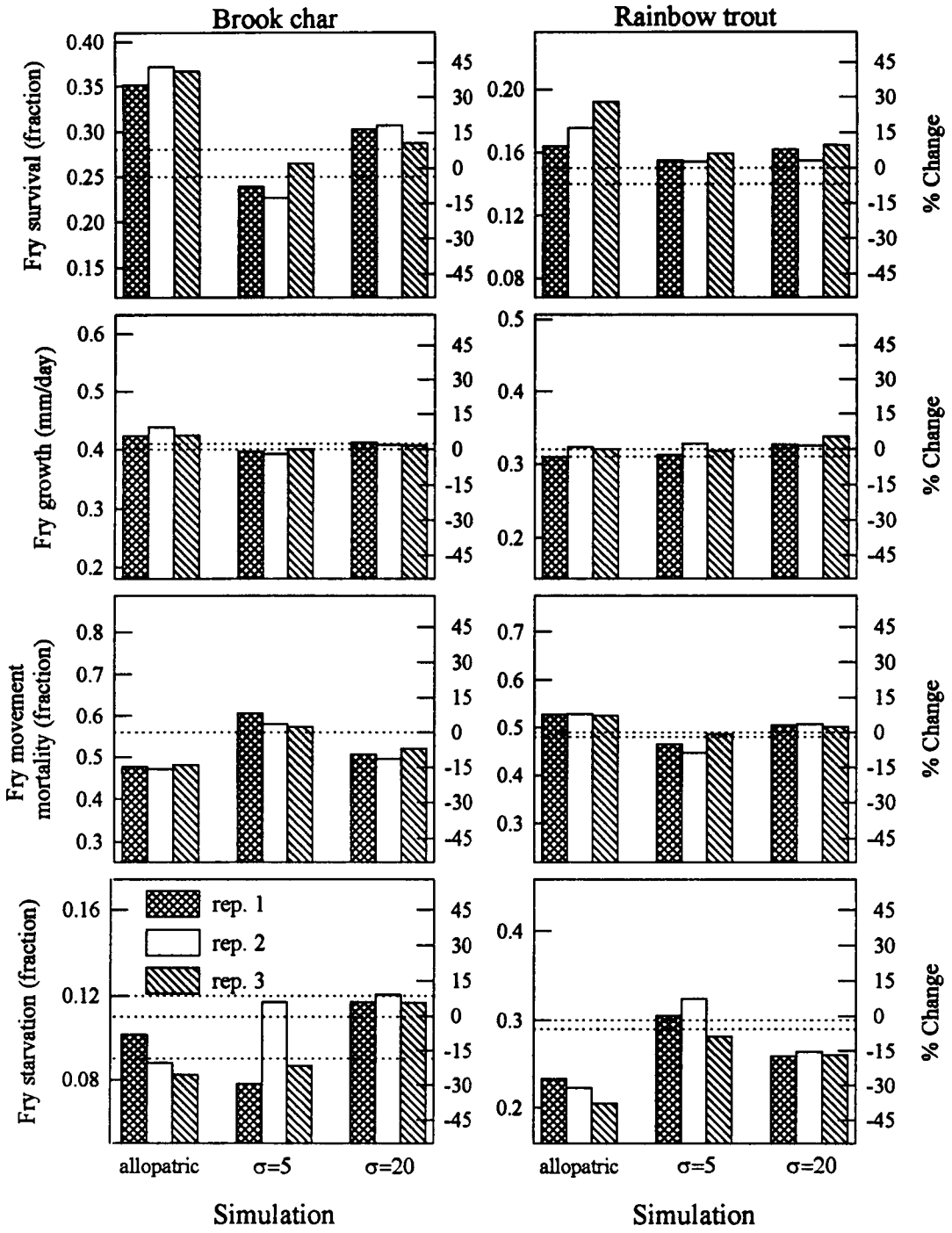

Figure 15: Average and percent change from baseline of brook char and rainbow trout fry stage survival, growth, movement-based mortality, and starvation-related mortality for the transition period (years 1 to 5) for the 3 replicate allopatric, decreased spawning season duration (sympatric), and increased spawning season duration (sympatric) simulations. Baseline replicate values are given by dashed lines (which may overlap). Percent change is computed as $100*(y-y_B)/y_B$, where y is the variable (i.e., survival, growth, etc.) and y_B is the corresponding baseline value. Note that the percent change axes are scaled similarly, but the axes of rates can differ between species.

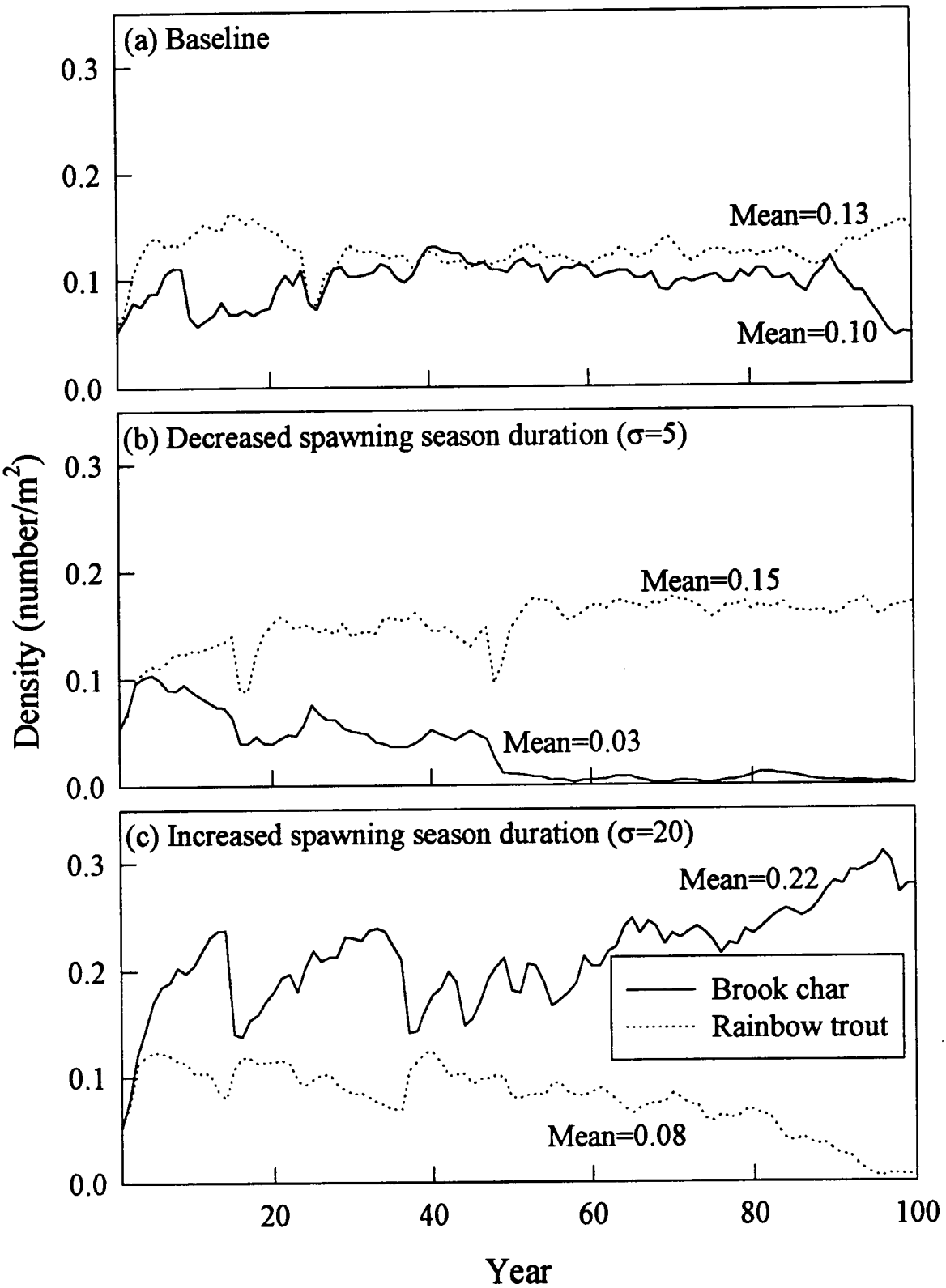

Figure 16: Annual brook char and rainbow trout post-fry densities for the replicate 2 baseline, decreased spawning season duration, and increased spawning season duration simulations.

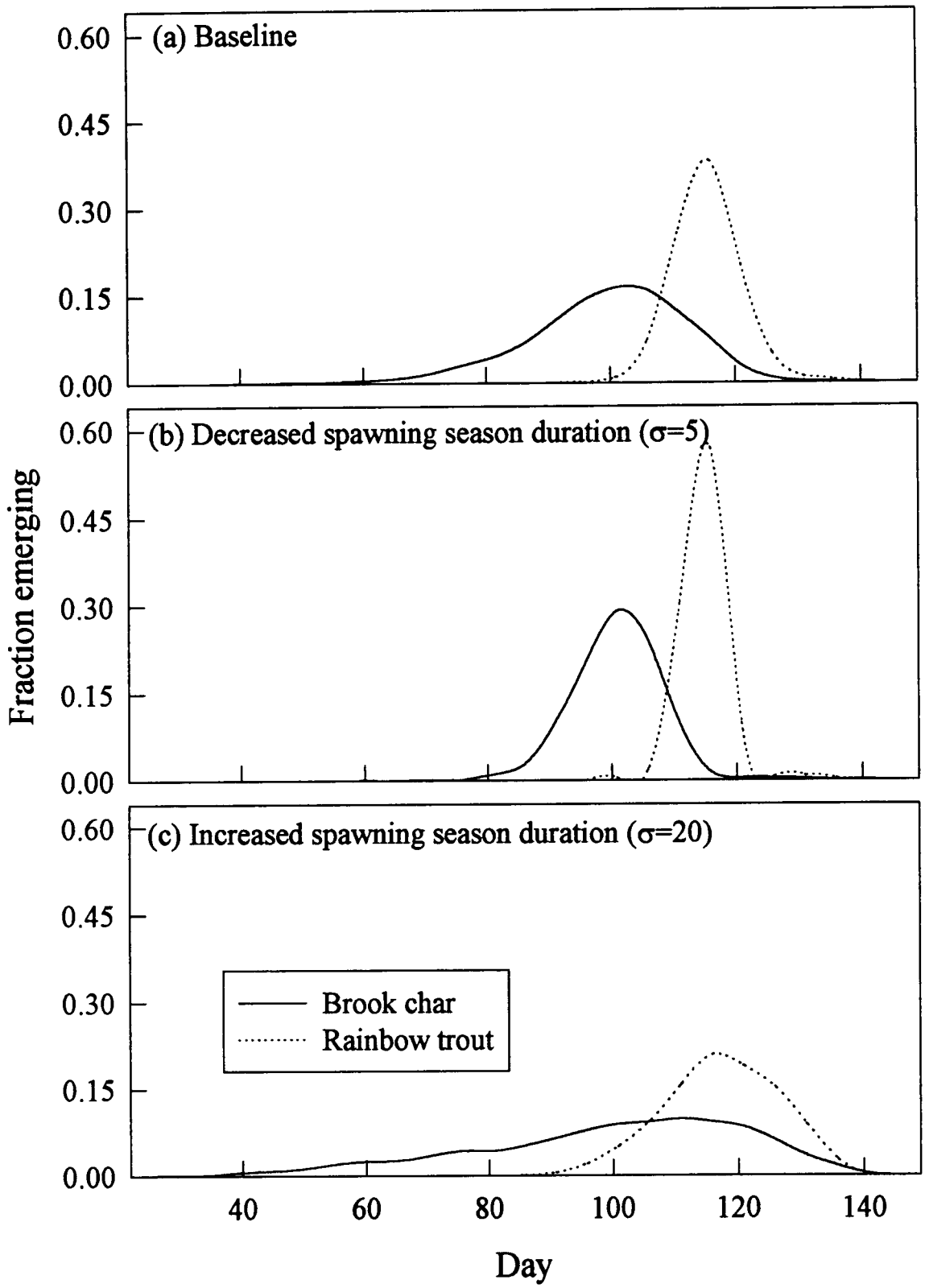

Figure 17: Probability density distributions of emergence dates of brook char and rainbow trout for the replicate 2 baseline, decreased spawning season duration, and increased spawning season duration simulations.

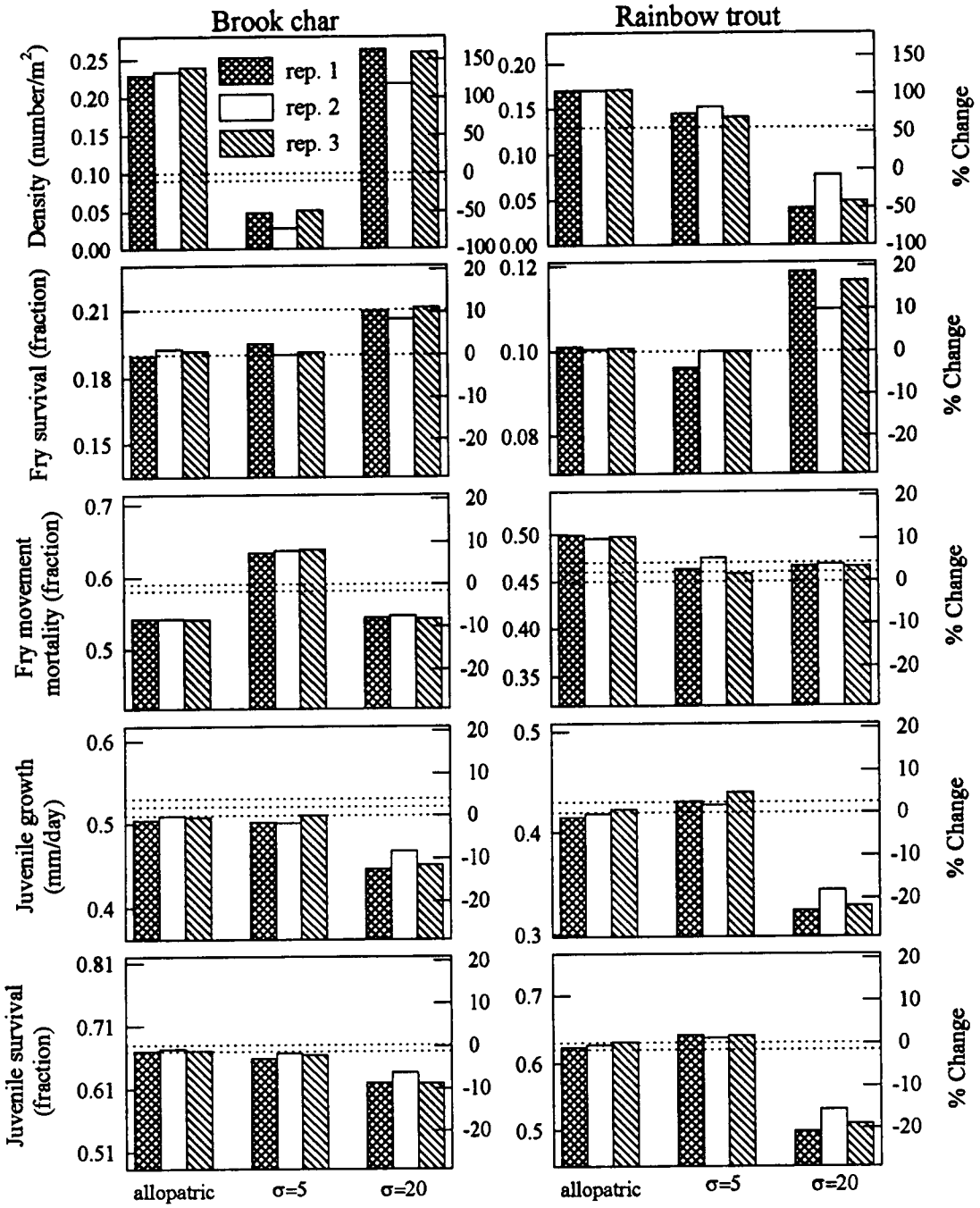

Figure 18: Average and percent change from baseline of brook char and rainbow trout fry stage survival and movement-based mortality, and juvenile stage survival and growth rate for years 6 to 100 for the 3 replicate allopatric, decreased spawning season duration (sympatric), and increased spawning season duration (sympatric) simulations. Baseline replicate values are given by dashed lines (which may overlap). Percent change is computed as $100*(y-y_B)/y_B$, where y is the variable (i.e., survival, growth, etc.) and y_B is the corresponding baseline value. Note that the percent change axes are scaled similarly, but the axes of rates can differ between species.

Part 3

Factors Affecting Competitive Dominance of Rainbow Trout over Brook Char in Southern Appalachian Streams: Implications of an Individual-Based Model

Abstract

An individual-based model was used to examine possible explanations for rainbow trout (*Oncorhynchus mykiss*) dominance over brook char (*Salvelinus fontinalis*) in southern Appalachian streams. Model simulations were used to quantify the effects on interspecific competition of: (1) greater aggressiveness in rainbow trout, (2) latitudinal differences in stream temperatures, flows, and daylight, (3) year-class failures, (4) lower fecundity of brook char, and (5) reductions in spawning habitat. The model tracks the daily spawning, growth, and survival of individuals of both species throughout their lifetime in a series of connected stream cells (pools, runs, or riffles). Average densities of each species based on 100 year simulations were compared for several levels of each of the five factors, and for sympatric and allopatric conditions. Based on model results and empirical information, it was concluded that more frequent year-class failures and the lower fecundity of brook char are both possible and likely explanations for rainbow trout dominance, warmer temperatures due to latitude and limited spawning habitat are possible but unlikely explanations, and rainbow trout aggressiveness is a highly unlikely explanation. Additional field work should focus on comparative studies of the reproductive success and the early life stage mortalities of brook char and rainbow trout among Appalachian streams with varying rainbow trout dominance.

Introduction

Large reductions in the range of native brook char, *Salvelinus fontinalis*, have been coupled to the expanded distribution of exotic rainbow trout, *Oncorhynchus mykiss*,

in the Appalachian streams of the southeastern United States (Kelly et al. 1980; Larson and Moore 1985). A traditional approach to competition (i.e., niche shift in the presence of a superior competitor; Roughgarden 1989) has failed to explain exclusion of brook char by rainbow trout (Ensign 1988). Field studies have revealed insignificant differences in the diets and behavior of brook char and rainbow trout between sympatric and allopatric conditions (Ensign et al. 1989; Lohr and West 1992). A systematic examination of other possible factors influencing competition among southern Appalachian trout populations is warranted.

Aggression of rainbow trout, water temperature, episodic mortalities, low fecundity of brook char, and limited spawning habitat have received some attention as possible factors influencing trout population dynamics. A general notion of more aggressive rainbow trout subordinating brook char when in sympatry has been cited as a factor leading to exclusion of brook char (Fausch 1988, 1989). Warmer water temperatures, which favor rainbow trout, have been used to explain the increasing dominance of rainbow trout with decreasing latitude in Appalachian streams (Fausch 1989; Flebbe 1994). Episodic mortalities of young-of-the-year, eliminating cohorts or year-classes, have been linked to the timing of spring and winter floods, droughts, and freezing temperatures. These episodic events can strongly affect brook char and rainbow trout interactions (Lennon 1961, 1967; Onodera and Ueno 1961; Seegrist and Gard 1972; Harshbarger 1975). High variability in fecundity has been observed among brook char populations (McFadden 1961; Wydoski and Cooper 1966), likely due to environmental (rather than genetic) factors (Scott 1962). Lennon (1967) found that brook char in lower

latitudes of the Appalachians have lower fecundity compared to higher latitude, northern populations. Kelly et al. (1980) mentioned that brook char females in Great Smoky Mountains National Park produced considerably fewer eggs than rainbow trout females. Availability of spawning habitat has been shown to control population levels and species dominance in competing trout populations in general (Larkin 1956; Lennon and Parker 1960; Hayes 1987). An evaluation is needed of which, if any, of these factors can explain the dominance of rainbow trout over brook char in southern Appalachian streams.

In this paper, a spatially-explicit, individual-based model is used to compare the effects of aggressiveness of rainbow trout, latitude, year-class failures, brook char fecundity, and reductions in spawning habitat on the population dynamics and competitive interactions between brook char and rainbow trout. The model was developed for sympatric, stream-resident brook char and rainbow trout in southern Appalachian streams (Clark and Rose, *in press*). First, a brief model description is given along with a summary of the baseline simulation and corroboration results. One-hundred year simulations designed to evaluate the potential importance of each of the five factors in affecting rainbow trout dominance are then presented. Part 3 concludes with a shortened list of possible factors that could explain rainbow trout dominance and with suggestions for future field efforts.

Model Description

The brook char - rainbow trout individual-based model is described in detail in Part 2 (or see Clark and Rose, *in press*). The model is briefly described here. Flow charts

summarizing the major computations of the model are presented in Figures 1-3; differences in how brook char and rainbow trout are represented in the model are compared in Figure 4. Figure 1 shows the overall model loops over years, days, and stream cells, and computations involving redds. Figures 2 and 3 show the computations for fry cohorts and individual juveniles and adults for a single stream cell. All computations are performed on a daily basis.

Environment

The stream is represented as a linear reach (with closed ends) divided into cells corresponding to pools, runs, and riffles. Sets of pools, runs, and riffles are stochastically generated to form the stream reach from mean lengths of pools (2.0 m), runs (1.6 m), and riffles (0.4 m), and a mean stream slope of 0.10 m/m. Water temperature, water flow, and daylength are assumed uniform throughout the entire stream reach but vary daily. The long-term average values of water temperature, flow, and daylength, estimated from data measured on southern Appalachian streams (35°N latitude), are shown in Figure 5. For temperatures and flows, daily stochasticity is imposed on the long-term average values. Water velocity, water depth, and cell width are calculated from water flow using relationships for the southern Appalachian region, and vary from cell to cell and over time.

Spawning, Eggs, and Alevins

Mature females (those greater than 100 mm) spawn once per year during the appropriate spawning season (Figure 4b) and establish redds in stream cells. Spawners

move as close to their natal cell as possible for spawning, and place their redd randomly within the chosen cell. Both males and females swim to and select cells for spawning, but only females lay eggs. Fecundity for fish of the same length is higher for rainbow trout than for brook char (Figure 4d). Individual redds are then followed as a cohort until development of the alevin stage is completed. Egg and alevin development rates in the redd are temperature-based, and differ between brook char and rainbow trout (Figure 4a). A constant instantaneous rate of mortality (0.013/day for brook char, 0.03/day for rainbow trout) is applied daily to each redd cohort. Location of the individual redds is tracked on a fine-scale grid inside each cell, permitting computation of additional mortality from dewatering when low flow exposes portions of the redd and from superimposition (overcutting) by later spawning fish. Complete loss of a redd occurs due to freezing (temperature < 0.1 °C) and excessive heat (temperature > 21 °C).

Fry

At swim-up (i.e., completion of alevin development), each redd is followed as a cohort of fry with initial length of 20 mm. Fry are initially located in the same cell as their redd, but may move downstream after two days due to slow growth or crowding. Fry always remain in the shallow stream margins (< 10 cm depth) feeding on drift until becoming juveniles. Metamorphosis occurs between 30 and 40 mm; fry greater than 30 mm become juveniles if slow growth or crowding triggers movement. The change in mean weight of an individual for a fry cohort is based on a bioenergetics formulation (see *Juveniles and Adults*, Equation 1).

Downstream fry movement occurs in response to weight loss or crowding. If fry growth rate today (g/g/day) is less than their past average growth rate, cohorts move downstream. Crowding-induced movement occurs when the total area of individual fry habitat exceeds the available fry habitat in a cell (defined as the surface area from 10 cm depth to each bank). Fry cohorts then move downstream (from smallest to largest in mean length) until the sum of fry habitats in the cell is less than the available habitat. For fry less than 30 mm, moving cohorts are relocated to the first available downstream fry habitat (water depth < 10 cm). For fry greater than 30 mm, moving cohorts become juveniles and enter the stream habitats utilized by juveniles and adults (water depths > 10 cm).

Mortality of fry reduces the numbers in each cohort. Fry mortality rate depends on their mean length, mean weight, and movement. Length-based and weight-based mortality for fry is as described for juveniles and adults. Movement mortality is assessed to moving fry cohorts by reducing the cohort size by 15% on the day of movement.

Juveniles and Adults

Juvenile and adult fish feed, grow, move, suffer mortality and (if mature and ripe) spawn on a daily basis. Each fry surviving to metamorphosis is followed as an individual. Juveniles and adults can exhibit either of two feeding strategies: stayers or floaters. Stayers establish territories (approximated by 60 cm x 60 cm squares in a cell) in the portion of a cell with water depth greater than 10 cm and slope less than 0.6 (i.e., not in riffles). Sites within a cell are allocated daily to both species in descending order of their lengths. Larger fish prevent smaller fish from occupying territories in the same cell.

Smaller fish are prevented from using squares adjacent to or in front of larger individuals within 5 body lengths of the larger individual. Fish become floaters if all sites in the cell are occupied or guarded from occupation. Floaters are located at the back of their cell.

Four size classes of drift prey are represented. Weights per individual associated with the four prey types are: 3.6, 9.5, 32.0 and 104.0 mg wet weight. Total prey biomass is 2.7 mg wet weight/m^3, similar to values reported for southern Appalachian trout streams (O'Hop and Wallace 1983; Ensign 1988). Fish less than 30 mm eat the smallest prey type; fish between 30 mm and 50 mm eat the two smallest prey types; fish between 50 mm and 60 mm eat the three smallest prey types; fish between 60 mm and 80 mm eat all prey types; and fish greater than 80 mm eat the three largest prey types. The number of prey from each size class encountered is determined by the prey density, cross sectional area of the stream at the territory site, and stream velocity in the cell. For stayers, prey densities are reduced by consumption by fish located upstream in the same cell. Prey remaining in the cell after consumption by all stayers are divided equally among the floaters. Floaters and stayers feed for all daylight hours except when temperatures are less than 2°C, when feeding is restricted to one hour per day. Fish moving upstream through a cell may feed on the prey remaining after all floaters and stayers have fed. Upstream movers encounter food based on volume of water searched and the remaining prey density.

Growth in weight (W, g wet weight) is represented using a bioenergetics equation:

$$W_{t+1} = W_t + 0.28pC_{max}A - 0.19M, \quad (1)$$

where C_{max} is the maximum daily consumption (g wet weight/day), p is the proportion of

C_{max} realized, A is assimilation efficiency, and M is total metabolism (g wet weight/day). Maximum consumption (C_{max}) is a function of the fish's weight and temperature developed from data reported in Elliott (1975a and b). The proportion of C_{max} realized (p) is determined by the biomass (number times weight per individual) of prey items eaten by the individual fish. Assimilation is assumed to be 0.65 for all fish. Metabolism (M) is a sum of routine (based on weight and a Q_{10} temperature adjustment) and active (based on weight and swimming speed/current velocity) components developed for each species, with brook char metabolism slightly lower than rainbow trout (Figure 4c). Optimum temperatures for growth are 9°C for brook char and 11°C for rainbow trout.

Weight is converted to length on a daily basis. Fish cannot lose length, but may lose weight, and length cannot be added until the fish weight is at or above the predicted value from the length-weight relationship. The length-weight relationships used for brook char and rainbow trout differ by less than 1%.

Fish move from a cell if their growth rate is slow, water depths have receded due to low flow, or high flow is above their maximum swimming speed. Direction of movement is random, except for mandatory downstream movement when flow is greater than their maximum swimming speed. During upstream movement feeding may occur and swimming costs are incurred. No feeding is allowed and no swimming costs are incurred during downstream movement. Distance moved is limited to 25 m per day, by obstruction from an upstream barrier (i.e., flow greater than maximum swimming speed), or by the upstream and downstream boundaries of the stream.

Mortality of fry, juveniles and adults is both length (L, mm total length) and

weight-based. Length-based instantaneous mortality (Z, 1/day) is given by:

$$Z = 0.0021 + 0.0012e^{-\frac{L}{8952}}. \quad (2)$$

Individual fry cohorts are reduced by multiplying by e^{-Z} each day until reaching the juvenile stage or the cohort size is below 1. Individual juvenile and adult fish die if a uniform random number between 0 and 1 (chosen daily for each fish) is less than $1-e^{-Z}$. Weight-based mortality of fry occurs when the mean weight of an individual in the cohort is below 70% of the weight corresponding to the length-weight relationship. Cohorts are reduced proportionately by the ratio of their actual mean weight divided by the weight from the length-weight relationship. For juveniles and adults, weight-based mortality occurs if the weight of an individual falls below 50% of the weight from the length-weight relationship.

Baseline Simulation and Corroboration

The baseline simulation demonstrates model realism and provides a basis for evaluating the effects of factors potentially affecting brook char and rainbow trout competition. The baseline simulation was for 100 years using a 600 m stream reach consisting of 50% pools, 40% runs, and 10% riffles. Mean pool length was 2.0 m and the average stream slope was 0.1 m/m (Moore et al. 1983; Larson and Moore 1985). Three replicate baseline simulations that differ in their random number sequence were performed. Different random number sequences affect the outcome of stochastic processes, such as stream morphology (lengths and slopes of individual pools, runs, and riffles), prey encounters, mortality, and direction of movement. In general, pools were approximately

40 cm deep with water velocities less than 30 cm/sec, runs were typically 15 cm deep with water velocities between 50 and 180 cm/sec, and riffles were approximately 9 cm deep with water velocities greater than 200 cm/sec.

Model predictions of brook char and rainbow trout densities and growth rates under baseline conditions (Figure 6; Table 1) were similar to values observed for sympatric populations in southern Appalachian streams. Predicted population densities (juveniles and adults averaged over the year) were stable through time, with mean annual rainbow trout densities about 1.3-fold higher than those of brook char (Figure 6). Predicted densities were similar in magnitude to those reported for southern Appalachian streams (0.02 - 0.22 brook char/m^2 and 0.02 - 0.18 rainbow trout/m^2, see Larson and Moore 1985 and Ensign et al. 1989). Predicted growth rates and lengths were also similar to values from the literature (Table 1). Pools were the most frequently used habitat (> 50% of all fry and > 90% of all juveniles and adults were found in pools), and movement of individuals was limited (< 8 m downstream for fry; < 20 m either upstream or downstream for juveniles and adults). Density-dependence was strongest in the fry stage, with fry growth rates negatively related to initial fry densities for both species (mean R^2 equal to 0.28 for brook char; 0.53 for rainbow trout). Fry survival was positively correlated to growth rate (R^2 approximately 0.42 for brook char; 0.62 for rainbow trout). Slower growth translated to higher mortality because mortality rate decreases with length (Equation 2). Higher fry density also caused higher movement mortality because overcrowding triggers fry movement. Predicted probability of survival, growth rates, and densities varied less than 11% among five replicate simulations (see Table 4, **Part 2**).

Clark and Rose (*in press*) present additional comparisons between model results and observed data.

Allopatric (single species) simulations under baseline conditions showed brook char to be more affected by competition than rainbow trout (Figure 7). Without rainbow trout present, brook char densities increased 2.5-fold, whereas rainbow trout increased only 1.3-fold when alone.

Factors Affecting Competition

General Design of Simulations

Model simulations were performed to evaluate the effect on competition of: (1) aggression of rainbow trout, (2) latitude, (3) year-class failures, (4) brook char fecundity, and (5) reduction in spawning habitat. For all of the factors except latitude, three to five levels of increasing intensity of each factor were examined. Latitude was treated as changes in daylength, temperature, and water flow singly and all together. For each level of each of the factors, three replicate simulations under sympatric and allopatric conditions were performed. Allopatric simulations provide a basis of comparison for assessing the effects of each factor. Allopatric predictions are the most predicted brook char or rainbow trout densities can change in response to each factor because the effects of interspecific competition have been removed.

All simulations were for 100 years using the same 600 m stream reach consisting of 50% pools, 40% runs, and 10% riffles as used in the baseline simulation. Simulations began with 200 56-mm individuals of either species (allopatric) or both species (200 from

each; sympatric). Stream morphology, flow and temperature (except in the latitudinal treatments), and prey density were identical across factors but varied among replicates. Thus, replicate simulation 1 had the same stream arrangement, water flows, and temperatures for all levels of all factors, but these were different than those used for replicate simulation 2. Model predictions of annual average densities (juveniles and adults) through time are presented for baseline and each level of a factor for one of the replicate simulations; average annual densities computed for years 6 to 100 are presented for all three replicates.

Aggressiveness of Rainbow Trout

Increased aggressiveness of rainbow trout was simulated by increasing the perceived length of juvenile and adult rainbow trout. Juvenile and adult feeding is based on a length hierarchy (in which fish of both species in a cell select feeding sites from longest to smallest fish). When comparing brook char and rainbow trout, rainbow trout lengths were artificially increased by a multiplying factor. Three levels of increasing rainbow trout aggressiveness were simulated by using multiplying factors of 1.5, 2.0, and 2.5. Thus, a 100 mm rainbow trout was perceived by a brook char in the same cell to be 150 mm, 200 mm, and 250 mm in each of the simulations.

Latitude

Latitudinal effects were simulated by altering water temperature, water flow, and daylength (Figure 5). Baseline simulations of the model were configured for temperature,

flow, and daylength from streams within the southern Appalachians at approximately 35°N latitude and an elevation of 914 m (Clark and Rose, *in press*). To simulate sympatric populations in a northern portion of their distribution (where brook char dominate), data from Appalachian streams (United States Geological Survey 1993b) at approximately 38°N latitude and 914 m elevation were used to generate curves for long-term mean temperature and water flow. Flow was adjusted to equate watershed size with that used for the baseline simulations (1,088 ha) by multiplying 38°N latitude flows by the ratio of 1088 ha to the watershed areas of each of five streams used. Daylength was calculated according to Brock (1981) for 38°N latitude. Replicate simulations with temperature, flow, and daylength changed together (latitude effect) and separately were performed. Simulations with only temperature, flow, or daylength changed allow determination of which of the components of the total latitude effect were causing the predicted response.

Because daylength is a principal determinant triggering spawning in trout (Henderson 1963), spawning seasons were also changed for simulations using the 38°N daylengths. The spawning season for brook char was shortened from October 1 to December 31 for the 35°N baseline simulation to October 1 to December 14 for the 38°N simulation. The spawning season for rainbow trout was shortened from January 1 to March 31 for the baseline simulation to January 15 to March 31. The shortened spawning seasons resulted in brook char and rainbow trout spawning during the same minimum and maximum values of daylengths as in baseline conditions.

Year-class Failures

Simulations were performed in which all eggs and alevins of both species were killed in specified years to represent episodic mortality events. Year-class failures were imposed every 3, 5, 10, and 20 years. No year-class failures were imposed until after year 10 to allow formation of realistic populations from initial conditions.

Increased Brook Char Fecundity

Simulations were performed with increased brook char fecundity. The relatively low brook char fecundity used in baseline simulations was based on data by Lennon (1967) for southern Appalachian populations of the Great Smoky Mountains National Park. Brook char fecundity was increased by multiplying the length-based baseline fecundity by 1.5, 2.0, and 2.7. McFadden (1961) reported fecundities (eggs/mm) for several northern latitude brook char populations that were 1.5-fold to 2.7-fold higher than baseline values. Fecundity of rainbow trout under baseline conditions was approximately 2.5-fold higher than brook char fecundity (Figure 4d). Increased fecundity is equivalent to decreased egg mortality in model simulations. Thus, effects of increased fecundity are indistinguishable from lowered egg mortality.

Reduced Spawning Habitat

Spawning habitat was reduced by 20%, 50%, and 80% to investigate its role in influencing brook char and rainbow trout competition. In baseline simulations, all cells with gradients less than 0.6 m/m, velocities less than or equal to 50 cm/sec, and depths

greater than or equal to 6 cm were available for spawning. Spawning habitat was reduced by randomly eliminating these cells at the beginning of each 100 year simulation based on probabilities of 0.2, 0.5, or 0.8.

Results

Aggressiveness of Rainbow Trout

Predicted annual densities of brook char and rainbow trout changed little from baseline values for all three levels of increased rainbow trout aggressiveness (Figures 8 and 9). Rainbow trout densities under increased rainbow trout aggressiveness remained well below allopatric densities. Feeding sites that provide adequate prey for growth are not limiting in the model. Growth and survival rates of juveniles and adults of each species for all three levels of increased aggressiveness varied less than 1% from baseline values.

Latitude

Brook char densities increased under 38°N latitude conditions resulting in their numerical dominance over rainbow trout (Figure 10a and leftmost simulation in Figure 11). However, brook char densities in the 38°N latitude simulations remained below their allopatric densities. The shift in competitive advantage to brook char in the higher latitude simulations was due to differential effects between species on egg and alevin survival. Lower temperature was the primary effect causing these changes, as changing temperature only resulted in similar predicted densities as with changing temperature, flow, and

daylength together (Figures 10a and b; two leftmost simulations in Figure 11). Flow changed alone caused a reduction in brook char densities due to reduced availability of prey (number of prey encountered is proportional to flow and the prey density), while daylength changed alone had little effect on either species (Figures 10c and d; two rightmost simulations in Figure 11).

Brook char were favored in the 38°N latitude simulation because egg and alevin survival decreased less for brook char than for rainbow trout. Lower temperatures during incubation caused increased egg and alevin development times in the 38°N latitude simulations. Mean temperatures experienced by brook char redds averaged 0.3°C lower in the 38°N latitude simulations compared to the baseline simulation (5.3°C versus 5.6°C), while mean temperature for rainbow trout redds was 0.8°C lower (5.6°C versus 6.4°C). Lower temperatures caused rainbow trout egg and alevin stage duration to increase from an average of 69 days in baseline simulations to 79 days in the 38°N simulations. The increase in brook char average egg and alevin stage duration was not as great (from 158 days in baseline to 163 days in 38°N simulations). Egg and alevin mortality rates are constant in the model, and the increased stage durations lowered average survival rate more for rainbow trout (0.09 versus 0.12) than for brook char (0.12 versus 0.13).

Fry survival increased similarly for both species in the 38°N latitude simulations because of reduced starvation mortality. Average brook char fry survival increased from 0.19 in the baseline simulations to 0.29 in the 38°N latitude simulations. Average rainbow trout fry survival increased from 0.10 to 0.16. The average percentage of fry dying due to

length-based and movement mortalities were similar between the 38°N and baseline simulations for both species. The percentage of brook char fry dying due to weight-based (starvation) mortality decreased from 14% in baseline conditions to 9% for the 38°N latitude simulations. Rainbow trout fry showed a similar reduction in the percentage dying from starvation (37% to 23%).

Lower starvation in both species was due to density-dependent growth and bioenergetic effects of lowered temperature. Reduced egg and alevin survival resulted in fewer fry. Because prey are divided equally among fry in a cell, lower fry densities results in more prey per fry and decreased likelihood of starvation. Average temperatures experienced by both species decreased by about 1°C between the 38°N latitude and baseline simulations, reducing routine metabolism of both species. Neither species was feeding at their maximum consumption rate, so the reduction in maximum consumption rates corresponding to 1°C colder water had no effect on their growth.

Year-class Failures

Imposition of year-class failures favored rainbow trout (Figures 12 and 13). Brook char densities decreased more with decreasing interval between year-class failures than rainbow trout densities. Under infrequent year-class failures (every 10 and 20 years), brook char densities were adequate to keep rainbow trout densities below their allopatric densities. At year-class failures every 3 and 5 years, brook char densities became so low that rainbow trout densities approached their allopatric densities. This pattern is more clearly seen in annual densities over time (Figure 12) than in the means of the three

replicate simulations (Figure 13).

Both populations compensated for lost year-classes through increased fry survival. In the three years immediately following a failed year-class, mean rainbow trout fry survival was 0.17, 0.15, and 0.14 for year-class failures every 20 years, 10 years, and 5 years, respectively. In the two years immediately following year-class failures every 3 years, rainbow trout fry survival was 0.16. Rainbow trout fry survival averaged 0.10 in baseline simulations. Brook char fry survival also increased in the years following year-class failures (0.26 for failures every 20, 10, 5, and 3 years compared to 0.19 in baseline). The percent of fry suffering movement mortality after year-class failures was 30% (failures every 20, 10, and 5 years) and 26% (failures every 3 years) for rainbow trout compared to 37% in baseline, and 10% (failures every 20, 10, 5, and 3 years) for brook char compared to 28% in baseline. Fry survival increased following year-class failures because lower egg production led to lower fry densities and thus less movement.

Rainbow trout were less affected by year-class failures because their higher fecundity at length resulted in a smaller reduction in their egg production compared to brook char. In the years following a year-class failure, the number of spawners decreased and the mean length of spawners increased for both species. Egg production in the three years immediately following year-class failures was 34 to 42% below baseline values for brook char, while only approximately 25% below baseline for rainbow trout. For year-class failures every 3 years, the combination of reduced egg production and increased fry survival resulted in little change in the number of fry survivors for rainbow trout (409 versus 428 for baseline), but approximately a 50% decrease for brook char (135 versus

318 for baseline). The mean length of spawners increased from approximately 138 mm in baseline to approximately 154 mm for year-class failures for both species. Increased mean length is advantageous to rainbow trout because the difference between their fecundity and brook char fecundity increases with length (Figure 4d).

Increased Brook Char Fecundity

Competitive advantage shifted to brook char in simulations in which their fecundity was increased (Figures 14 and 15). Brook char densities approached allopatric levels and rainbow trout densities decreased markedly with increasing brook char fecundity. The major effects of increased brook char fecundity were observed in the first three years of the simulations, after which new, dynamic equilibrium conditions were obtained (Figure 14). Annual egg production increased and fry survival decreased for both species during the first three years of the simulations (Figure 16). The increase in brook char egg production more than offset their reduced fry survival, resulting in a net increase in fry survivors for each of the first 3 years (e.g., 387, 495, and 534 for the 2.7-fold increase versus 300, 354, and 379 for baseline). The slight decrease in rainbow trout egg production and reduced fry survival resulted in a net loss of fry survivors each year (e.g., 329, 320, and 306 for the 2.7-fold increase versus 389, 444, and 659 for baseline). Fry survival rates of brook char remained low for years 6 to 100 of the increased fecundity simulations (0.13, 0.10, and 0.07 compared to 0.19 in baseline). All other life stage-specific growth and survival rates were similar between baseline and increased fecundity simulations for both species.

Reduced Spawning Habitat

Decreasing available spawning habitat reduced densities of both species and favored rainbow trout (Figures 17 and 18). Predicted densities of both species generally decreased under allopatric and sympatric conditions. Rainbow trout densities under sympatric conditions decreased the least, resulting in densities similar to their allopatric densities under the 80% reduction in spawning habitat. Brook char densities under allopatric and sympatric conditions decreased the most with reductions in spawning habitat.

Decreasing the spawning habitat resulted in lowered densities of both species because not all females were able to reach spawning areas. Mean annual number of female spawners between baseline conditions and an 80% reduction in habitat decreased from 149 to 83 for rainbow trout and from 140 to 32 for brook char. A larger fraction of mature female brook char (37% versus 21% of mature rainbow trout females) were unable to reach the sparsely located spawning cells because low flow during their spawning season (average flow of 0.25 m^3/s) restricted movement more than when rainbow trout spawn (average flow of 0.47 m^3/s). Corresponding to reduced numbers of spawners, annual egg production between baseline and 80% reduction in habitat decreased 35% for rainbow trout and 62% for brook char. Once the populations adjusted to the reduced number of spawners, growth and survival rates by life stage were similar between baseline and reduced spawning habitat conditions for rainbow trout and for brook char.

Discussion

Using a spatially explicit, individual-based model of sympatric, stream-resident brook char and rainbow trout, the effects on interspecific competition of: (1) aggressiveness of rainbow trout, (2) latitude, (3) year-class failures, (4) increased brook char fecundity, and (5) reductions in spawning habitat were simulated. Model results indicated that aggression of rainbow trout did not significantly affect population densities of either species, northern latitude conditions and increased fecundity favored brook char populations, and year-class failures and reduced spawning habitat reduced rainbow trout densities less than brook char. At the highest levels of each factor, increased brook char fecundity resulted in near-allopatric brook char densities, while year-class failures and reduced spawning habitat resulted in allopatric rainbow trout densities. Below, model results and a review of empirical information are used to judge the likelihood that each of the factors explains the dominance of rainbow trout over brook char in southern Appalachian streams.

Evidence from recent studies (Fausch 1988, 1989) and model simulations both suggest that rainbow trout dominance over brook char is not due to rainbow trout juveniles and adults outcompeting brook char for food or space. Ensign et al. (1989) found no differences in the diets of juvenile and adult brook char and rainbow trout, and Lohr and West (1992) reported insignificant differences in habitat use between the species in southern Appalachian streams. Large differences in either would be expected when an inferior competitor is sympatric with a superior one (Diamond 1978), especially when food is limiting as in southern Appalachian streams (Cada et al. 1987; Ensign et al. 1990).

Baseline simulations indicated only moderate density-dependence during the juvenile stage and very little during the adult stage (Clark and Rose, *in press*), and simulations artificially forcing subordination of brook char juveniles and adults had little impact on predicted population dynamics (Figures 8 and 9).

While model results suggest that limited spawning habitat favors rainbow trout, empirical evidence leads us to deem limited spawning habitat as an unlikely explanation for rainbow trout dominance. Predicted densities of both species declined with reductions in spawning habitat, but rainbow trout declined less than brook char (Figures 17 and 18). Only under the highest reduction in spawning habitat (80%) did rainbow trout densities approach allopatric densities. However, most empirical evidence indicates that spawning habitat in the southern Appalachians is not limiting. Dechant and West (1985), Kelly et al. (1980), and Lennon (1967) observed conditions affecting trout redds in Appalachian streams and did not mention inadequate habitat (but see Harshbarger (1975) for a contrasting opinion). Appalachian populations rebound rapidly from low levels (Lennon 1961), implying spawning areas are generally available. Furthermore, Lennon and Parker (1959) observed large numbers of spawning trout followed by good hatching success in streams of Great Smoky Mountains National Park.

Model simulations showed that all three of the remaining factors (latitude, brook char fecundity, year-class failures) provide possible explanations for the dominance of rainbow trout. Simulations with streams typical of 38°N latitude or with increased brook char fecundity were dominated by brook char populations (Figures 10 and 11). Colder temperatures in 38°N simulations increased egg and alevin incubation times, especially for

rainbow trout, giving brook char an advantage. Increased brook char fecundity favored brook char (Figures 14 and 15), with effects observed during the first 3 years of simulations (Figure 16). Increased fecundity of brook char resulted in more fry survivors despite reduced fry survival. Rainbow trout egg production was insufficient to offset reduced fry survival, resulting in lower annual fry survivors compared to baseline. Brook char populations declined sharply with decreasing interval between year-class failures, but rainbow trout densities remained high (Figures 12 and 13). Rainbow trout recovered more quickly from year-class failures than brook char because of a shift to fewer, but longer female spawners in years immediately following a year-class failure. Fecundity of rainbow trout increases more rapidly with length than brook char fecundity (Figure 4d). Lower movement-induced mortality (due to decreased egg production) resulted in higher fry survival for both species.

Based on empirical evidence, reduced brook char fecundity and year-class failures are judged to be likely, and latitude conditions less likely, explanations of rainbow trout dominance. All three factors show differences related to latitude. McFadden (1961) noted that brook char fecundity can vary greatly among populations; Lennon (1967) observed that the brook char fecundity in Great Smoky Mountains National Park was very low compared to females from northern latitude populations. Intermittent flooding is known to increase mortality of eggs, fry, and small trout (Onodera and Ueno 1961; Seegrist and Gard 1972), particularly in southern Appalachian streams (Harshbarger 1975). Mean winter and spring flows in streams draining Great Smoky Mountains National Park (approximately 35°N latitude) are much higher than those in streams

draining Shenandoah National Park (approximately 38°N latitude) (Figure 5; United States Geological Survey 1993a, b). The higher flows are directly related to more frequent freshets and floods during heavy precipitation events (Shanks 1954; Harshbarger 1975). Lennon (1967) also observed that streams of Great Smoky Mountains National Park are less homothermous than other trout streams and winter temperatures can exhibit rapid drops compared to temperatures in other streams better buffered by groundwater. In contrast, differences in long term mean temperatures (which caused the latitude effect in simulations) between 38°N and 35°N (baseline) latitude streams were small in magnitude (Figure 5). Indeed, the curve for 38°N fit data from baseline (35°N) streams as well as the baseline curve (both with $R^2 > 0.89$), and vice versa (both with $R^2 > 0.73$).

Some caution in interpretation is needed because other variables that could affect rainbow trout dominance also covary with latitude and results depend on several key model assumptions. For example, Lennon (1967) found lower dissolved solids in streams of the Great Smoky Mountains National Park than in those of the Shenandoah National Park and the White Mountains National Forest (approximately 44°N). Distinction between reduced fecundity and increased egg and alevin mortality (perhaps due to water quality differences) cannot be made in model simulations. Results based on increased fecundity of brook char could have been obtained with reduced egg mortality. The conclusions also depend on realistic model assumptions. Two major assumptions are the equal division of prey among fry in a stream cell and how brook char and rainbow trout differences are represented. Assuming all fry in a cell get equal prey resulted in density-dependent growth and survival in model simulations (Clark and Rose, *in press*).

Differences between brook char and rainbow trout were limited to egg and alevin development times, time of spawning, routine metabolism, and length-based fecundity (Figure 4). All of these assumptions affect model predictions, and thus could influence the conclusions concerning the possible role of different factors in explaining rainbow trout dominance.

Of the five hypotheses regarding dominance of rainbow trout over brook char in southern Appalachian streams, more frequent year-class failures and the lower fecundity of brook char were found to be both possible and likely explanations, warmer temperatures due to latitude and limited spawning habitat to be possible but unlikely explanations, and rainbow trout aggressiveness to be a highly unlikely explanation. Dominance by rainbow trout in southern latitudes could be explained by a higher frequency of flow-related episodic mortality events or a gradient in water quality reducing brook char fecundity (or egg survival). Additional field work should focus on a comparative study of the reproductive success and the mortality of early life stages of brook char and rainbow trout. The studies should focus on contrasting northern and southern Appalachian streams, or southern Appalachian streams that show different degrees of rainbow trout dominance. Measurement of short-term variation in water temperatures, flows, and water quality should be coordinated and integrated with estimates of egg, alevin, and fry survival.

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Appendix: Tables and Figures

Table 1: Average values (over replicates) of life stage-specific mean duration, survival, growth rate, and mean length for years 6 to 100 of the baseline (sympatric) simulations. Age-1 fish have lived 1 year, age-2 fish have lived 2 years, and age-3 fish have lived 3 years.

Stage	Duration (days)	Survival (fraction)	Growth rate (g/g/day)		Mean length (mm)	
Brook char			Predicted	Observed	Predicted	Observed
eggs and alevins	158	0.13	-	-	-	-
fry	33	0.19	0.05	0.06[a]	31[c]	-
juveniles (< 100mm)	137	0.68	0.027	-	100[d]	-
age-1	251	0.52	0.016	0.006[b]	116	86[b], 101[e], 149[f]
age-2	365	0.44	0.003	0.004[b]	164	139[b], 136[e], 174[f]
age-3	365	0.45	0.001	0.0006[b]	185	155[b], 160[e], 196[f]
Rainbow trout						
eggs and alevins	69	0.12	-	-	-	-
fry	41	0.10	0.04	0.04[a]	31[c]	-
juveniles (< 100mm)	173	0.63	0.021	-	100[d]	-
age-1	312	0.45	0.013	0.009[b]	115	104[b], 131[g]
age-2	365	0.43	0.003	0.005[b]	164	180[b], 170[g]
age-3	365	0.44	0.001	0.0002[b]	186	185[b], 208[g]

[a]Rose (1986), [b]Whitworth (1980), [c]Length at end of fry stage, [d]Length at maturity, [e]Konopacky and Estes (1986), [f]Lennon (1961), [g]Lennon and Parker (1959)

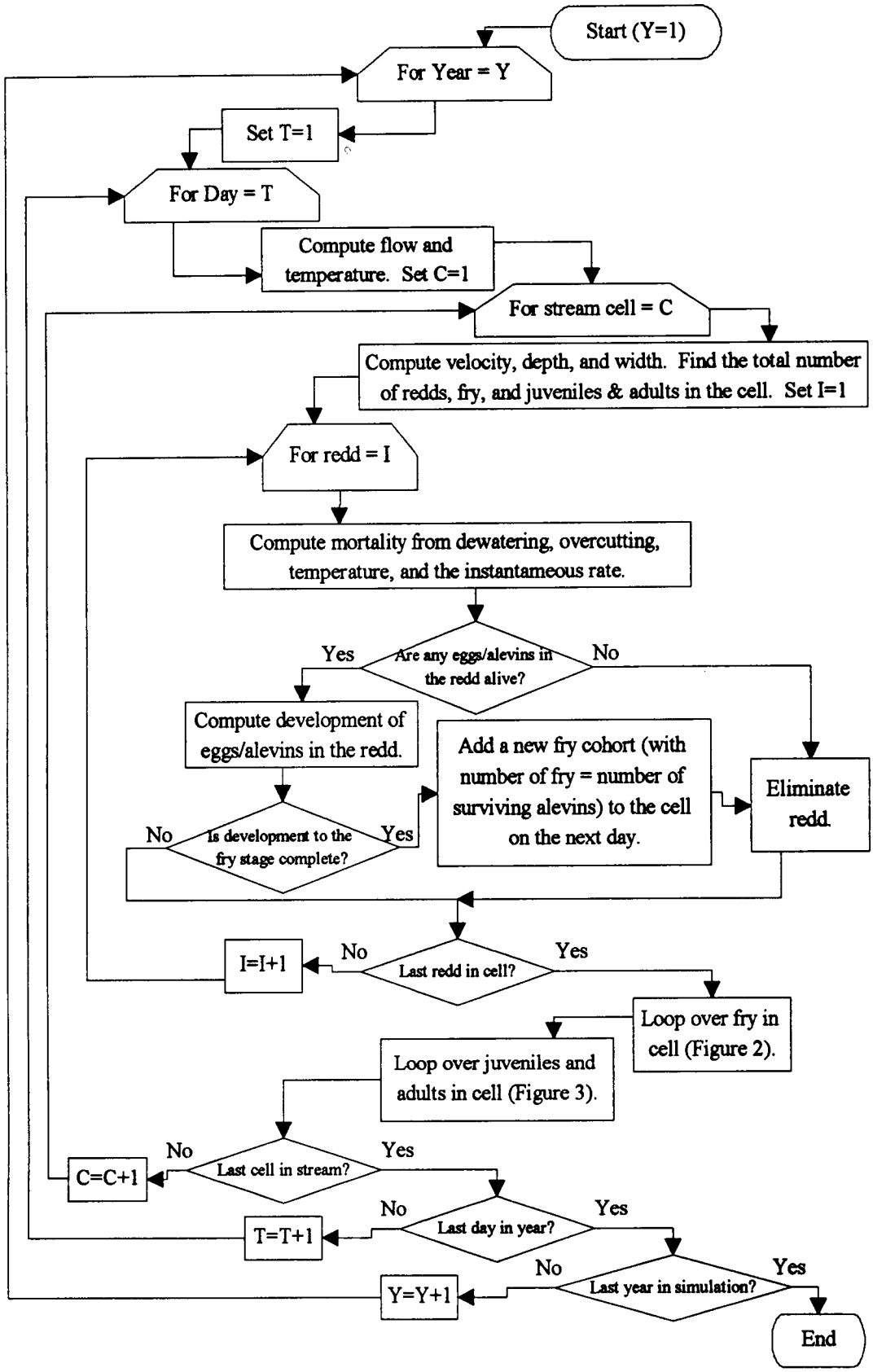

Figure 1: Flowchart of the major components of the brook char - rainbow trout model.

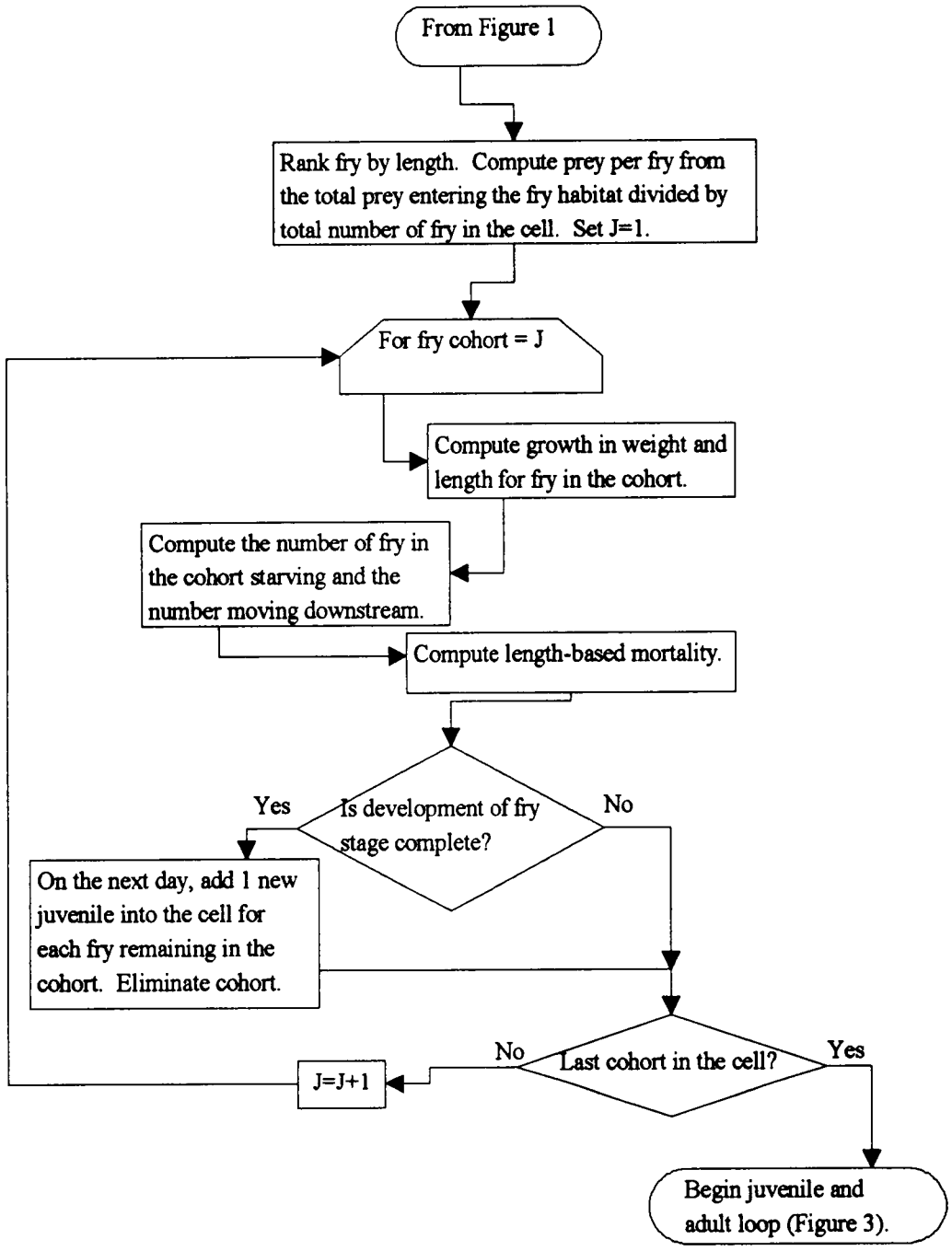

Figure 2: Flowchart of the daily processes performed for fry cohorts in a cell of the model stream.

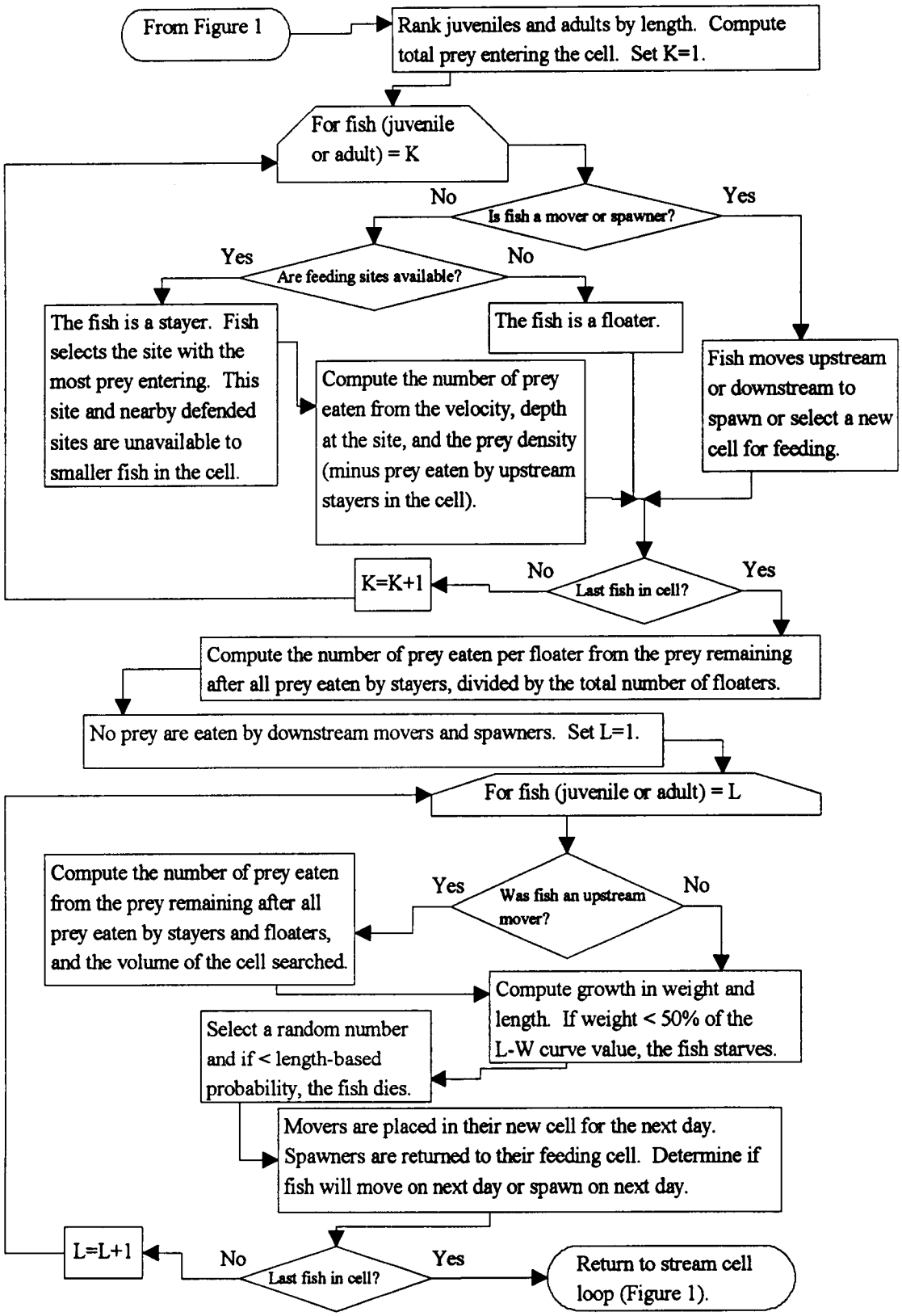

Figure 3: Flowchart of the daily processes performed for individual juveniles and adults in a cell of the model stream.

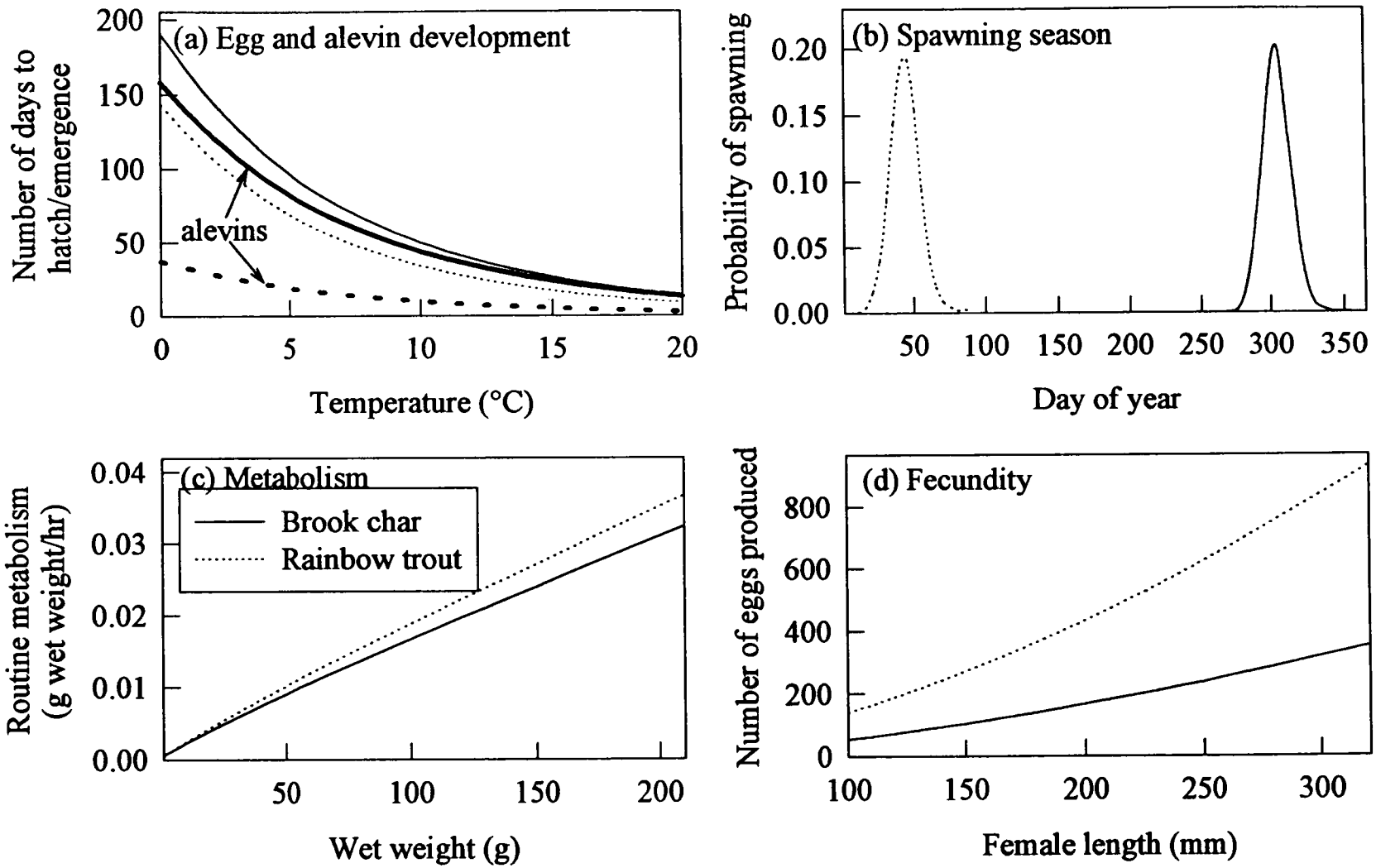

Figure 4: Species-specific differences between brook char and rainbow trout represented in the model: (a) egg and alevin development rates, (b) spawning season, (c) routine metabolism, and (d) fecundity. Minor differences (less than 1%) also exist between the species-specific length-weight relationships used in the model.

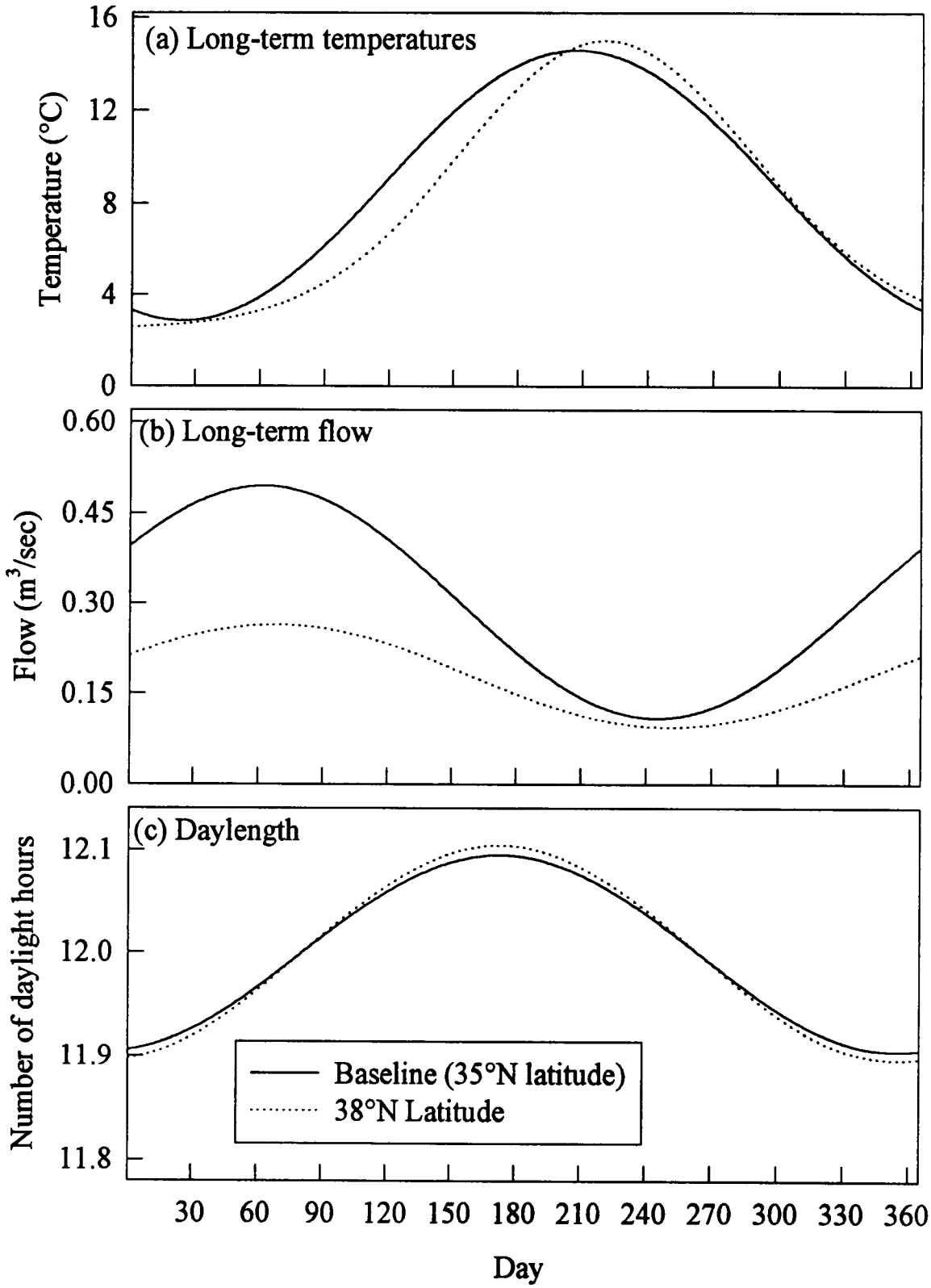

Figure 5: Long term mean (a) water temperature, (b) flow, and (c) daylength used in the baseline simulations (35°N) and simulations of 38°N latitude streams.

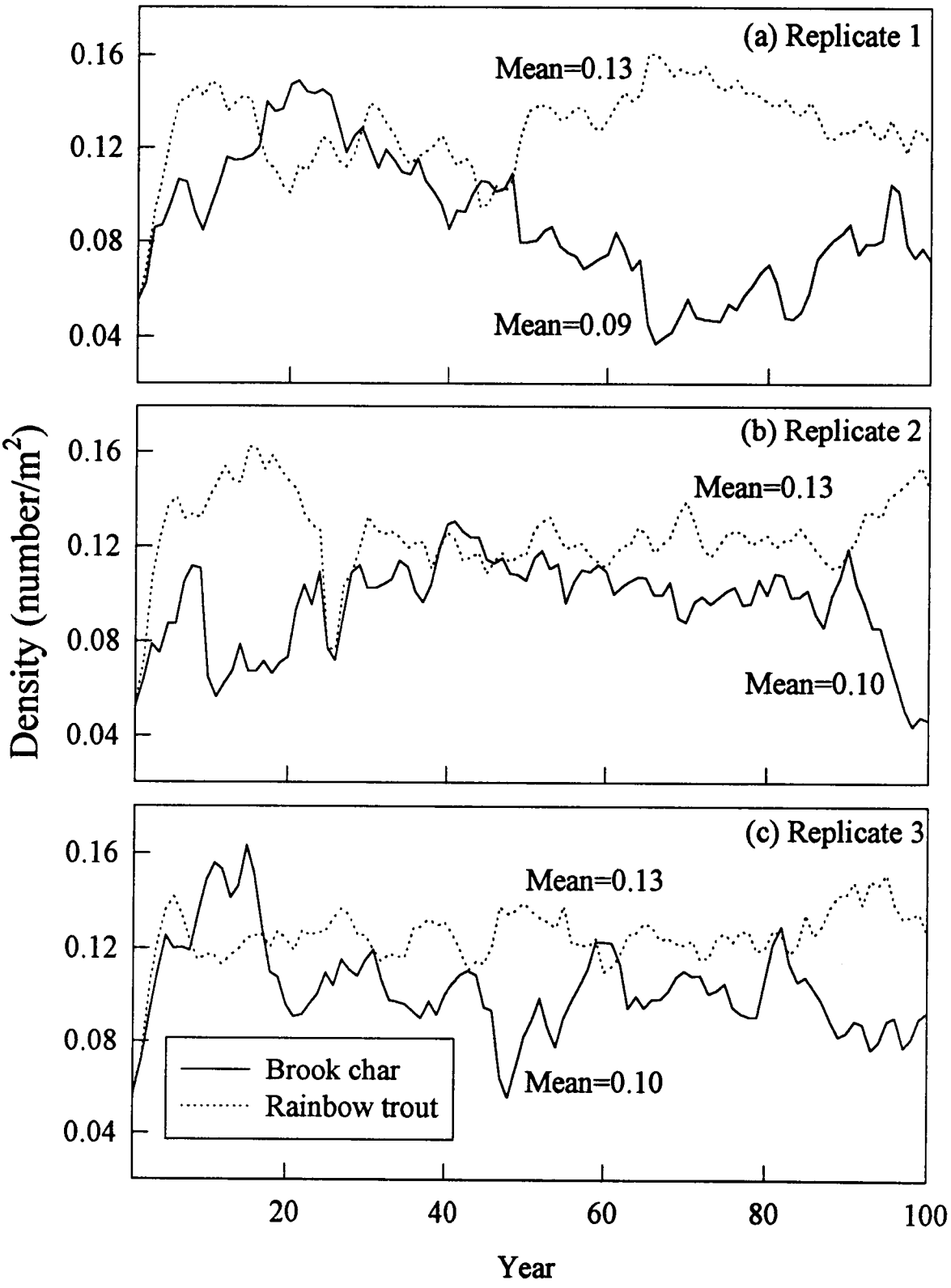

Figure 6: Annual brook char and rainbow trout post-fry densities for the 3 replicate baseline (sympatric) simulations.

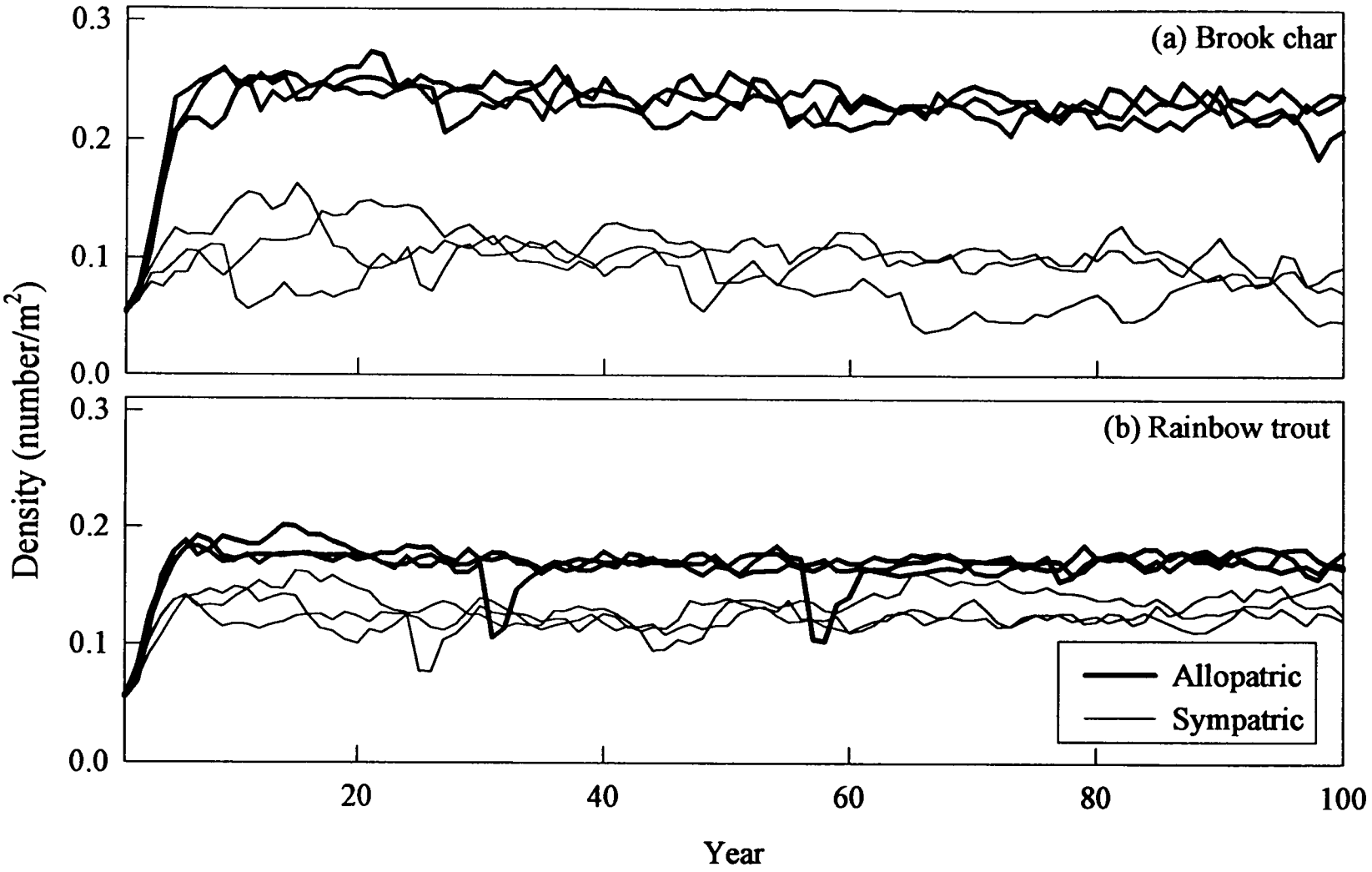

Figure 7: Sympatric and allopatric annual post-fry densities of (a) brook char and (b) rainbow trout for the 3 replicate simulations under baseline conditions.

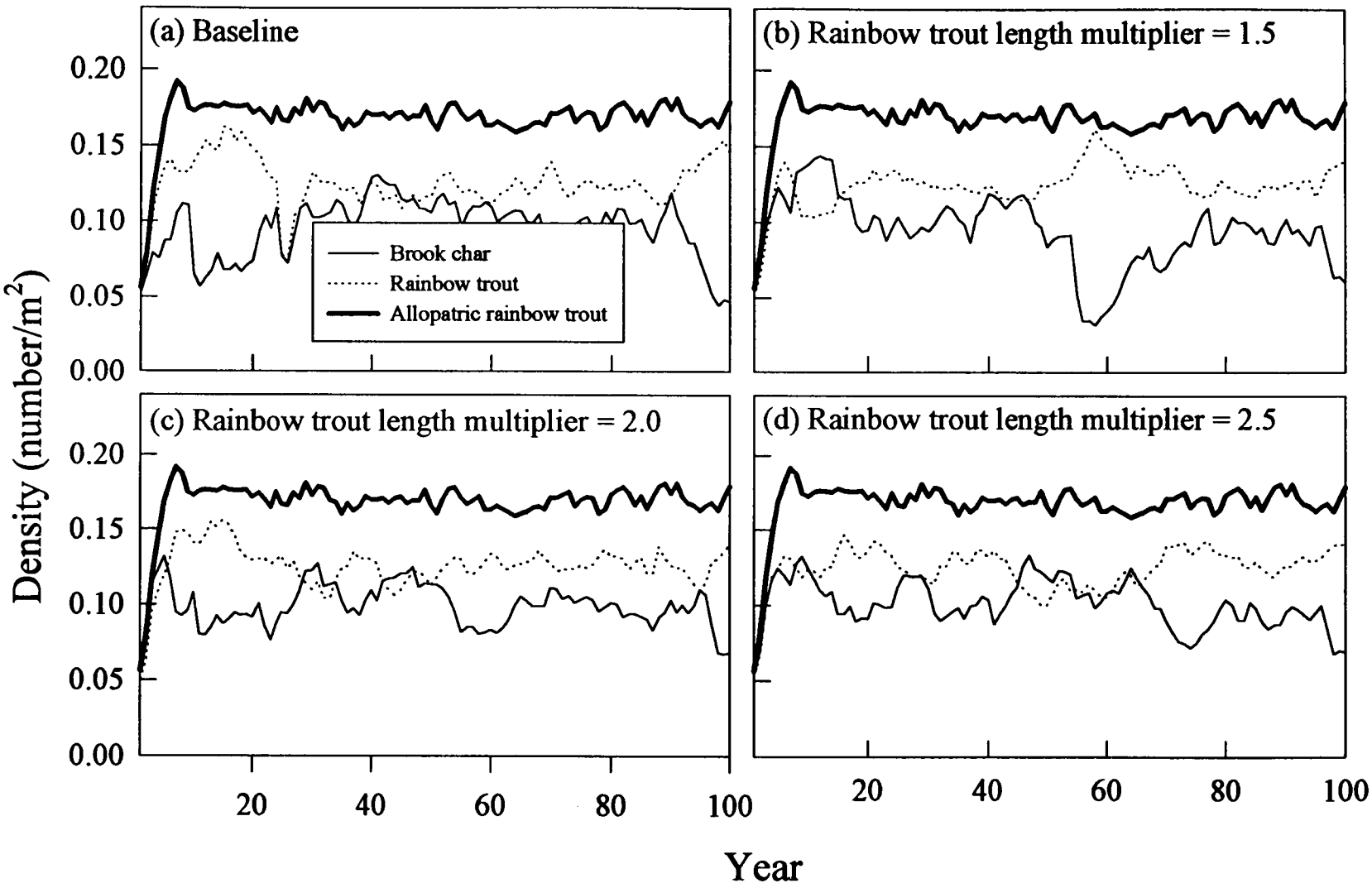

Figure 8: Annual sympatric brook char, sympatric rainbow trout, and allopatric rainbow trout post-fry densities for the replicate 2 baseline simulation under: (a) baseline conditions and increased rainbow trout aggressiveness with length multiplier of (b) 1.5, (c) 2.0, and (d) 2.5.

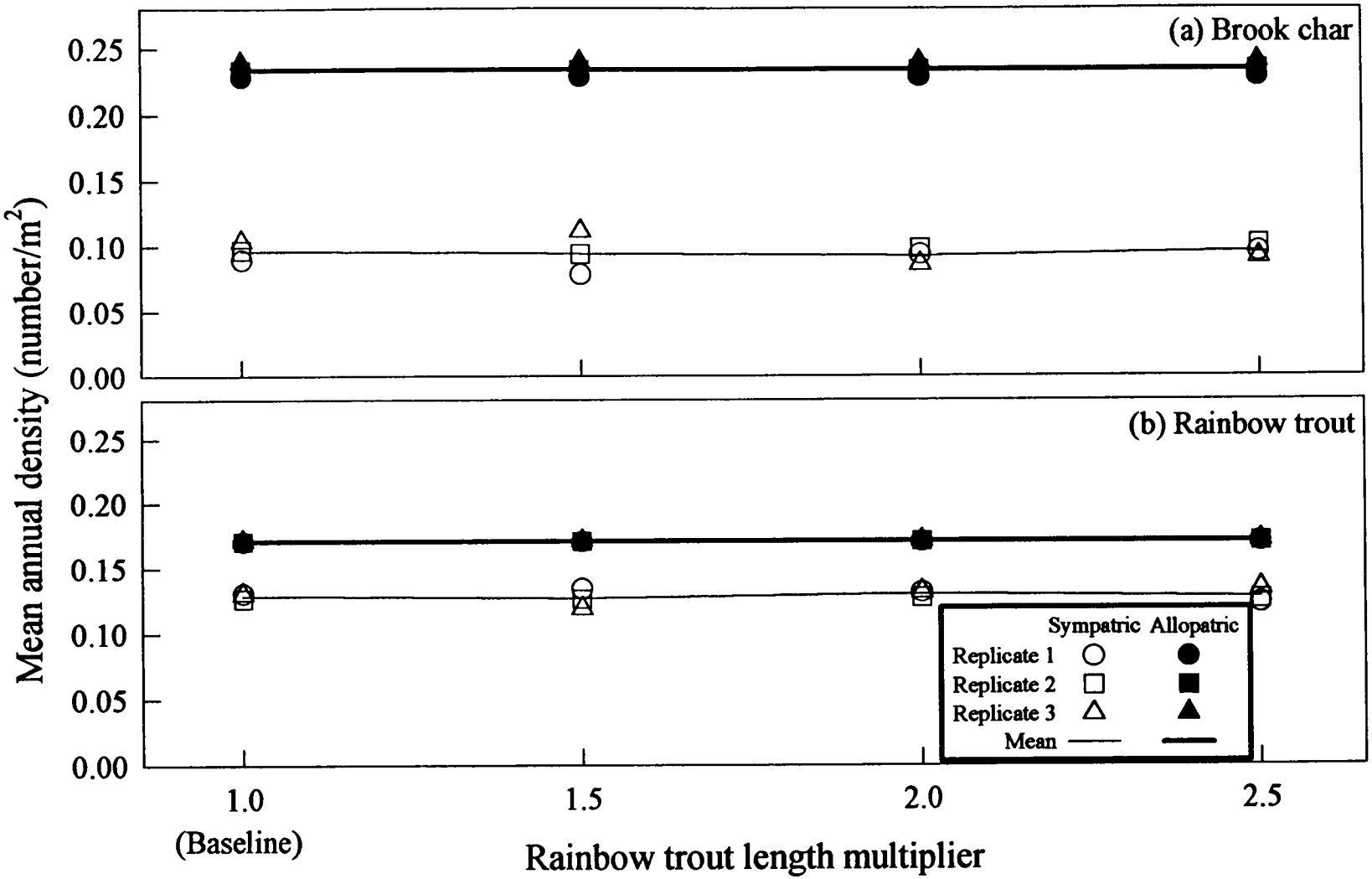

Figure 9: Mean (a) brook char and (b) rainbow trout post-fry densities (computed over years 6 to 100) for increasing rainbow trout length multipliers. Aggressiveness of rainbow trout was increased by multiplying their length by 1.5, 2.0, and 2.5 when competing for feeding sites with brook char (1.0 represents baseline).

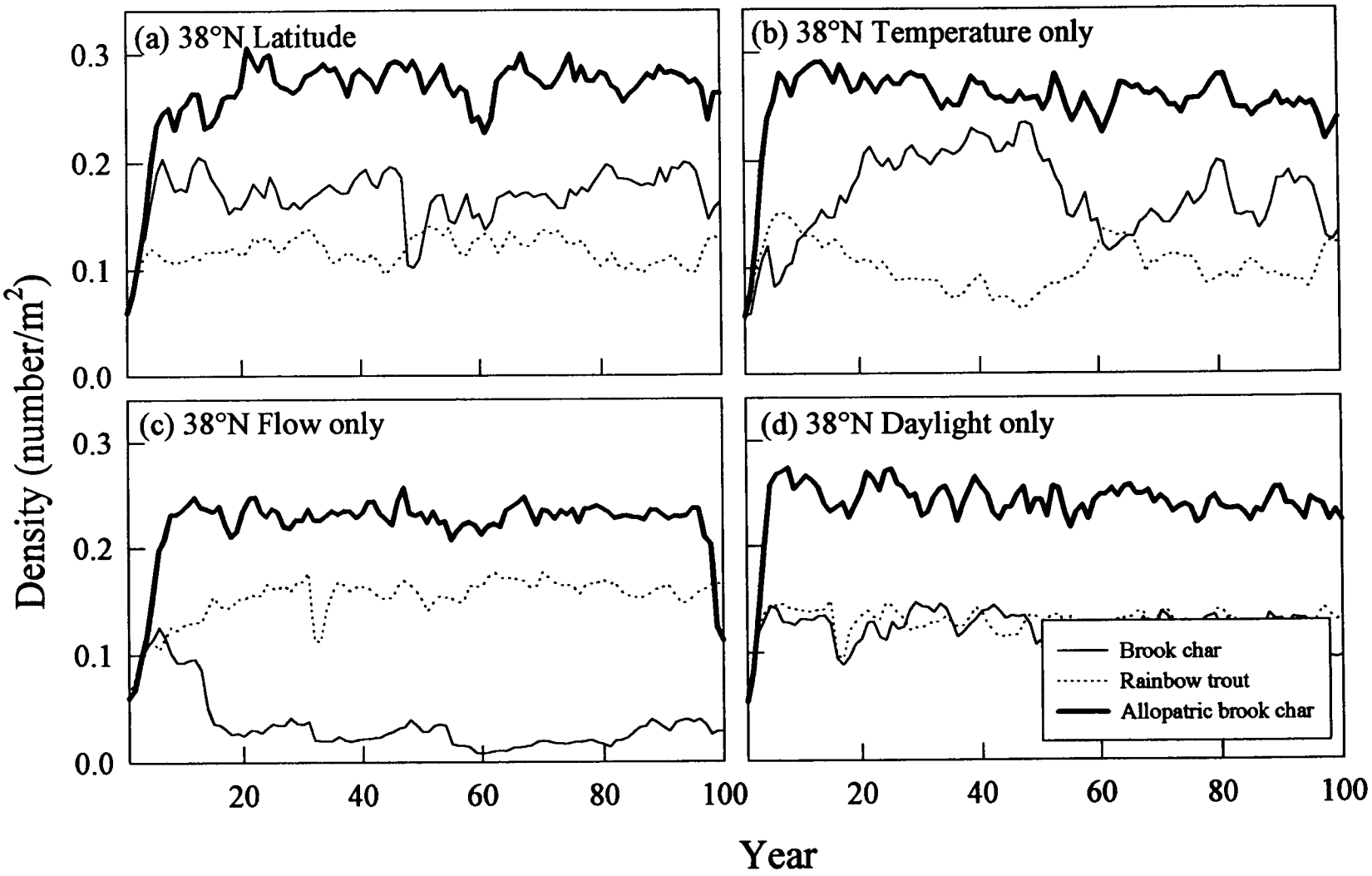

Figure 10: Annual sympatric brook char, allopatric brook char, and sympatric rainbow trout post-fry densities for the replicate 2 simulation under: (a) 38°N latitude, (b) 38°N temperature only, (c) 38°N flow only, and (d) 38°N daylight only.

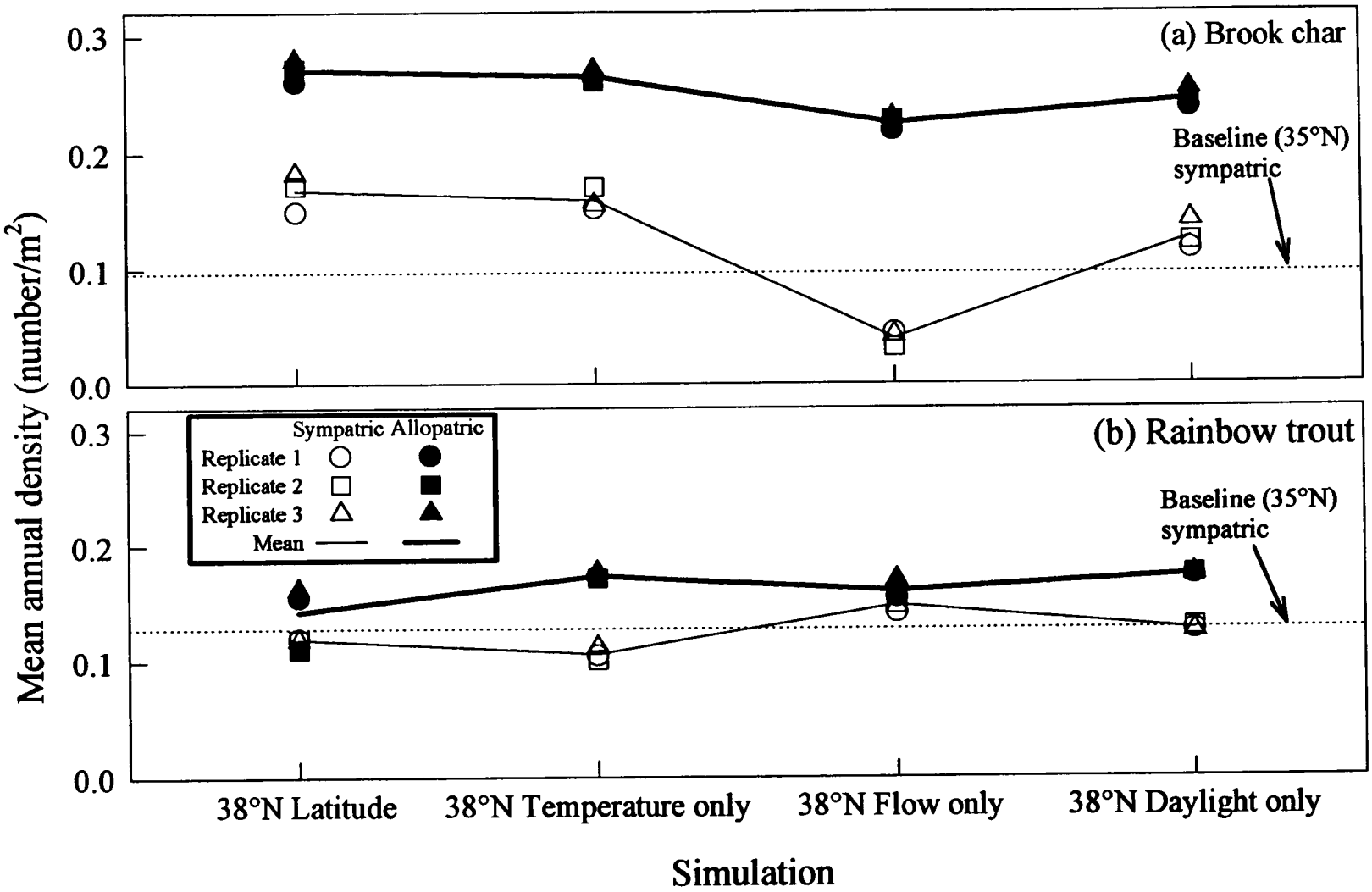

Figure 11: Mean (a) brook char and (b) rainbow trout post-fry densities (computed over years 6 to 100) for 38°N temperature, flow, and daylight used together (as latitude) and singly.

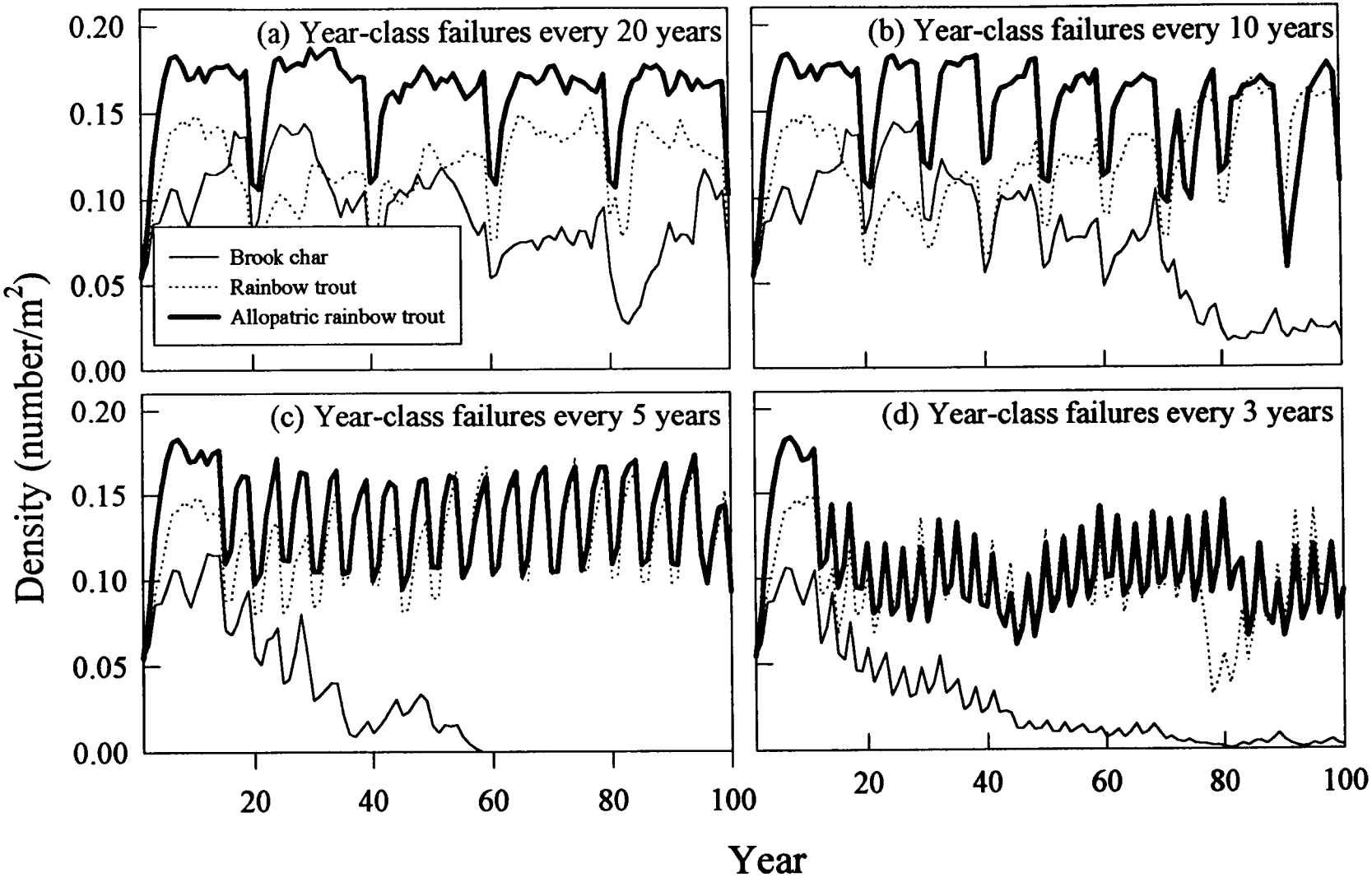

Figure 12: Annual sympatric brook char, sympatric rainbow trout, and allopatric rainbow trout post-fry densities for the replicate 1 simulation for year-class failures every (a) 20 years, (b) 10 years, (c) 5 years, and (d) 3 years.

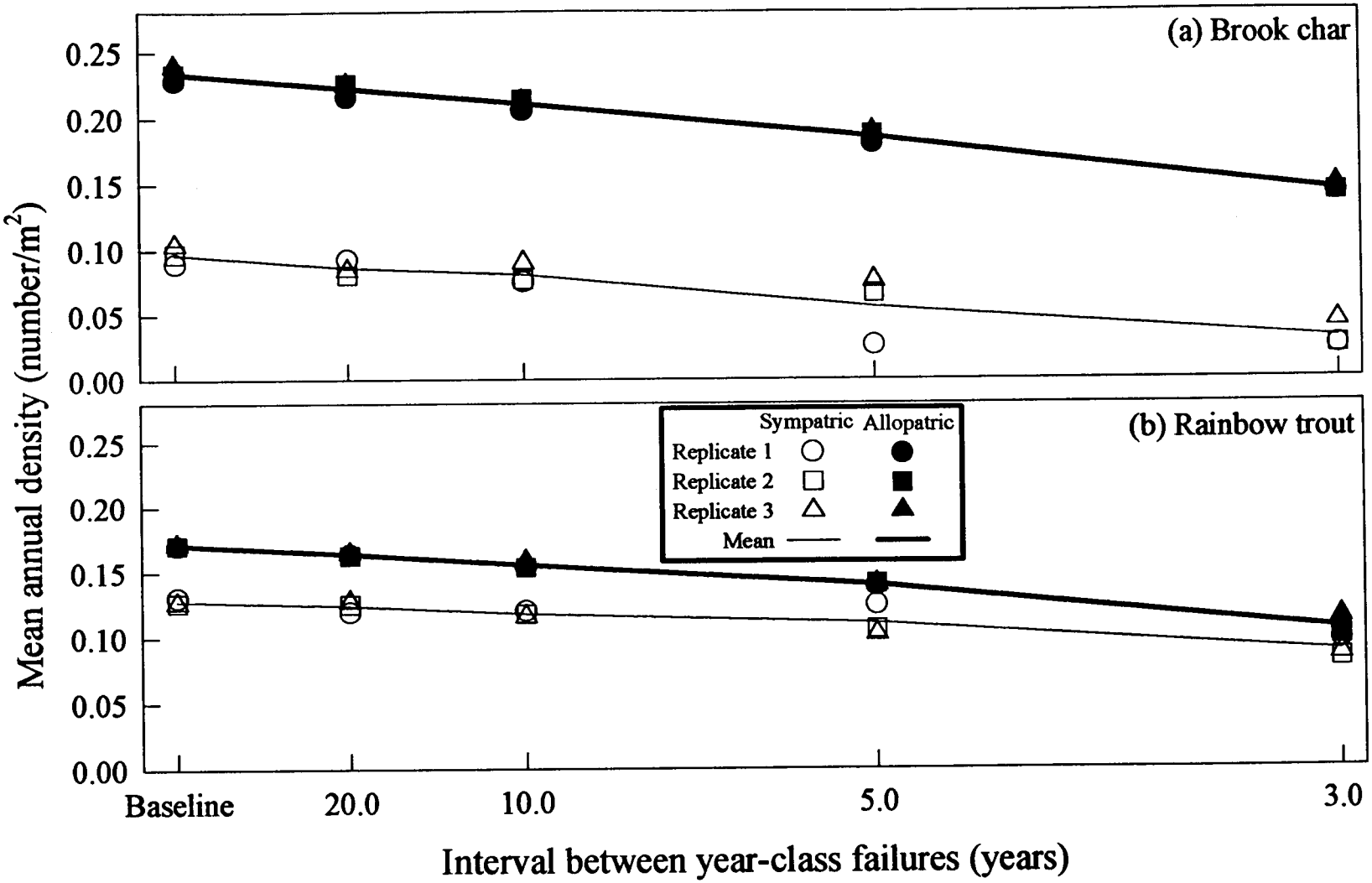

Figure 13: Mean (a) brook char and (b) rainbow trout post-fry densities (computed over years 6 to 100) with decreasing interval between year-class failures.

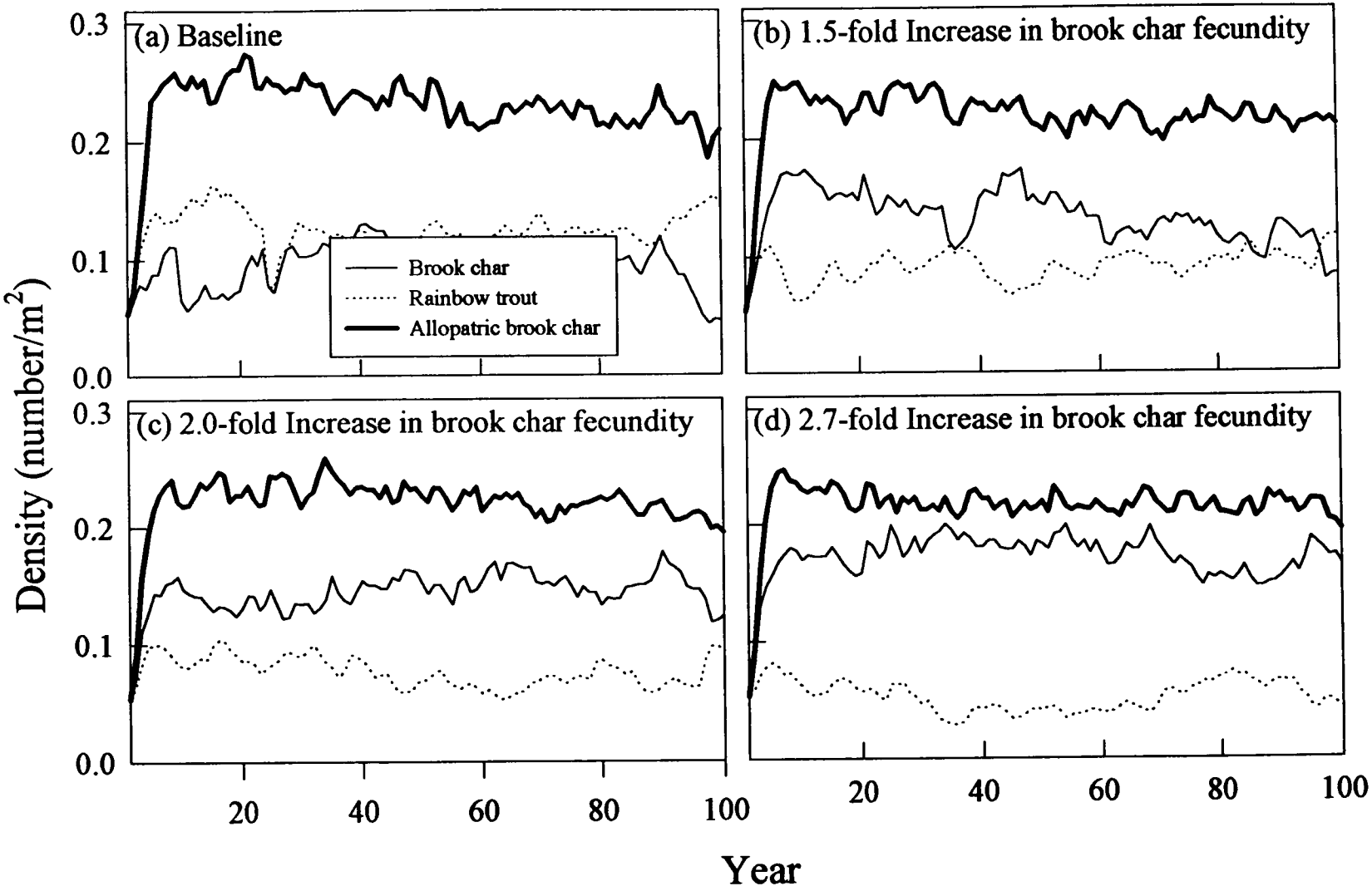

Figure 14: Annual sympatric brook char, allopatric brook char, and sympatric rainbow trout post-fry densities for the replicate 2 simulation under: (a) baseline fecundity and brook char fecundity increased (b) 1.5-fold, (c) 2.0-fold, and (d) 2.7-fold.

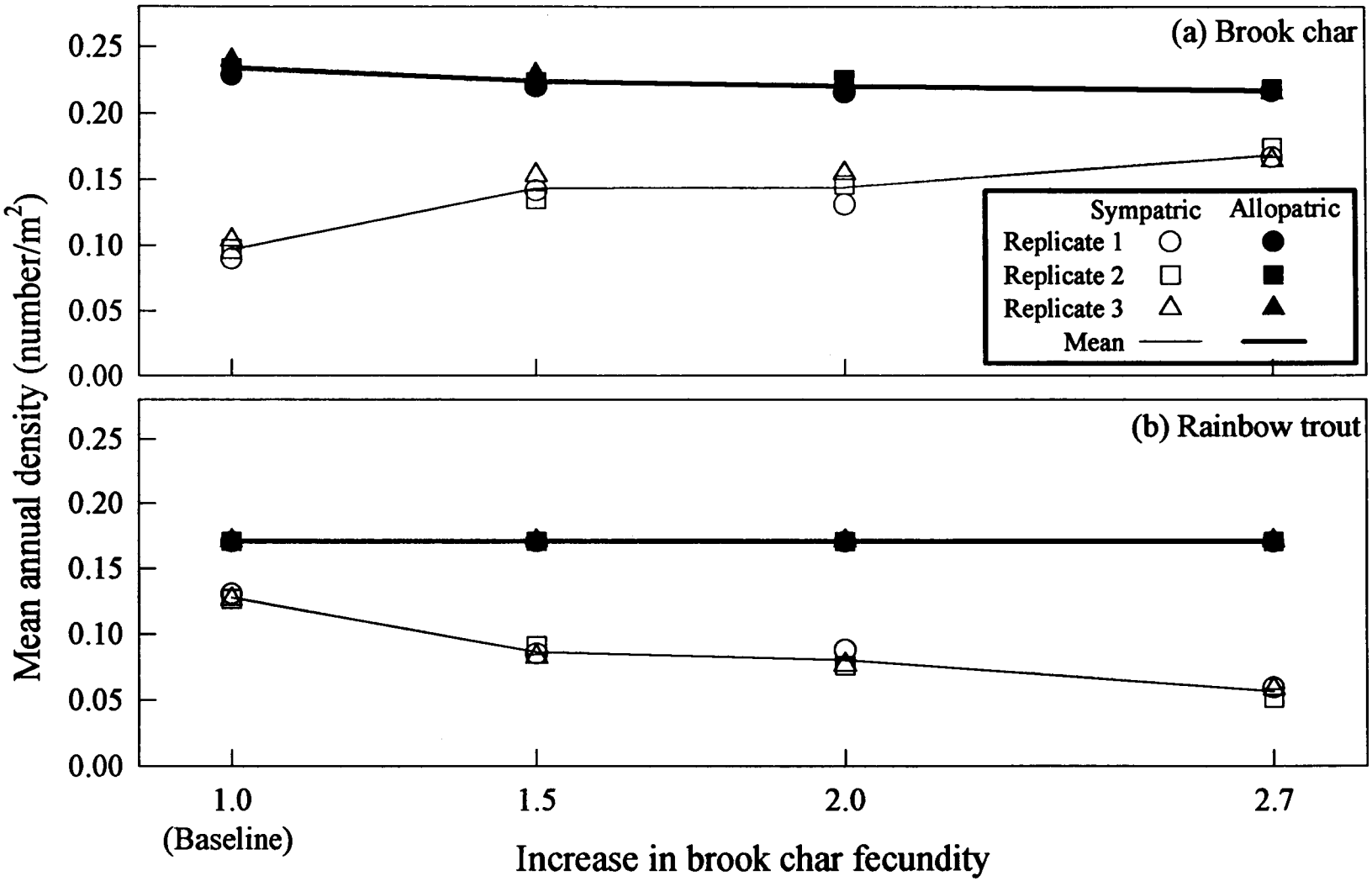

Figure 15: Mean (a) brook char and (b) rainbow trout post-fry densities (computed over years 6 to 100) with increasing brook char fecundity.

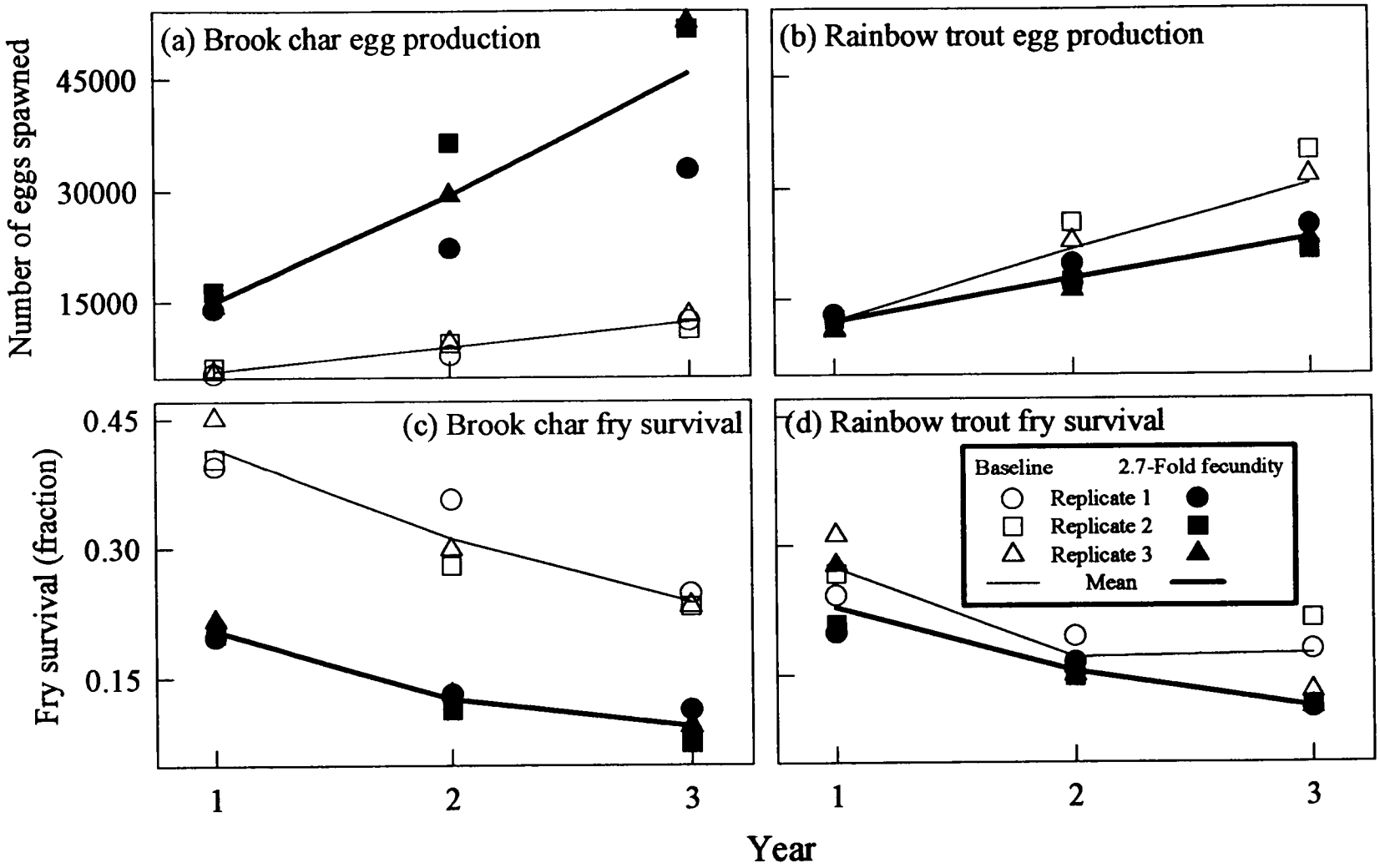

Figure 16: Egg production and fry survival of brook char (a and c) and rainbow trout (b and d) in the first 3 years of the baseline and 2.7-fold higher brook char fecundity simulations.

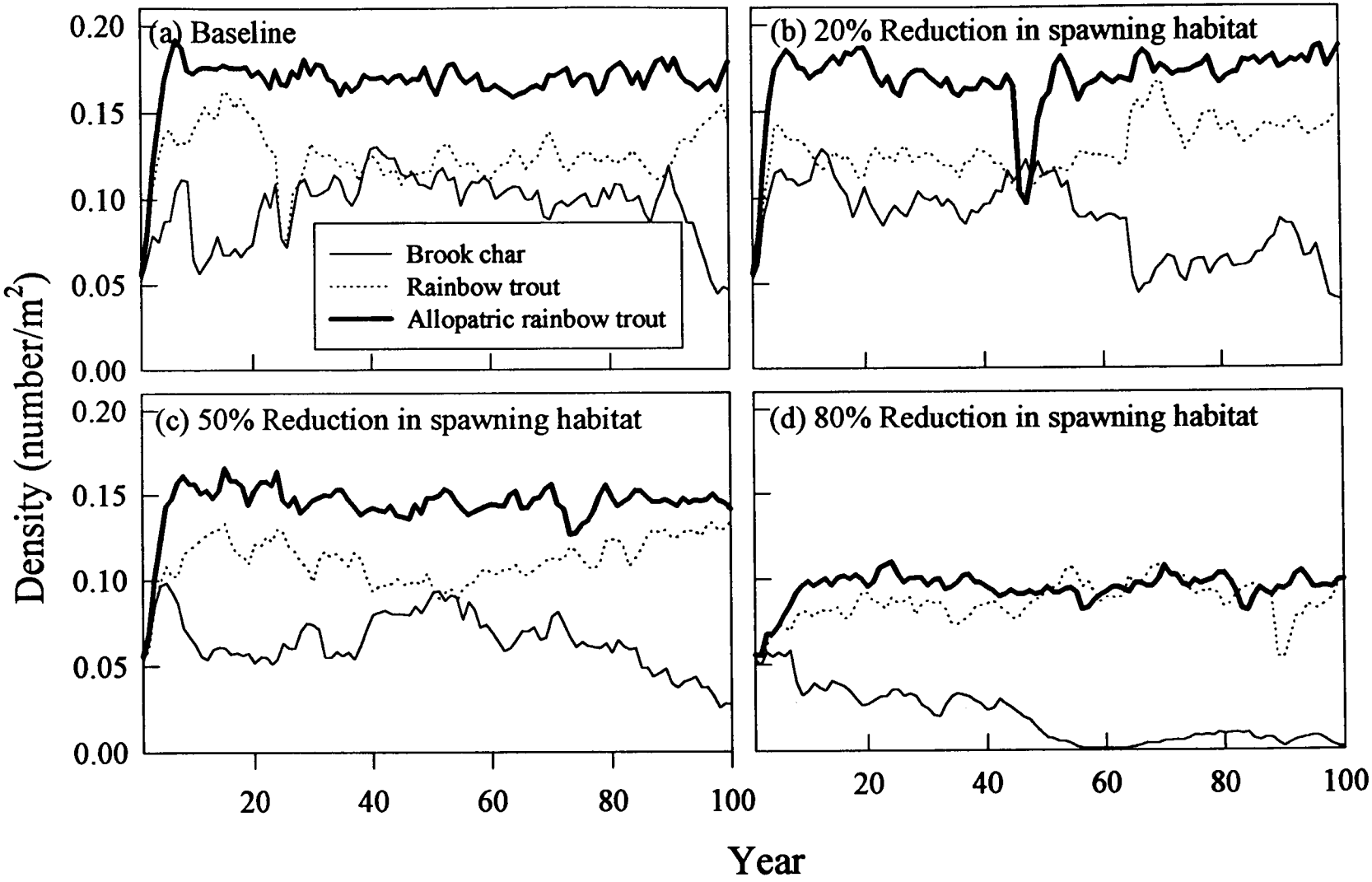

Figure 17: Annual sympatric brook char, sympatric rainbow trout, and allopatric rainbow trout post-fry densities for the replicate 2 simulations under (a) baseline (0%) and reduced spawning habitat of (b) 20%, (c) 50%, and (d) 80%.

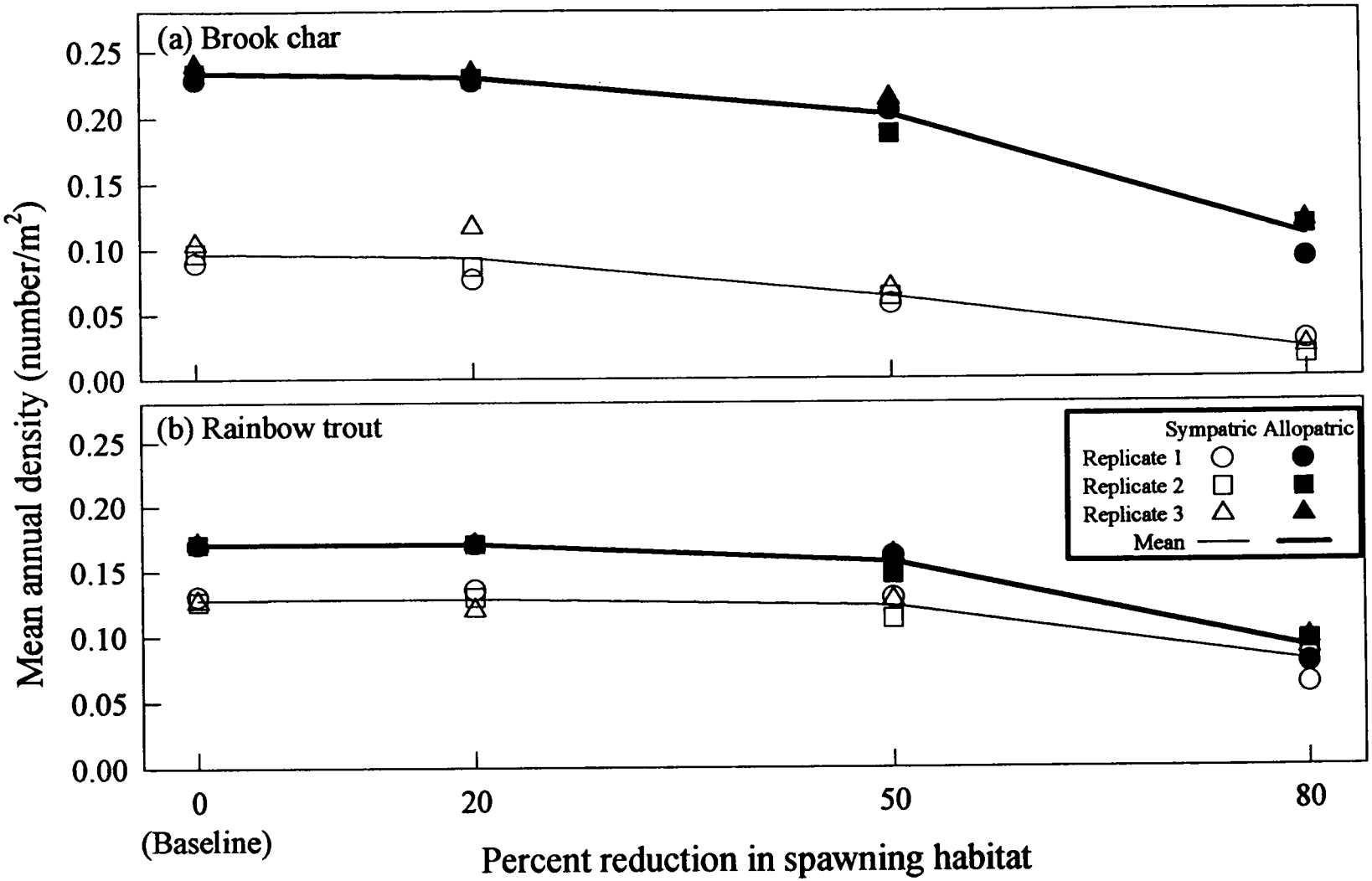

Figure 18: Mean (a) brook char and (b) rainbow trout post-fry densities (computed over years 6 to 100) with increasing reductions in spawning habitat.

Part 4

An Individual-Based Modeling Analysis of Management Strategies for Enhancing Brook Char Populations in Southern Appalachian Streams

Abstract

An individual-based model of sympatric rainbow trout (*Oncorhynchus mykiss*) and brook char (*Salvelinus fontinalis*) was used to evaluate management strategies for enhancing brook char densities in southern Appalachian streams. Management strategies were compared for 100 year simulations under: (1) electrofishing removal of rainbow trout, (2) stocking of brook char, (3) habitat alteration (changing mean size of pools in the stream), and (4) angler harvest of rainbow trout. Results indicated that realistic levels of electrofishing removal of rainbow trout and stocking of brook char juveniles could produce allopatric brook char densities, but that habitat alteration and rainbow trout fishing would not significantly increase brook char densities. Electrofishing and stocking results were robust as similar predictions were obtained under conditions that favored rainbow trout (invasion of rainbow trout adults, frequent year-class failures, reductions in spawning habitat). Approximately 10 to 20 years are required for allopatric densities to be achieved. Management strategies that reduce competition in the young-of-the-year life stages offer the most promise for restoring brook char stocks in southern Appalachian streams.

Introduction

In the Appalachian streams of the southeastern United States, large reductions in the range of native brook char, *Salvelinus fontinalis*, have been coupled with an expansion of the distribution of exotic rainbow trout, *Oncorhynchus mykiss* (Kelly et al. 1980; Larson and Moore 1985). Controlling populations of exotic species and restoring native

species are an important part of trout fisheries management in the southern Appalachians (Moore et al. 1986). Alternative management options for enhancing native species are difficult to compare and assess prior to implementation. Quantitative, objective comparisons among alternative strategies would be useful to fishery managers faced with attempting to restore native trout species.

Management strategies that have been employed in Appalachian streams to enhance brook char populations include electrofishing removal of rainbow trout (Moore et al. 1983; Riley 1986), stocking of brook char (King 1942; Lennon and Parker 1959), and fishing for rainbow trout but not brook char (Larson and Moore 1985). Electrofishing removal of rainbow trout has generally enhanced brook char stocks, but the degree of enhancement has been highly variable (Moore et al. 1983; Riley 1986; Habera 1987). Limited evidence suggests that supplemental stocking (and restocking) and reduced fishing of brook char results in only marginal benefits as brook char range has continued to decline in Appalachian streams (Kelly et al. 1980).

Habitat alteration as a means of trout management has been used in streams outside of the Appalachians. Riley and Fausch (1995) found that in Colorado streams increased pool volume and decreased current velocity resulted in higher immigration of trout but only temporary increases in survival. However, studies of Canadian streams have shown significant increases in brook char survival when pool habitat was increased (Saunders and Smith 1962; Burgess and Bider 1980). Habitat alteration has potential application for Appalachian streams. Flebbe and Dolloff (1995) found that two streams in old-growth forests of the Appalachians supported greater trout biomass and had smaller

and more numerous pools than a stream in a maturing second-growth forest.

A spatially explicit, individual-based model developed for sympatric, stream-resident brook char and rainbow trout was used to quantitatively compare alternative strategies for restoring brook char populations. The management strategies compared are: (1) electrofishing removal of rainbow trout, (2) stocking of brook char, (3) habitat alteration, and (4) angler harvest of rainbow trout. Each strategy was applied at various levels to a baseline case typical of sympatric populations in southern Appalachian streams. Strategies that showed significant enhancement of brook char densities were further evaluated for their robustness. The successful management strategies were applied under conditions likely to be encountered in Appalachian streams that favor rainbow trout (invasions, episodic high mortality, and reduced spawning habitat) to determine if they still resulted in enhanced brook char densities.

Model Description

The brook char - rainbow trout individual-based model is described in detail in Part 2 (or see Clark and Rose, *in press*). The model is briefly described here. Flow charts summarizing the major computations of the model are presented in Figures 1-3; differences in how brook char and rainbow trout are represented in the model are compared in Figure 4. Figure 1 shows the major loops over years, days, and stream cells, and the computations for redds. Figures 2 and 3 show the computations for fry cohorts, and juvenile and adult individuals, respectively, in each stream cell. All computations are performed on a daily basis.

Environment

The stream is represented as a linear reach (with closed ends) divided into cells corresponding to pools, runs and riffles. Sets of pools, runs, and riffles are stochastically generated to form the stream reach from mean lengths for pools (2.0 m), runs (1.6 m), and riffles (0.4 m), and a mean stream slope of 0.10 m/m. Water temperature, water flow, and daylength are assumed uniform throughout the entire stream reach but vary daily. The long-term average values of water temperature, flow, and daylength, were estimated from data measured on southern Appalachian streams. For temperatures and flows, daily stochasticity is imposed on the long-term average values. Water velocity, water depth, and cell width are calculated from water flow using relationships for the southern Appalachian region, and vary from cell to cell and over time.

Spawning, Eggs, and Alevins

Mature females (those greater than 100 mm) spawn once per year during the appropriate spawning season (Figure 4b) and establish redds in stream cells. Spawners move as close to their natal cell as possible for spawning, and place their redd randomly within the chosen cell. Both males and females swim to and select cells for spawning, but only females lay eggs. Fecundity (eggs/mm) is higher for rainbow trout compared to brook char (Figure 4d). Individual redds are then followed as a cohort until development of the alevin stage is completed. Egg and alevin development rates in the redd are temperature-dependent, and differ between brook char and rainbow trout (Figure 4a). A constant instantaneous rate of mortality is applied (0.013/day for brook char, 0.03/day for

rainbow trout) daily to each redd cohort. Location of the individual redds is tracked on a fine-scale grid inside each cell, permitting computation of additional mortality from dewatering when low flow exposes portions of the redd and from superimposition (overcutting) by later spawning fish. Complete loss of a redd occurs due to freezing (temperature < 0.1 °C) and excessive heat (temperature > 21 °C).

Fry

At swim-up (i.e., completion of alevin development), individual redds are followed as individual cohorts of fry with initial lengths of 20 mm. Fry are initially located in the same cell of the stream in which the redd was located, but may move downstream after two days due to slow growth or crowding. Fry always remain in the shallow stream margins (< 10 cm depth) feeding on drift (divided among all fry in the cell) until becoming juveniles. Metamorphosis occurs between 30 mm and 40 mm; fry greater than 30 mm become juveniles if slow growth or crowding triggers movement.

Growth of fry is based on the same bioenergetics as juveniles and adults (Equation 1). All individual fry in a cohort are assumed to grow uniformly.

Downstream fry movement occurs in response to weight loss or crowding. If fry growth rate today (g/g/day) is less than their past average growth rate, cohorts move downstream. Crowding-induced movement occurs when the total area of individual fry habitat exceeds the available fry habitat in a cell (defined as the surface area from 10 cm depth to each bank). Fry cohorts then move downstream (from smallest to largest in mean length) until the sum of fry habitats in the cell is less than the available habitat. For fry less

than 30 mm, moving cohorts are relocated to the first available downstream fry habitat (water depth < 10 cm). For fry greater than 30 mm, moving cohorts become juveniles and enter the stream habitats utilized by juveniles and adults (water depths > 10 cm).

Mortality of fry is length-based, weight-based, and movement-based. Length-based and weight-based mortality for fry is as described for juveniles and adults (see below). Movement mortality is assessed to moving fry cohorts by reducing the cohort size by 15% on the day of movement.

Juveniles and Adults

Juvenile and adult fish feed, grow, move, suffer mortality and (if mature and ripe) spawn on a daily basis. Each fry surviving to metamorphosis is followed as an individual. Juveniles and adults can exhibit either of two feeding strategies: stayers or floaters. Stayers establish territories (60 cm x 60 cm in size) in the portion of a cell with depth greater than 10 cm and in cells with slopes less than 0.6 m/m (i.e., not in riffles). Sites within a cell are allocated daily to both species in descending order of their lengths. Larger fish prevent smaller fish from occupying territories in the same cell that are within 5 body lengths upstream or adjacent to their site. Floaters locate at the back of a cell if no sites are available in a cell.

Four size classes of drift prey are represented. Weights per individual associated with the four prey types are: 3.6, 9.5, 32.0 and 104.0 mg wet weight. Total prey biomass is 2.7 mg wet weight/m^3, similar to the 0.3 to 8.0 mg wet weight/m^3 reported for southern Appalachian trout streams (O'Hop and Wallace 1983; Ensign 1988). Fish less than 30 mm

eat the smallest prey type; fish between 30 mm and 50 mm eat the two smallest prey types; fish between 50 mm and 60 mm eat the three smallest prey types; fish between 60 mm and 80 mm eat all prey types; and fish greater than 80 mm eat the three largest prey types. The number of prey from each size class encountered is determined by the prey density, cross sectional area of the stream at the territory site, and stream velocity in the cell. For stayers, prey densities are reduced by consumption by fish located upstream in the same cell. Prey densities remaining in the cell after consumption by all stayers is divided equally among the floaters. Floaters and stayers feed for all daylight hours except when temperatures are less than 2°C, when feeding is restricted to one hour per day. Fish moving upstream through a cell may feed on the prey remaining after all floaters and stayers have fed. Upstream movers encounter food based on volume of water searched and the remaining prey density.

Growth in weight (W, g wet weight) is represented using a bioenergetics equation:

$$W_{t+1} = W_t + 0.28pC_{max}A - 0.19M, \quad (1)$$

where C_{max} is the maximum daily consumption (g wet weight/day), p is the proportion of C_{max} realized, A is assimilation efficiency, and M is total metabolism (g wet weight/day). Maximum consumption (C_{max}) is a function of the fish's weight and temperature developed from data reported by Elliott (1975a; 1975b). The proportion of C_{max} realized (p) is determined by the biomass (number times weight per individual) of prey items eaten by the individual fish. Assimilation is assumed to be 0.65 for all fish. Metabolism (M) is a sum of routine (based on weight and a Q_{10} temperature adjustment) and active (based on

weight and swimming speed/current velocity) components developed for each species. Brook char metabolism is slightly lower than rainbow trout metabolism (Figure 4c). Optimum temperatures for growth are 9°C for brook char and 11°C for rainbow trout.

Weight is converted to length on a daily basis. Fish cannot lose length, but may lose weight, and length cannot be added until the fish weight is at or above the predicted value from the length-weight curve. Brook char and rainbow trout length-weight relationships were estimated from southern Appalachian populations and differ by less than 1%.

Fish can move from a cell if growth is slow, depths have receded due to low flow, or high flow is above their maximum swimming speed. Direction of movement is randomly determined; only downstream movement is allowed when flow is greater than maximum swimming speed. During upstream movement feeding is allowed and swimming costs are incurred. During downstream movement, feeding is not allowed and no swimming costs are imposed. Distance moved is limited to 25 m per day or less if obstructed by an upstream barrier (i.e., flow greater than maximum swimming speed) or the upstream and downstream boundaries of the stream..

Mortality of fry, juveniles and adults is both length (L, mm total length) and weight-based. Length-based instantaneous mortality (Z, 1/day) is given by:

$$Z = 0.0021 + 0.0012e^{-\frac{L}{8952}}. \qquad (2)$$

Individual fry cohorts are reduced by multiplying by e^{-Z} each day until reaching the juvenile stage or the numbers in a cohort become less than one. Individual juvenile and adult fish

die if a random number (chosen daily for each fish) is less than $1-e^{-Z}$. Weight-based mortality of fry occurs when the average weight of an individual in the cohort becomes less than 70% of the weight predicted by their length-weight relationship. Cohorts are then reduced proportionately by the fraction of actual weight divided by the correct length-weight value. For juveniles and adults, weight-based mortality occurs if the weight of an individual becomes less than 50% of the weight predicted by their length-weight relationship.

Baseline Conditions and Model Corroboration

Baseline conditions were defined to be representative of typical conditions in southern Appalachian streams (see Clark and Rose, *in press*). A 600 m stream reach was simulated, comprised of 50% pools, 40% runs, and 10% riffles. Mean pool length was 2.0 m and average stream slope was 0.1 m/m (Moore et al. 1983; Larson and Moore 1985). As described above, daily water temperatures, flows, and prey densities were specified using data from southern Appalachian streams. Pools averaged 40 cm deep with water velocities less than 30 cm/sec. Water depth averaged 15 cm in runs with water velocities between 50 and 180 cm/sec. Riffles were shallow (approximately 9 cm deep) with relatively high water velocities (> 200 cm/sec). Simulations were initiated with 200 56-mm individuals of each species and were for 100 years duration. Replicate simulations can be performed that differ only in their random number sequences. Random number sequences affect the outcome of stochastic processes, such as stream morphology (dimensions of each cell), prey encounters, mortality, and direction of trout movement.

Previous analyses of the model showed that average predicted probability of survival and growth rates among five replicate simulations varied less than 8% and average predicted densities varied less than 11% (see Table 4, **Part 2**). Results in this part also indicated a consistent pattern in predicted time to equilibrium (see *Time to Equilibrium*) based on a single replicate simulation. Therefore, single simulations are analyzed in this part.

Model predictions of brook char and rainbow trout densities and growth rates under baseline conditions were similar to values observed for sympatric populations in southern Appalachian streams (Table 1). Predicted population densities (daily densities of juveniles and adults averaged over the year) were stable through time, with average annual rainbow trout densities approximately 1.4-fold higher than those of brook char (Figure 5a). Pools were the most frequently used habitat (> 50% of all fry and > 90% of all juveniles and adults were found in pools). Movement of individuals was limited (< 8 m downstream for fry; < 20 m either upstream or downstream for juveniles and adults). Density-dependence was strongest in the fry stage. Fry growth rates were negatively related to initial fry densities for both species (R^2 approximately 0.3 for brook char; R^2 approximately 0.5 for rainbow trout). Fry survival was positively related to fry growth rate (R^2 approximately 0.4 for brook char; R^2 approximately 0.6 for rainbow trout). Clark and Rose (*in press*) present additional model analyses and comparisons of model results to data.

Allopatric (single-species) simulations under baseline conditions showed brook char to be more affected by competition than rainbow trout (Figure 5b). Without rainbow trout present, brook char densities increased 2.5-fold, whereas rainbow trout increased

only 1.3-fold when alone.

Management Strategies: Methods

Management Simulations under Baseline Conditions

Model simulations were performed under conditions of: (1) electrofishing removal of rainbow trout, (2) stocking of brook char, (3) habitat alteration, and (4) angler harvest of rainbow trout. Daily water flows, temperature, prey densities, and arrangement and dimensions of pools, runs, and riffles were identical for all simulations. Predicted allopatric brook char densities were used as the metric for measuring the performance of the management strategies. The most effective management strategy would result in allopatric brook char densities. Allopatric densities generated under baseline conditions are identical to those for simulations involving electrofishing, stocking, and rainbow trout fishing because these changes did not affect the model configuration. Predicted allopatric densities corresponding to simulations involving habitat alterations were determined by performing brook char only simulations for each changed value of mean pool length.

Model predictions of average annual juvenile and adult (post-fry) densities of each species are compared among model simulations. Plots of average annual values over the 100 years are presented for selected levels of each management strategy; the means of the average annual values (computed over years 11 to 100) are presented for all simulations. The first 10 years of simulations are ignored to eliminate effects of initial conditions.

Electrofishing

Electrofishing of rainbow trout was simulated by randomly removing a fraction of rainbow trout (all sizes) on day 240 (August 31) of each year. If a random number chosen for each rainbow trout was less than the probability of removal then that fish was removed from the stream. Probabilities of removal simulated were: 0.0 (baseline), 0.1, 0.2, 0.3, 0.5, and 0.8. These probabilities span the range of possible values; 80 to 90% efficiency has been reported for multiple-pass electrofishing (Johnson 1965; Wiley and Tsai 1983). No removals were imposed during the first 10 years of the simulations to allow the populations to establish themselves. Electrofishing was assumed to have no effects on brook char.

Stocking of Brook Char

Stocking of brook char was simulated by placing a fixed number of eggs, fry, or juveniles in the model stream each year. Equivalent numbers of eggs, fry, and juveniles were stocked using model-generated survival rates under baseline conditions (0.12 for egg to fry stage and 0.25 to 0.33 for fry to juvenile stage; Clark and Rose, *in press*). Reported juvenile stocking levels in Appalachian streams (number/600 m) are 269 (Lennon 1961), 596 (Lennon and Parker 1959), and 746 (King 1942). Annual juvenile stocking levels simulated were: 0 (baseline), 200, and 600. Using survival estimates, corresponding annual stocking levels of eggs were 5,000 and 20,000, and of fry were 600 and 2,400.

Eggs, fry, and juveniles were stocked during times and in locations within the stream appropriate for each life stage. Eggs were stocked by placing artificial redds (each

with 250 eggs) in randomly chosen spawning cells (cells with gradients < 0.6 m/m, velocities ≤ 0.5 m/sec, and depths ≥ 6 cm) between day 295 (October 22) and day 304 (October 31) of each year. Fry stocking was achieved by placing groups of 25 fry (each 25 mm) in randomly chosen cells with gradients less than 0.6 m/m, velocities less than or equal to 0.43 m/sec, and depths greater than or equal to 10 cm on day 100 (April 10) of each year. Groups of 50 stocked juveniles (each 50 mm) were placed in randomly chosen cells with gradients less than 0.6 m/m, velocities less than or equal to 0.56 m/sec, and depths greater than or equal to 10 cm on day 120 (April 30) each year. For all simulations with stocking, no stocking occurred in the first 10 years of the simulation, and stocking was discontinued if rainbow trout went extinct.

Habitat Alteration

Habitat alteration was simulated by changing the mean pool length of the model stream. In baseline simulations, lengths of each pool were generated from a triangular probability distribution with mode of 2.0 m, minimum of 1.4 m, and maximum of 2.6 m. Because a symmetric triangular distribution was used, mean pool length equals modal length. Habitat was altered by decreasing and increasing the mode, minimum, and maximum of the triangular distribution. Changes simulated were mean pool lengths of: 1.5 m (mode of 1.5 m, minimum of 1.0 m, and maximum of 2.0 m), 4.0 m (mode of 4.0 m, minimum of 2.8 m, and maximum of 5.2 m), and 6.0 m (mode of 6.0 m, minimum of 4.2 m, and maximum of 7.8 m). Increasing pool lengths result in fewer, but larger pools in the model stream reach. Mean pool length was reduced below the baseline value to ensure

that predicted effects of mean pool length were consistent. Prey densities are specified per stream cell. Therefore, prey densities were changed corresponding to the different mean pool lengths to maintain the same amount of total prey in the stream reach as in baseline conditions.

Angler Harvest of Rainbow Trout

Angler harvest of rainbow trout was simulated by daily removing a percentage of adult rainbow trout larger than a fixed length (creel size) from day 60 (March 1) to day 304 (October 31). Two creel sizes were used in the simulations: 178 mm (approximately 7 inches) and 152 mm (approximately 6 inches). The 178 mm creel size is a common size limit for southern Appalachian trout fisheries (King 1942; Lennon and Parker 1959; Lennon 1961). The 152 mm limit was included to determine the potential benefits of using a smaller, but still realistic, creel size. On each day between day 60 and 304, if a random number selected for each adult rainbow trout (longer than the creel size) was less than the probability of harvest, then that fish was removed from the stream. Percentages harvested examined were: 0.0%/day (baseline), 0.3%/day, 0.7%/day, and 1.0%/day. Simulated harvest levels bracket reported values for trout fisheries (0.6%/day - Lennon and Parker 1959; 0.3%/day - McFadden 1961). No removals occurred in the first 10 years of the simulations to allow initial conditions to dissipate, and no effect was assumed on brook char.

Robustness of Strategies

For management strategies which resulted in significant increases in brook char densities under baseline conditions, additional simulations were performed to evaluate their robustness. The strategies were applied under three conditions: invasion by adult (spawning) rainbow trout, frequent year-class failures of both species, and a 50% reduction in spawning habitat. The introduction of a few, large rainbow trout is believed to be how rainbow trout invade allopatric brook char streams (Larson et al. 1995), and would be expected to occur in sympatric streams undergoing brook char restoration. Reduced spawning habitat and year-class failures were included because previous results indicated they favor rainbow trout populations (see **Part 3**). For a management strategy to be useful it must be successful under a variety of conditions that are likely to occur. Rainbow trout invasion, reduced spawning habitat, and year-class failures have been documented for a variety of trout streams (Lennon 1961; Kondolf et al. 1991; Larson et al. 1995; Sorensen et al. 1995). These three conditions provide a rigorous test of the robustness of a management strategy because they provide conditions that favor rainbow trout over brook char more than that which occurs under baseline conditions.

Annual average post-fry densities were predicted for invasions, reduced spawning habitat, and year-class failures imposed on the baseline model configuration (Figure 6). Invasions were simulated by randomly placing five 200 mm adult female rainbow trout in the model stream on day 265 (September 22) of each year. Year-class failures were represented by killing all eggs of both species every 5 years. No invasions or year-class failures were imposed during the first 10 years of the simulation. Reduced spawning

habitat was simulated by randomly eliminating, with probability of 0.5, potential spawning cells (cells with gradients < 0.6, velocities ≤ 0.5 m/sec, and depths ≥ 6 cm) at the beginning of the simulation. Compared to baseline conditions (Figure 5), rainbow trout invasions had little effect on brook char densities, reduced spawning habitat resulted in decreased brook char densities, and year-class failures resulted in brook char extinction (Figure 6).

Time to Equilibrium

The time to reach equilibrium was computed for those management strategies that resulted in significant increases in brook char densities. Time to equilibrium was computed based on the number of years required for average annual densities to reach the long-term mean annual densities. Long-term mean annual brook char and rainbow trout densities were computed over years 11 to 100 for each management strategy simulation. For brook char, the first year (after year 10) the annual average density exceeded the long-term mean value was used because brook char densities were increasing under management simulations. For rainbow trout, which were decreasing to lower densities under management strategy simulations, time to equilibrium was computed by taking the first year (after year 10) annual density was less than the long-term mean density. Time to equilibrium values provide a rough estimate of how quickly the results of different management strategies would be observed.

Management Strategies: Results

Baseline Conditions

Predicted annual post-fry densities of brook char increased to allopatric levels for the rainbow trout electrofishing and several brook char stocking strategies, but not for the habitat alteration and angler harvest of rainbow trout strategies (Figures 7-11). For electrofishing, probability of removal greater than or equal to 0.3 resulted in allopatric brook char densities (Figures 7a and 8). The high level of fry stocking (2,400/year) and both levels of juvenile stocking also produced near allopatric brook char densities (Figures 7b and 9). Habitat alteration (increasing mean pool length in the stream) (Figures 7c and 10) and angler harvest of rainbow trout (Figures 7d and 11) increased brook char densities, but even at the highest levels examined, predicted densities were less than allopatric densities.

Electrofishing lowered rainbow trout fry densities, by lowering juvenile and adult survival, which resulted in increased brook char fry survival. At a capture probability of 0.5, average juvenile rainbow trout survival was 23% lower than under baseline conditions (0.48 versus 0.63), and average age-2 survival was 16% lower (0.36 versus 0.43). Lower juvenile and adult survival resulted in fewer rainbow trout spawners and lowered fry densities. There were an average of 12 rainbow trout spawners per year and 339 individuals entering the fry stage for the capture probability of 0.5, compared to 156 spawners and 4,382 individuals entering the fry stage under baseline conditions. Brook char fry survival increased during the first five years following implementation of electrofishing (0.24 for 0.5 capture probability versus 0.21 for baseline), and their numbers

quickly increased to new equilibrium levels comparable to allopatric densities (Figure 8).

Stocking of juvenile brook char caused reduced juvenile survival for both species. For a stocking level of 600 juveniles per year, average juvenile growth rates were reduced compared to baseline conditions for brook char (0.51 to 0.37 mm/day) and for rainbow trout (0.42 to 0.30 mm/day). Lower juvenile growth rates lead to lower survival (0.68 to 0.44 for brook char; 0.63 to 0.49 for rainbow trout). The combination of adding brook char and lower juvenile survival resulted in a net increase in the average annual number of brook char spawners (from 131 for baseline to 373). Reduced juvenile survivorship resulted in fewer annual rainbow trout spawners (from average of 156 for baseline to 16).

Stocking eggs and small numbers of fry (600 annually) increased brook char densities to less than allopatric levels and decreased rainbow trout densities (Figure 7b). Stocking eggs and 600 brook char fry per year increased the average number of brook char fry, and fry survival is negatively correlated to the total number of fry present (for baseline, $R^2 = 0.44$ for brook char and $R^2 = 0.73$ for rainbow trout). For example, the average number of fry under stocking 5,000 eggs was 3,234 (compared to 1,607 in baseline) and fry survival was 0.16 (compared to 0.19 in baseline). Similar changes were predicted for stocking 20,000 eggs and 600 fry. Stocked eggs and fry offset the decrease in brook char fry survival resulting in an increase in the average number of brook char spawners (e.g., 215 with 5,000 eggs stocked versus 131 in baseline). More spawners resulted in higher brook char densities, but the increased egg production was not enough to produce allopatric densities. Rainbow trout densities decreased due to higher brook char densities causing reduced rainbow trout juvenile survival (e.g., average of 0.60 with

5,000 eggs stocked versus 0.63 in baseline). Reduced juvenile survival lowered the average number of rainbow trout spawners (115 with 5,000 eggs stocked versus 156 in baseline), and ultimately their densities.

Stocking large numbers of brook char fry (2,400 annually) resulted in allopatric densities (Figure 5b). As with stocking of eggs and 600 fry, adding 2,400 fry lowered fry brook char survival (0.12 versus 0.19 in baseline). However, adding 2,400 fry was enough to result in an annual average of 315 spawners, which was similar to an average of 335 spawners under allopatric conditions. As with stocking of eggs and 600 fry, rainbow trout juvenile survival was reduced compared to baseline conditions (0.58 versus 0.63 in baseline), but not enough for them to be eliminated from the stream.

Increasing pool length slightly favored brook char, but effects were not enough to result in allopatric densities. The major effects were a greater reduction in juvenile survival of rainbow trout compared to brook char, and an increase in the lengths of older trout of both species. Mean juvenile survival of rainbow trout decreased from 0.63 under baseline conditions to 0.55 for 4 m and 6 m mean pool length simulations. Mean juvenile survival of brook char decreased less (0.68 to 0.62). Corresponding to reduced juvenile survival, mean number of rainbow trout spawners decreased from 156 under baseline to 94 for the increased mean length simulations. Mean number of brook char spawners were similar for baseline and increased mean pool length simulations (approximately 140). Mean length of spawners increased by approximately 10 mm for both species because of higher adult growth rates. Mean growth rates of age-2 brook char and rainbow trout increased from 0.13 mm/day under baseline to 0.16 mm/day for mean pool lengths of 4

and 6 m. Age-2 and older trout benefitted from increased pool length because they occupied feeding positions near the front of pools (allocation of feeding location was based on length). Prey drift rates were increased with increasing pool lengths to maintain the same total prey as in baseline conditions. Fish located in the front of a cell, before the consumptive effects of other trout are accounted for, would experience the most increase in prey. However, survival of age-2 and age-3 fish did not change because the instantaneous mortality rate (Equation 2) is relatively flat for lengths greater than 120 mm. The similar number of spawners and their longer length resulted in a slight increase in average egg production for brook char (12,360 eggs under baseline to 16,300 for 4 and 6 m pool lengths). The increased length of rainbow trout spawners was not enough to offset their reduced numbers, and mean egg production decreased from baseline conditions (38,170 eggs to 26,210). Thus, while increased mean pool length favored brook char, the effects were not sufficient to cause significant increases in brook char densities.

The two creel sizes resulted in lowered rainbow densities and higher, but less than allopatric, brook char densities. Changes in trout densities and survival rates showed a consistent pattern for increasing probabilities of removal and between the 152 mm and 178 mm creel sizes. Predicted brook char densities increased and rainbow trout densities decreased with increasing probabilities of removal. For a given probability of removal, brook char densities were consistently higher and rainbow trout densities consistently lower, for the 152 mm compared to the 178 mm creel size. Results for the highest probability of removal (1%) with the 152 mm creel size are used because these conditions

exhibited the greatest changes in survival rates and trout densities.

Under the 1%/day probability of rainbow trout removal and a 152 mm creel limit, older rainbow trout survival decreased, eliminating years of extremely low brook char juvenile survival. Age-2 survival of rainbow trout averaged 0.23 for the 1%/day harvest and 152 mm creel size compared to 0.43 under baseline conditions. However, survival of age-1 trout was not affected because in mid-summer more than 75% of age-1 rainbow trout were shorter than the 152 mm creel size. Fewer, but still significant, numbers of rainbow trout spawn before reaching 152 mm. An average of 52 first-time rainbow trout spawners are less than 152 mm under the 1%/day rainbow trout fishing rate (compared to 156 for baseline). The reduction in adults under the 1%/day removal rate did lead to reduced egg production and lower average numbers of rainbow trout juveniles (192 versus 441 in baseline). Rainbow trout fry survival increased (0.10 to 0.15) in response to lower trout densities and acted to offset some, but not all, of the reduced egg production. Lower juvenile densities reduced the number of years of low brook char juvenile survival associated with low summer flows or large year-classes of rainbow trout. Under low flow or high juvenile trout densities, juvenile brook char growth rates are reduced leading to decreased survival. Low flow and high trout densities reduce the amount of prey available to brook char juveniles, causing slower growth rates. Under baseline conditions, brook char juvenile survival was positively correlated to growth rate (R^2 approximately 0.20), and growth rate was negatively related to flow and total juvenile and adult trout biomass (Clark and Rose, *in press*). Brook char juvenile survival less than 0.63 occurred for 13 years under baseline conditions. In 10 of the 13 years of low brook char juvenile survival,

either the summer flow was below average or the total number of juveniles and adults was above average. A 1%/day fishing removal rate of rainbow trout decreased juvenile and adult biomass, reducing the number of years with low juvenile brook char survival to only four years. However, fewer years of low juvenile brook char survival were not sufficient for brook char to reach allopatric densities.

Robustness of Electrofishing and Stocking Strategies

Electrofishing and stocking under conditions favoring rainbow trout had similar effects on brook char as under baseline conditions. Under conditions of invasion by rainbow trout, year-class failures, and reduction in spawning habitat, predicted mean annual post-fry brook char densities increased asymptotically toward their allopatric levels for increasing probabilities of removal (Figure 12) and from egg to juvenile stocking (Figure 13). Predicted brook char and rainbow trout densities were similar to those predicted under baseline conditions. The only difference was that annually stocking 600 brook char fry resulted in allopatric densities for the year-class failures condition but not for baseline conditions. During years of year-class failures, eggs of both species were eliminated. Stocked brook char fry compensated for the failed natural reproduction in years with year-class failures, and brook char persisted at high levels whereas rainbow trout did not (Figure 13).

Time to Equilibrium

Times to equilibrium for the electrofishing (Figure 14) and stocking (Figure 15)

strategies under conditions favoring rainbow trout were similar to, or less than, those under baseline conditions. For the electrofishing strategy, time to equilibrium peaked at the intermediate fractions of removal (Figure 14). Low probability of rainbow trout removal had little impact on the populations, which were then able to quickly reach their near-baseline, new equilibrium densities. High probability of removal (0.8) resulted in rapid responses because of the large effects imposed. The descending portion of the time to equilibrium relationship with probability of removal corresponds to probabilities (≥ 0.3) that resulted in allopatric densities. Among effective stocking strategies (2,400 fry and 200 and 500 juveniles), quickest and longest times to equilibrium varied among conditions. In general, brook char densities reached their long-term mean densities in about 13 years for eggs (predicted densities well below allopatric), and in about 10 to 20 years for fry and juvenile stocking. An exception was the greater than 30 year time to equilibrium for stocking 200 juveniles/year under the 50% reduction in spawning habitat. Except under conditions of rainbow trout invasions, stocking the highest numbers (500) of the oldest life stage (juveniles) resulted in the quickest times to equilibrium.

Discussion

Using a spatially explicit, individual-based model of brook char and rainbow trout, four management strategies for enhancing brook char populations in typical high gradient streams of the southern Appalachians were simulated. Management strategies examined were: (1) electrofishing removal of rainbow trout, (2) stocking of brook char, (3) habitat alteration, and (4) angler harvest of rainbow trout. Model results indicated that

electrofishing of rainbow trout and stocking of large number of fry or juvenile brook char could produce allopatric brook char densities, but that habitat alteration and angler harvest of rainbow trout would not significantly increase brook char densities. Further analyses showed that electrofishing and stocking results were robust. Similar predictions of brook char densities for electrofishing and for stocking were obtained under baseline conditions, and under conditions of rainbow trout invasions, year-class failures, and reduced spawning habitat. Allopatric densities were obtained (time to equilibrium) 10 to 20 years after initiation of the successful management strategies.

Model simulations found little enhancement of brook char populations by habitat manipulation and field studies have generated mixed results. Model simulations under increased mean pool length showed the appropriate direction of change in trout densities (brook char increased and rainbow decreased), but small magnitudes of change. Larger pools and higher prey resulted in increased predicted growth rates and size of age-2 and older trout. Flebbe and Dolloff (1995) found larger trout (but lower total trout densities) in streams in second-growth forests, where pools were larger but less numerous than those in streams in old-growth southern Appalachian forests. Kelly et al. (1980) found that brook char densities tend to be highest in undisturbed watersheds of the southern Appalachians. These observations may be related to factors other than pool size. For example, invertebrate production (Gurtz et al. 1980; Gurtz and Wallace 1984) and the magnitude of rainbow trout introduction (King 1942) can depend on the prior history of disturbances in watersheds. Riley and Fausch (1995) observed no long term changes in survival when pool sizes were artificially increased in a trout stream. The relationship

between pool size and brook char - rainbow trout dynamics remains unclear.

In agreement with model results, angling pressure on rainbow trout in southern Appalachian streams is generally low and inconsequential to brook char population trends. Despite year round fishing for rainbow trout (178 mm creel size) and closure of the brook char fishery in the 1970's in streams of the Great Smoky Mountains National Park (GSMNP), brook char densities have declined and rainbow trout distribution has increased (Larson and Moore 1985). Whitworth and Strange (1983) reported that "minimal" fishing pressure had negligible impact on sympatric populations of rainbow trout and brook char in a small southern Appalachian stream. King (1942) reported a high harvest (2.2%/day, 203 mm creel size) for a stream in GSMNP, but this was for a stocked, put-and-take rainbow trout fishery. Lennon (1961 and 1967) reported extremely light fishing pressure on streams in GSMNP containing brook char; maximum harvest rates of approximately 0.6%/day (203 mm creel size) have been reported (Lennon and Parker 1959). McFadden (1961) reported a lower harvest (0.3%/day) in a heavily fished Wisconsin stream. Even for the highest level of rainbow trout harvest (1%/day, 152 mm creel size), model simulations did not produce brook char populations at allopatric levels. Generally, only a small fraction of trout reach harvestable size in the model, as well as in the field (Konopacky and Estes 1986), and their removal has little impact on either their or brook char population dynamics.

Model simulations and field studies have shown electrofishing removal of rainbow trout to be effective in increasing brook char stocks. Rainbow trout capture probabilities can be quite high in small southern Appalachian streams. Moore et al. (1986) enhanced

brook char populations to near allopatric conditions in GSMNP streams by annual electrofishing removal of approximately 50% of the adult and 40% of the juvenile rainbow trout. Habera (1987) also reported increased brook char densities after rainbow trout electrofishing removal (50 to 70% efficiency) in streams of GSMNP. In model simulations under baseline conditions and conditions favoring rainbow trout, allopatric brook char densities resulted when removal probabilities were greater than or equal to 0.3. Increasing removal probability from 0.3 to 0.8 resulted in significant reduction in the time to equilibrium (> 25 years at 0.3 removal but < 10 years at 0.8 removal).

A critical aspect of electrofishing is the effective removal of young-of-the-year trout. Both Habera (1987) and Moore et al. (1983) saw the most dramatic effects of rainbow trout removal on young-of-the-year brook char growth and survival. In model simulations, density-dependent growth and survival were strongest in young-of-the-year life stages (Clark and Rose, *in press*). Model simulations incorporating electrofishing assumed equal capture probability for all sizes of trout. Evidence indicates that equal probability of capture is a reasonable assumption for many southern Appalachian streams (Moore et al. 1983; Whitworth and Strange 1983; Habera 1987); however, assuming equal capture probability is not always valid (Bohlin and Sundstrom 1977). Hence, electrofishing may be less effective in situations where small trout are less susceptible to capture.

Contrary to model results, brook char stocking efforts in the southern Appalachians have been ineffective in restoring brook char populations. Annual stocking of brook char juveniles created near allopatric densities within 10 to 20 years under all

conditions in model simulations. However, King (1942) failed to establish a viable population of brook char in a stream of GSMNP by stocking the stream with 75 to 150 mm juveniles and adults. Lennon and Parker (1959) later attempted to establish brook char in this same stream by stocking 50 to 100 mm juveniles, but this effort was also unsuccessful (Kelly et al. 1980). Lennon (1967) reported that numerous attempts at stocking New England strain brook char in GSMNP streams failed completely, as did attempts to stock brook char from GSMNP streams in streams at higher latitudes of the Appalachians (approximately 38°N in Shenandoah National Park). He attributed the poor survival of transplanted brook char to possible genetic differences between the strains. Subsequent work has shown significant genetic differences between southern Appalachian and northern Appalachian brook char (McCracken et al. 1993). Harned (1976) found that survival and dispersal were higher in native southern Appalachian brook char than in non-native brook char when both were stocked in a stream of GSMNP. Possible explanations for model success but field failure of stocking include wrongly assuming in the model that stocked and natural brook char are identical, inter-annual variation in factors affecting year-class strength in the field overwhelming the effects of stocking, or field stocking for too few years.

Additional considerations not included in the analysis could affect the feasibility of different management strategies. Cost (time, effort, and capital) of implementation of different strategies can vary greatly but is not considered in model analyses. In all model simulations, management strategies were implemented continually on an annual basis; in practice, management strategies can sometimes only be implemented for relatively few

years and not always annually. Negative effects on brook char due to electrofishing for rainbow trout were not included in model simulations. Though most studies from Appalachian streams using electrofishing techniques do not mention deleterious effects from the shocker (e.g., Whitworth and Strange 1983; Moore et al. 1986; Larson et al. 1995), increased egg mortality (Godfrey 1957; Dwyer and Erdahl 1995) and injury to juvenile and adult trout (Sharber and Carothers 1988) have been observed in brook char and other salmonids. Electrofishing effects on brook char could reduce the effectiveness of rainbow trout removal in enhancing brook char stocks. Moreover, stocking simulations ignored maintenance of genetic purity and behavioral ramifications imposed by hatcheries. Finally, any effects of the different management strategies, or their implementation, on other species or on critical habitats were ignored. Actual implementation of a management strategy would require consideration of these effects.

The results indicate that brook char densities could be enhanced to allopatric levels by electrofishing removal of rainbow trout and stocking of juvenile brook char, but not by using habitat alteration or angler harvest of adult rainbow trout. Electrofishing for rainbow trout and stocking of juvenile brook char enhanced brook char stocks over a wide range of conditions. Under annual implementation of electrofishing or stocking, achievement of allopatric brook char densities would require 10 to 20 years. Model results show that brook char populations are typically limited by dynamics affecting the early life stages. Electrofishing removed both small and large rainbow trout, which benefited young-of-the-year brook char. Stocking of juvenile brook char increased recruitment by bypassing the bottleneck in the fry stage. Efforts focused on enhancing

conditions for the early life stages of brook char appear to offer the most promise for enhancing brook char populations in southern Appalachian streams.

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Appendix: Tables and Figures

Table 1: Life stage-specific mean duration, survival, growth rate, and mean length for years 6 to 100 of the baseline (sympatric) simulation. Age-1 fish have lived 1 year, age-2 fish have lived 2 years, and age-3 fish have lived 3 years.

Stage	Duration (days)	Survival (fraction)	Growth rate (g/g/day)		Mean length (mm)	
Brook char			Predicted	Observed	Predicted	Observed
eggs and alevins	159	0.13	-	-	-	-
fry	33	0.19	0.05	0.06[a]	31[c]	-
juveniles (< 100mm)	139	0.68	0.027	-	100[d]	-
age-1	252	0.51	0.016	0.006[b]	116	86[b], 101[e], 149[f]
age-2	365	0.43	0.003	0.004[b]	164	139[b], 136[e], 174[f]
age-3	365	0.45	0.001	0.0006[b]	186	155[b], 160[e], 196[f]
Rainbow trout						
eggs and alevins	70	0.11	-	-	-	-
fry	41	0.10	0.04	0.04[a]	31[c]	-
juveniles (< 100mm)	173	0.63	0.021	-	100[d]	-
age-1	311	0.45	0.012	0.009[b]	116	104[b], 131[g]
age-2	365	0.43	0.003	0.005[b]	165	180[b], 170[g]
age-3	365	0.44	0.001	0.0002[b]	187	185[b], 208[g]

[a]Rose (1986), [b]Whitworth (1980), [c]Length at end of fry stage, [d]Length at maturity, [e]Konopacky and Estes (1986), [f]Lennon (1961), [g]Lennon and Parker (1959)

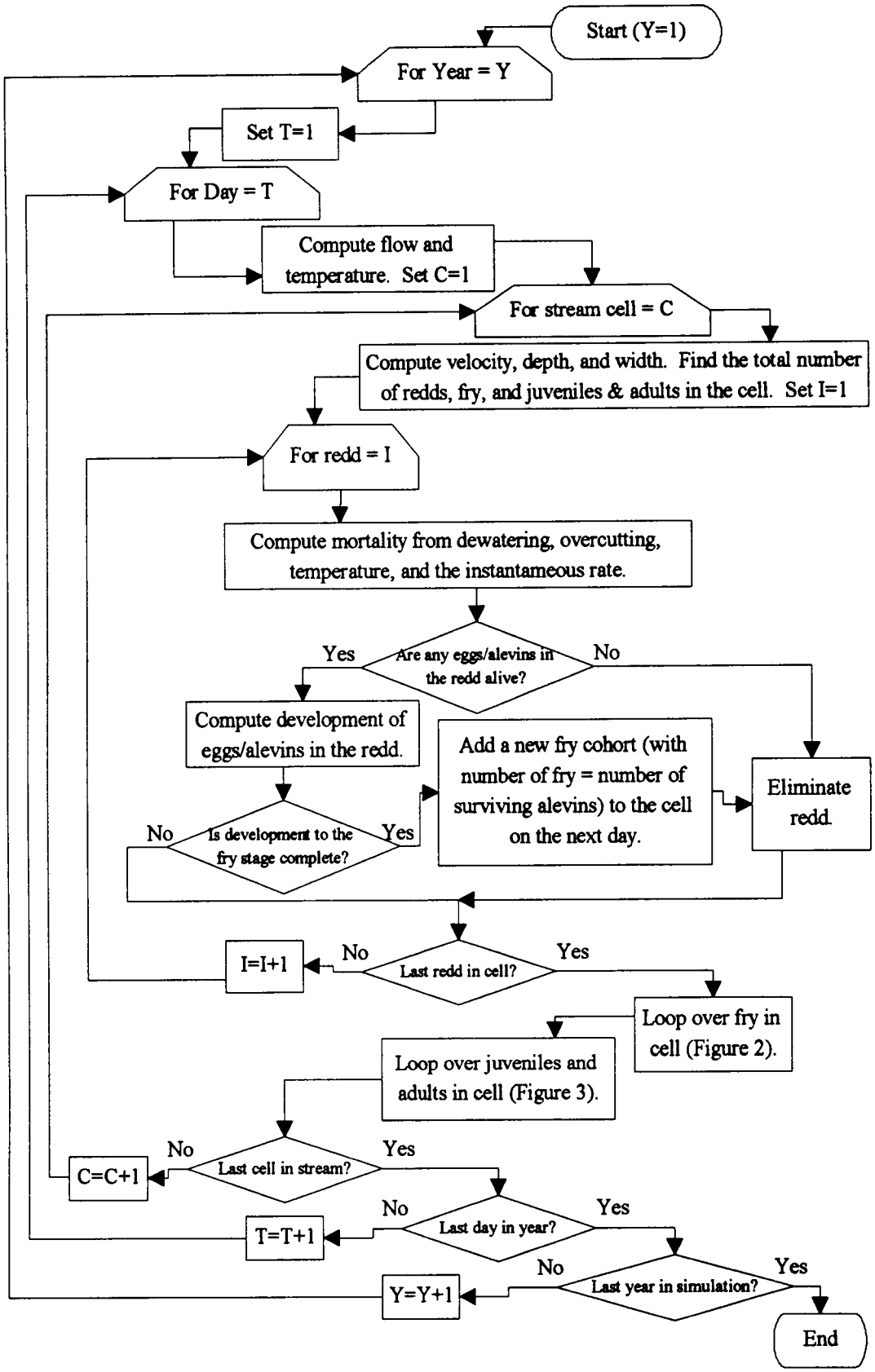

Figure 1: Flowchart of the major components of the brook char - rainbow trout model.

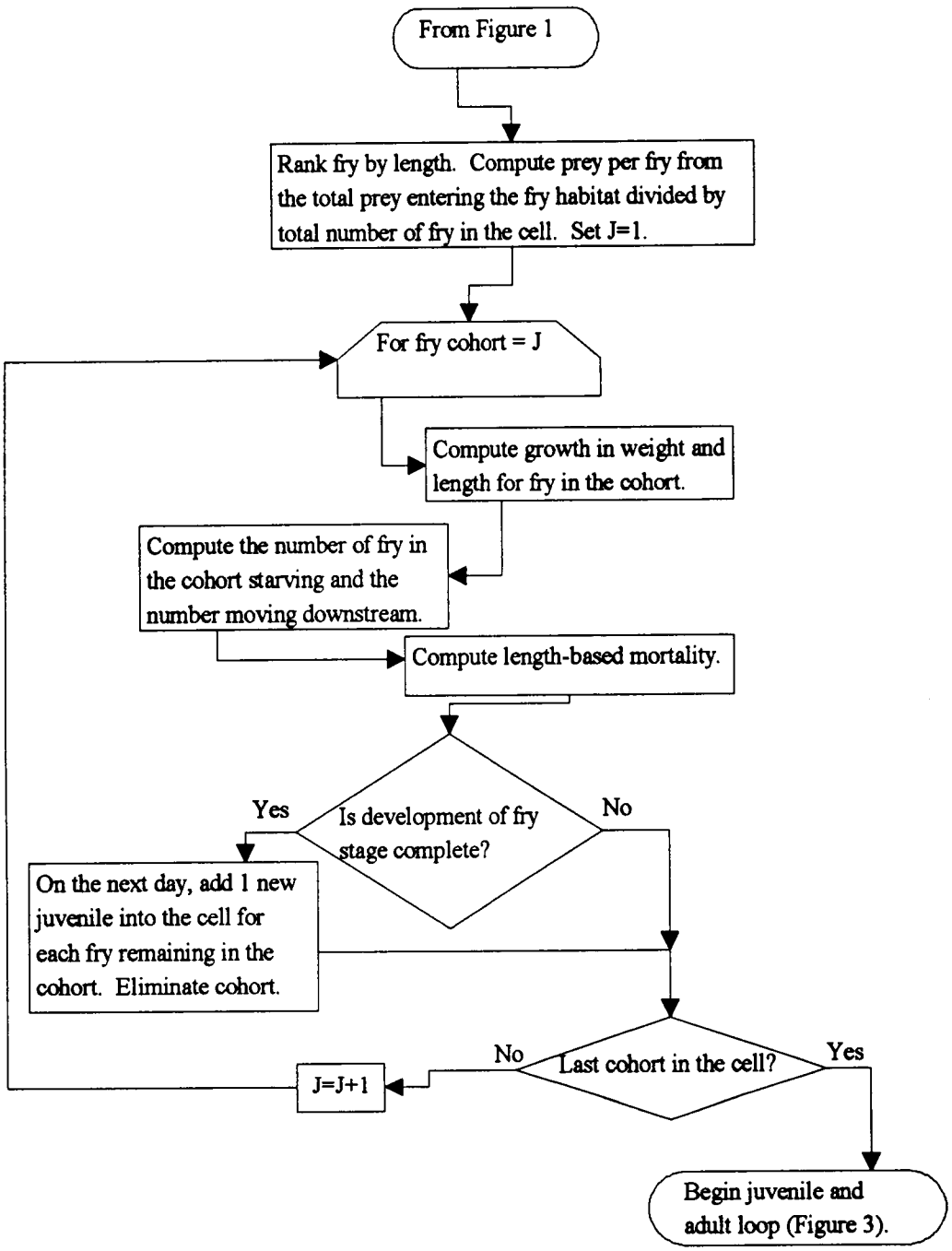

Figure 2: Flowchart of the daily processes performed for fry cohorts in a cell of the model stream.

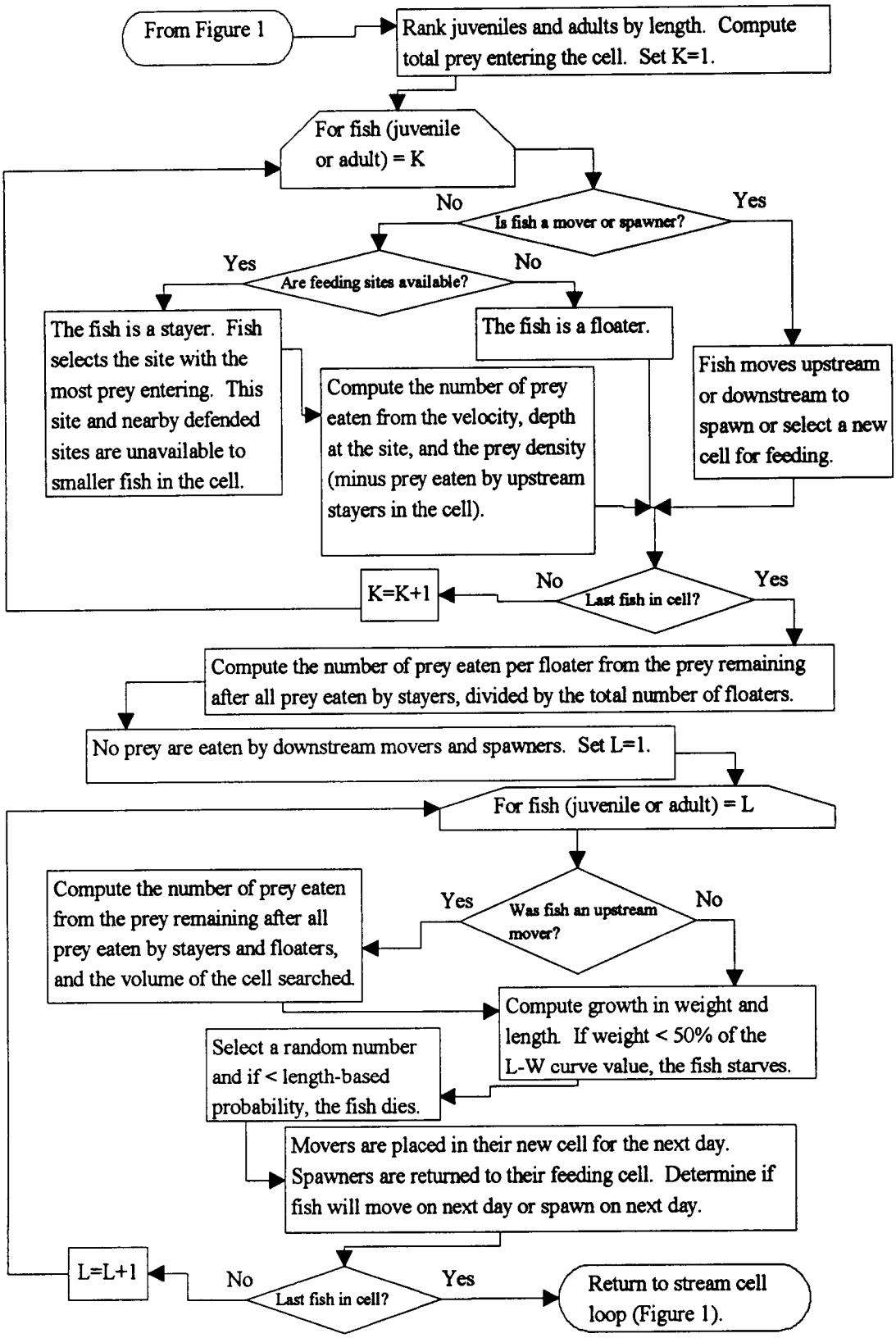

Figure 3: Flowchart of the daily processes performed for individual juveniles and adults in a cell of the model stream.

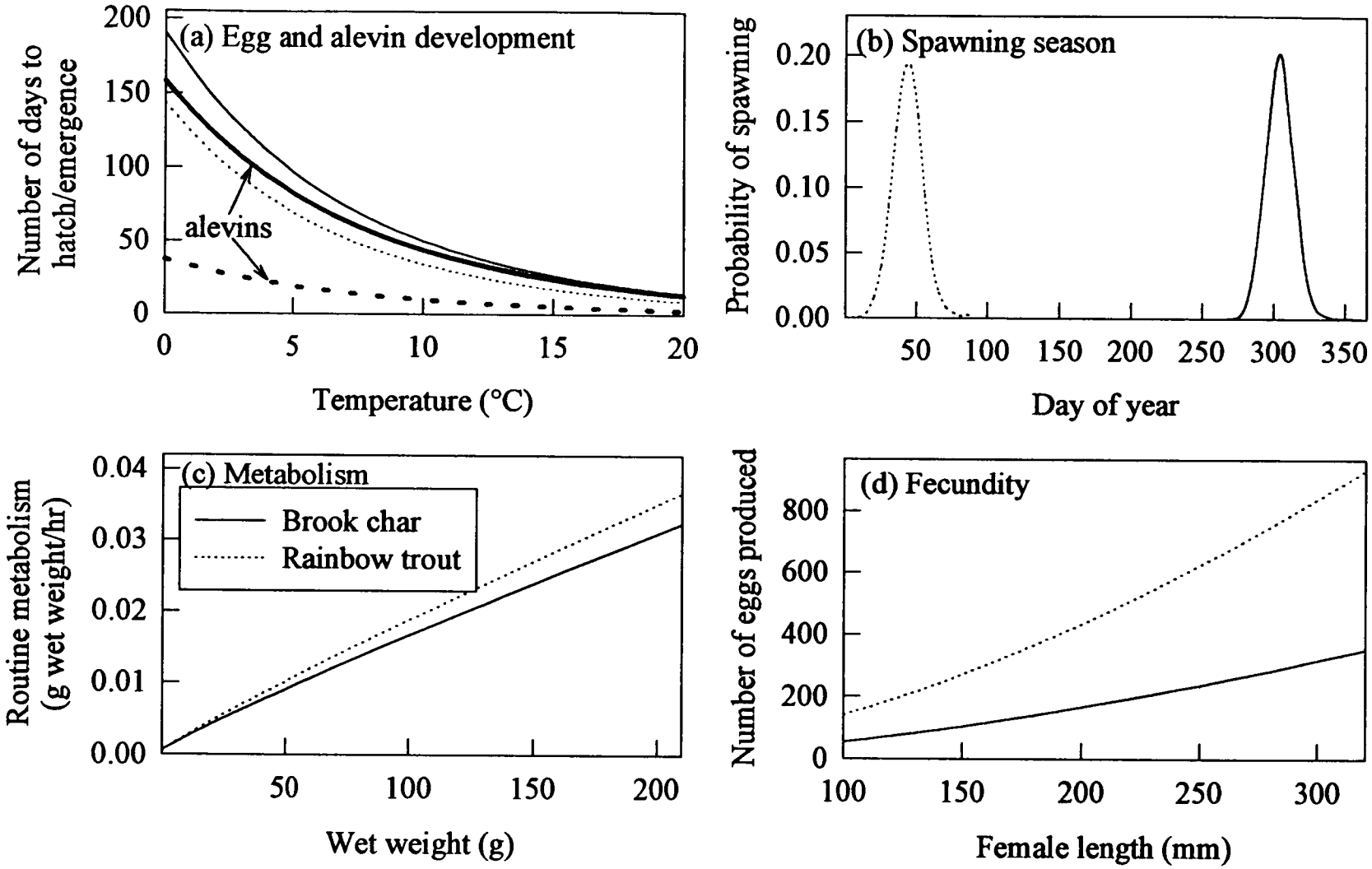

Figure 4: Species-specific differences between brook char and rainbow trout represented in the model: (a) egg and alevin development rates, (b) spawning season, (c) routine metabolism, and (d) fecundity. Minor differences (< 1%) also exist between the species-specific length-weight relationships used in the model.

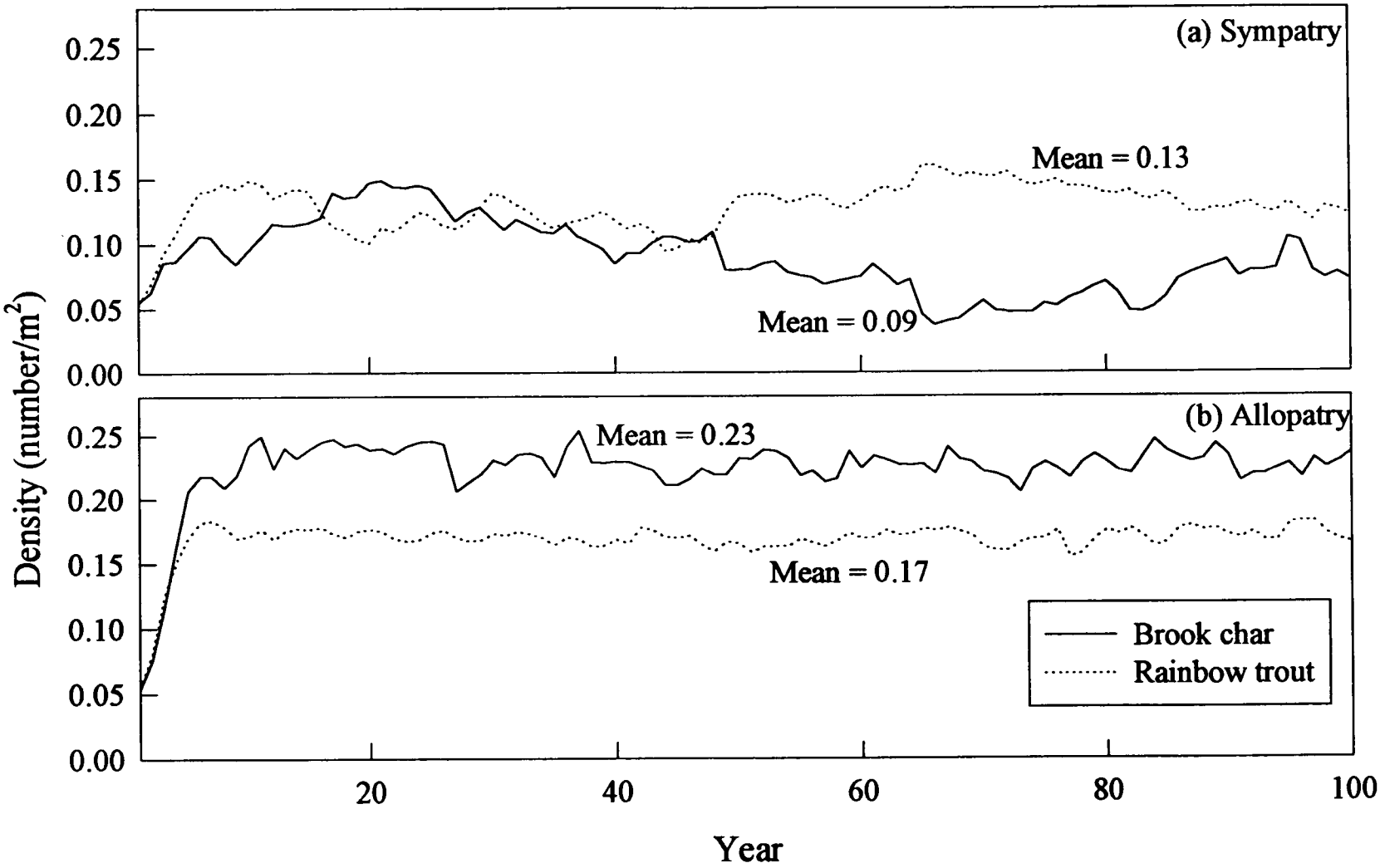

Figure 5: Annual brook char and rainbow trout post-fry densities under baseline conditions: (a) sympatry and (b) allopatry.

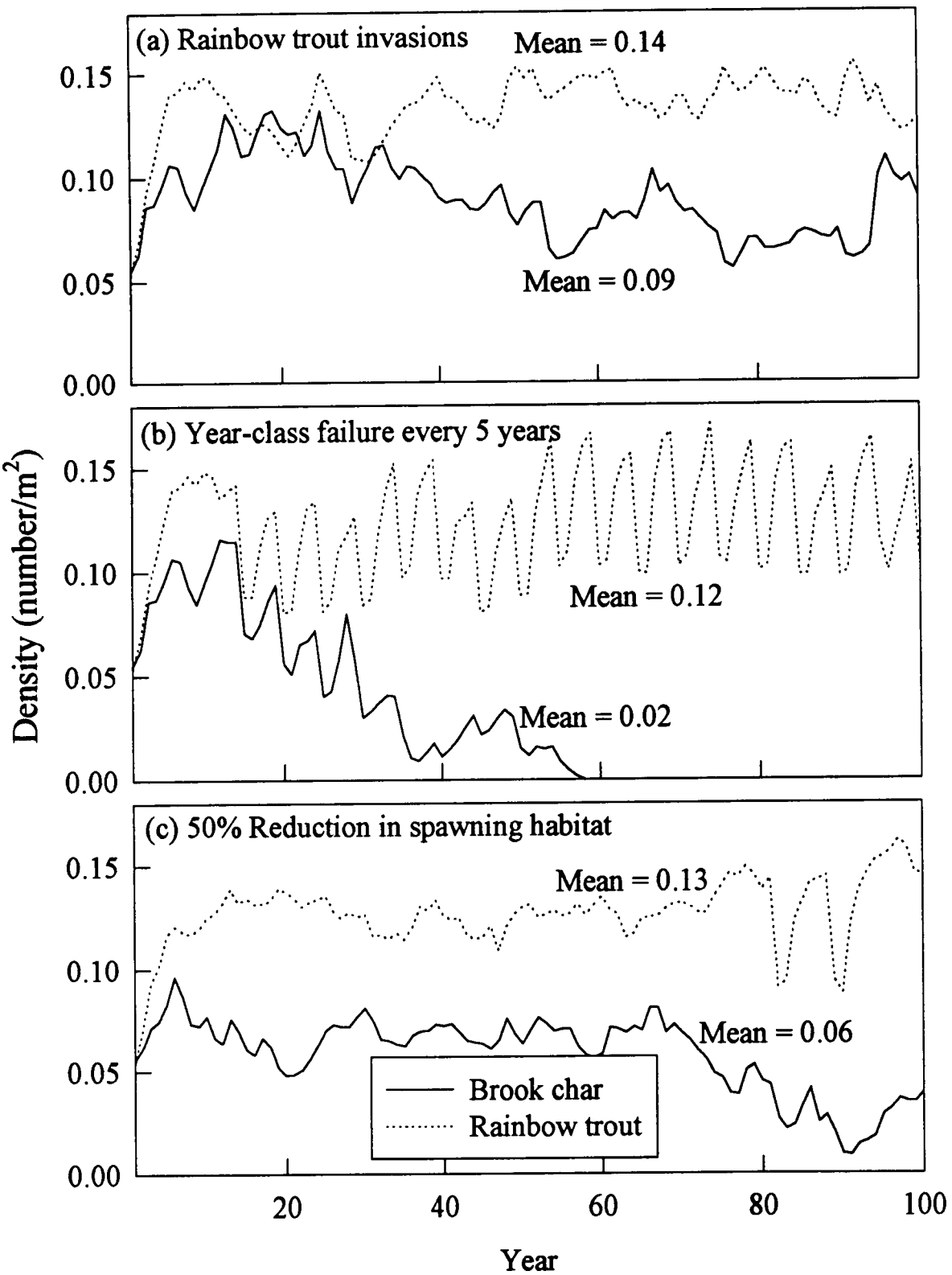

Figure 6: Annual brook char and rainbow trout post-fry densities under: (a) rainbow trout invasions, (b) year-class failures every 5 years, and (c) 50% reduction in spawning habitat.

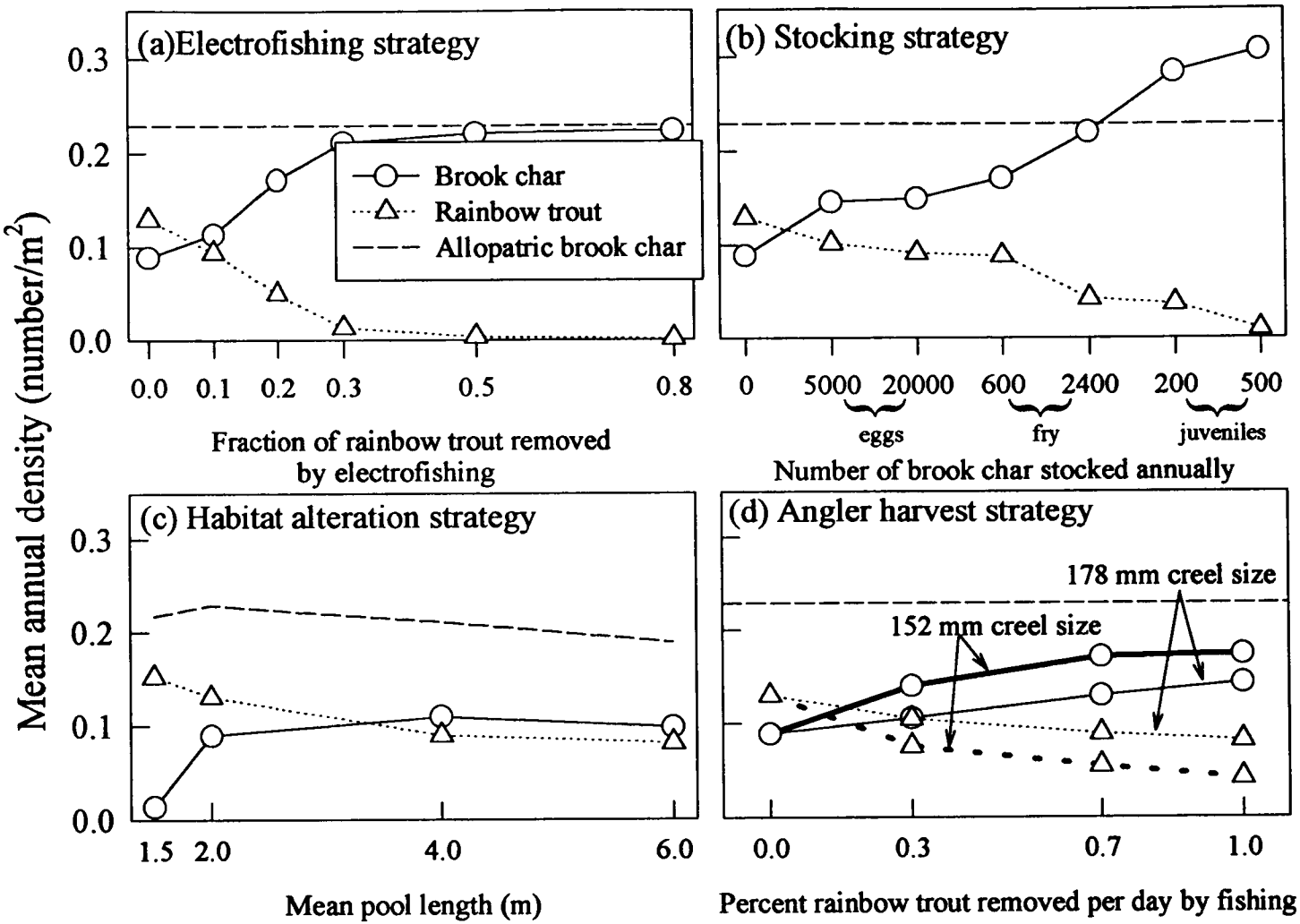

Figure 7: Mean annual brook char and rainbow trout post-fry densities at various levels of: (a) electrofishing removal of rainbow trout, (b) brook char stocking, (c) habitat alteration, and (d) angler harvest of rainbow trout. Mean annual allopatric densities of brook char are included on each figure.

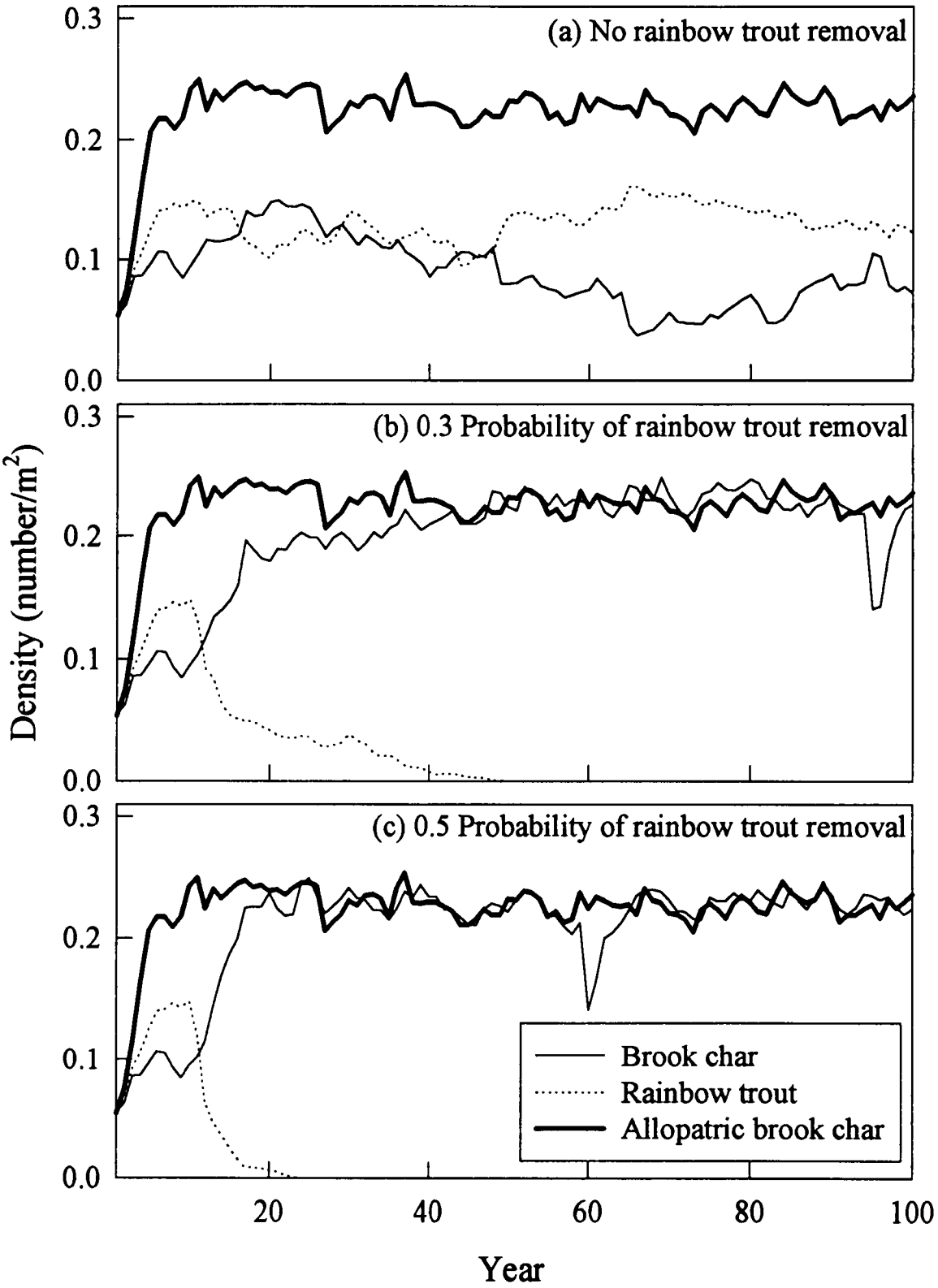

Figure 8: Annual allopatric brook char and sympatric brook char and rainbow trout post-fry densities for (a) baseline and electrofishing capture probabilities of (b) 0.3 and (c) 0.5.

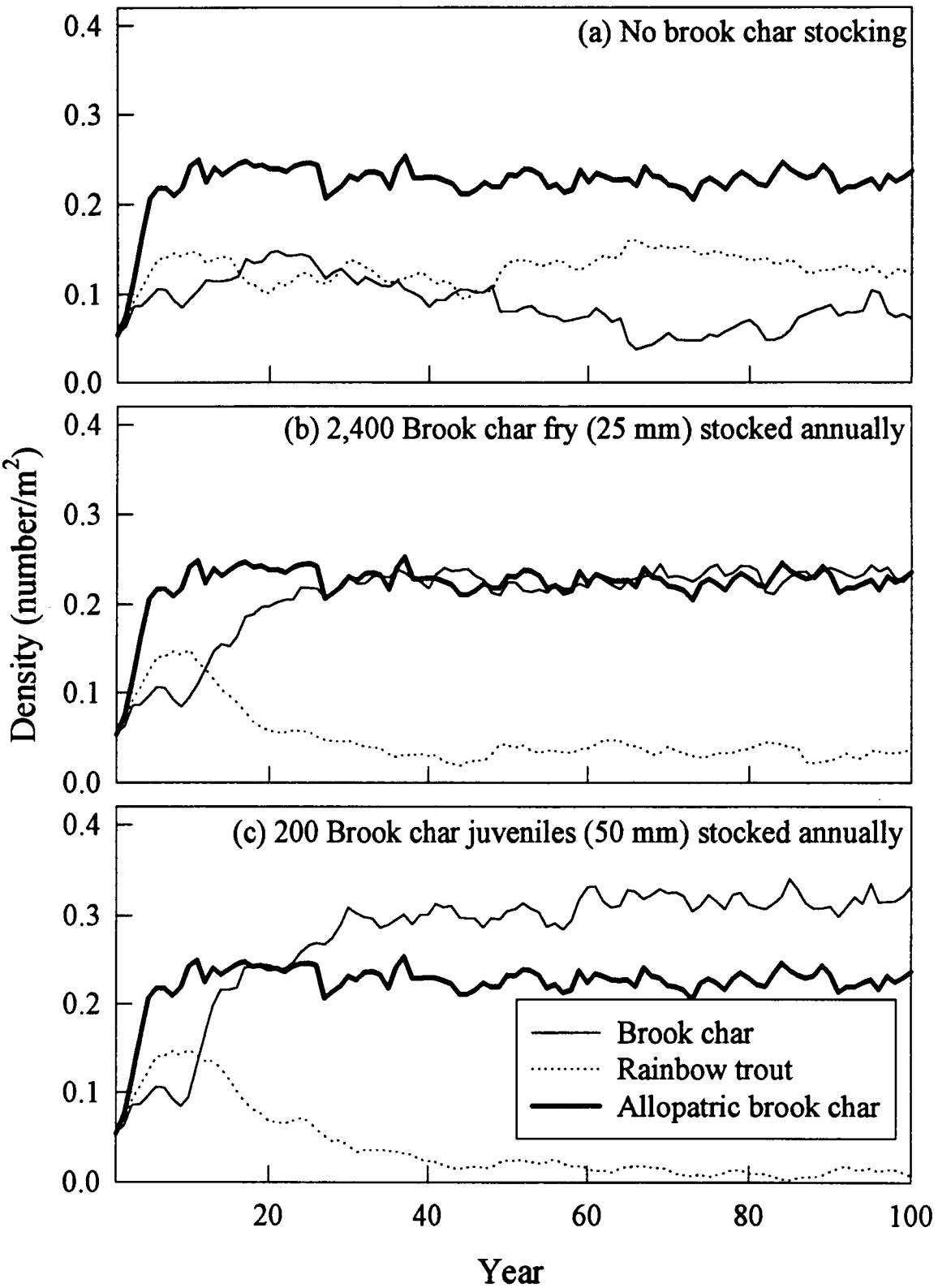

Figure 9: Annual allopatric brook char and sympatric brook char and rainbow trout post-fry densities for (a) baseline and brook char stocking of (b) 2,400 fry and (c) 200 juveniles.

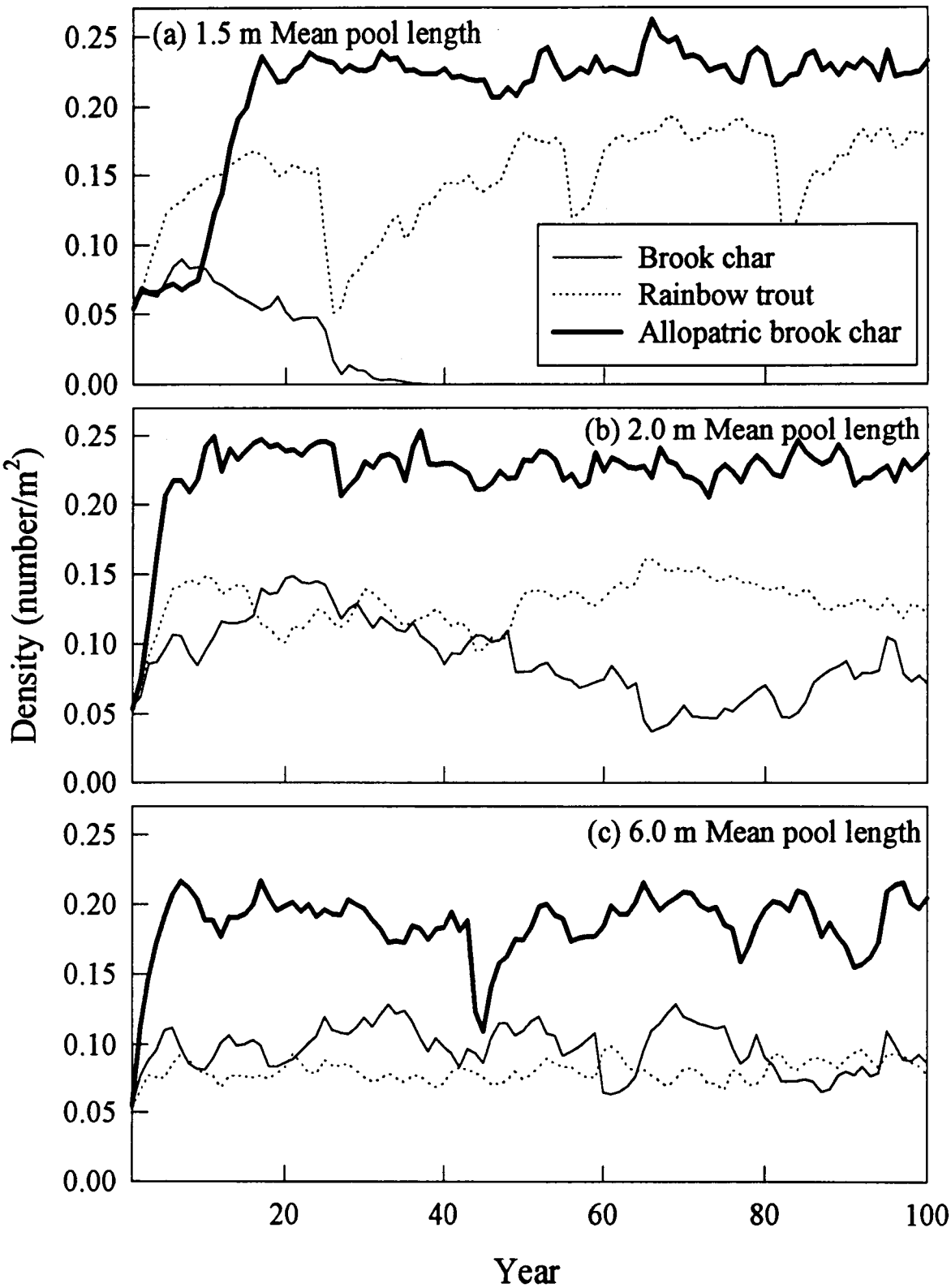

Figure 10: Annual allopatric brook char and sympatric brook char and rainbow trout post-fry densities for (a) mean pool length of 1.5 m, (b) baseline (mean pool length of 2.0 m), and (c) mean pool length of 6.0 m.

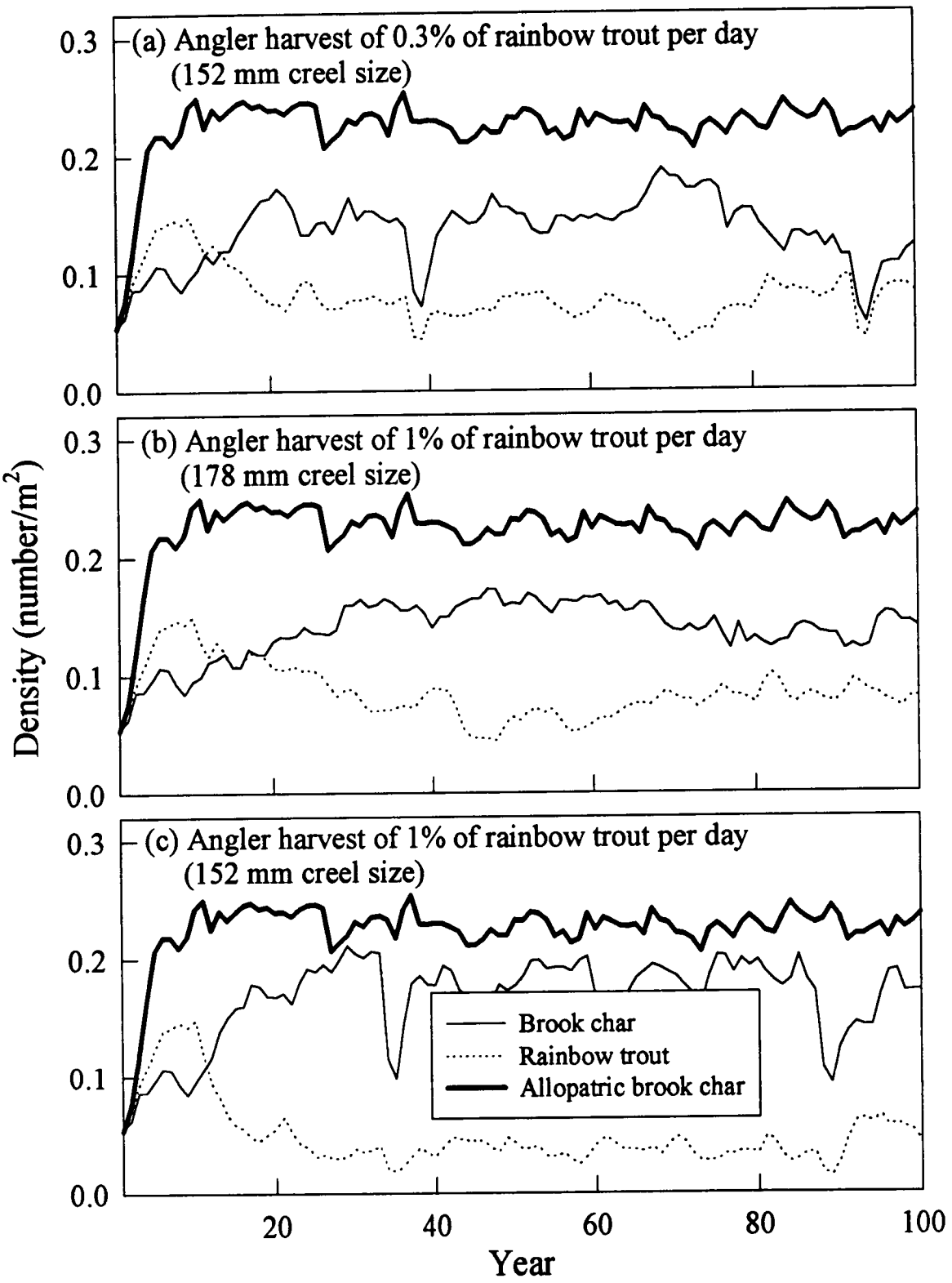

Figure 11: Annual allopatric brook char and sympatric brook char and rainbow trout post-fry densities for angler harvest of rainbow trout with (a) 0.3% daily harvest (152 mm creel size), (b) 1.0% daily harvest (178 mm creel size), and (c) 1.0% daily harvest (152 mm creel size).

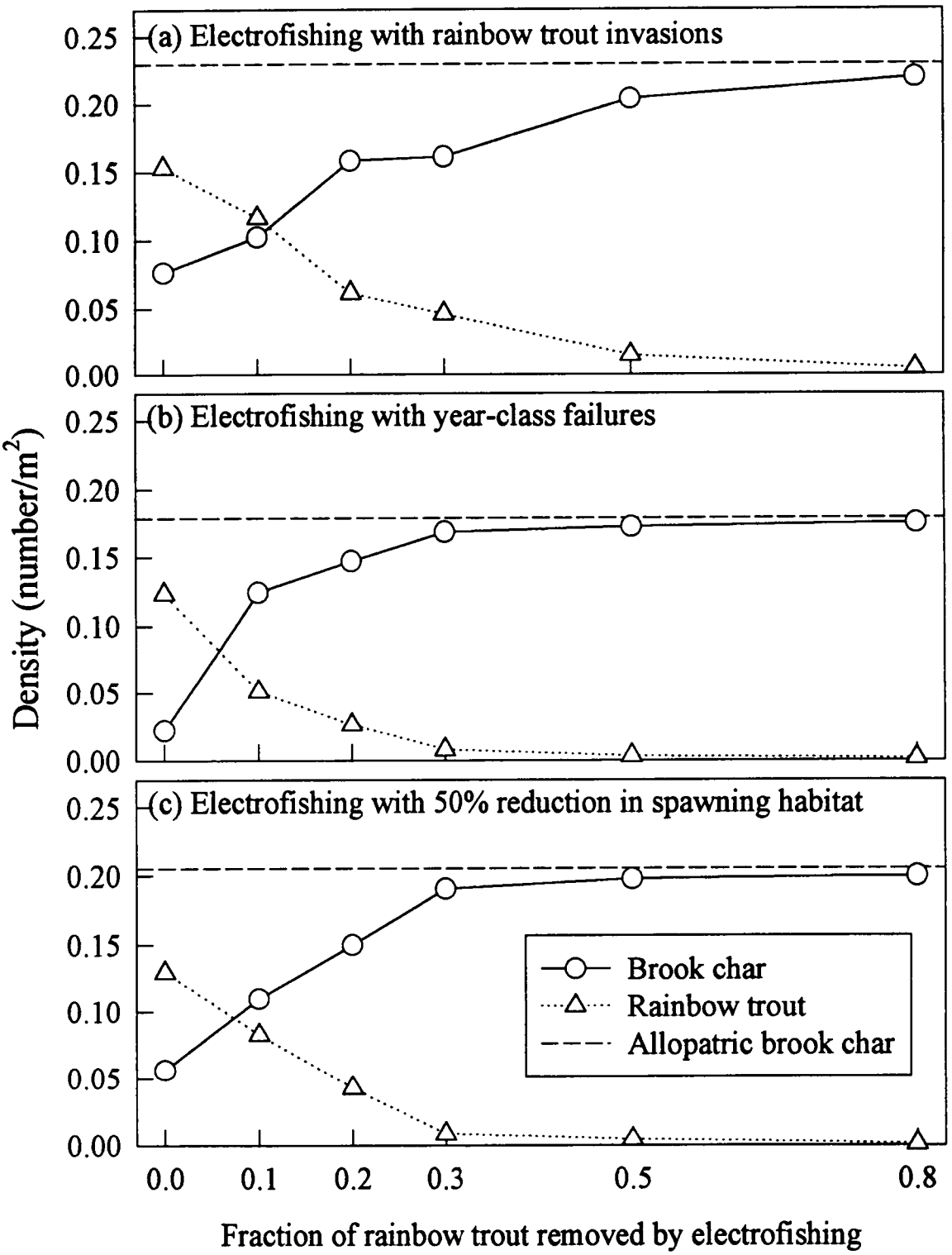

Figure 12: Mean annual brook char and rainbow trout post-fry densities for electrofishing removal of rainbow trout under (a) invasion from adult rainbow trout, (b) year-class failures every 5 years, and (c) 50% reduction in spawning habitat. Mean annual allopatric densities of brook char are included on each figure.

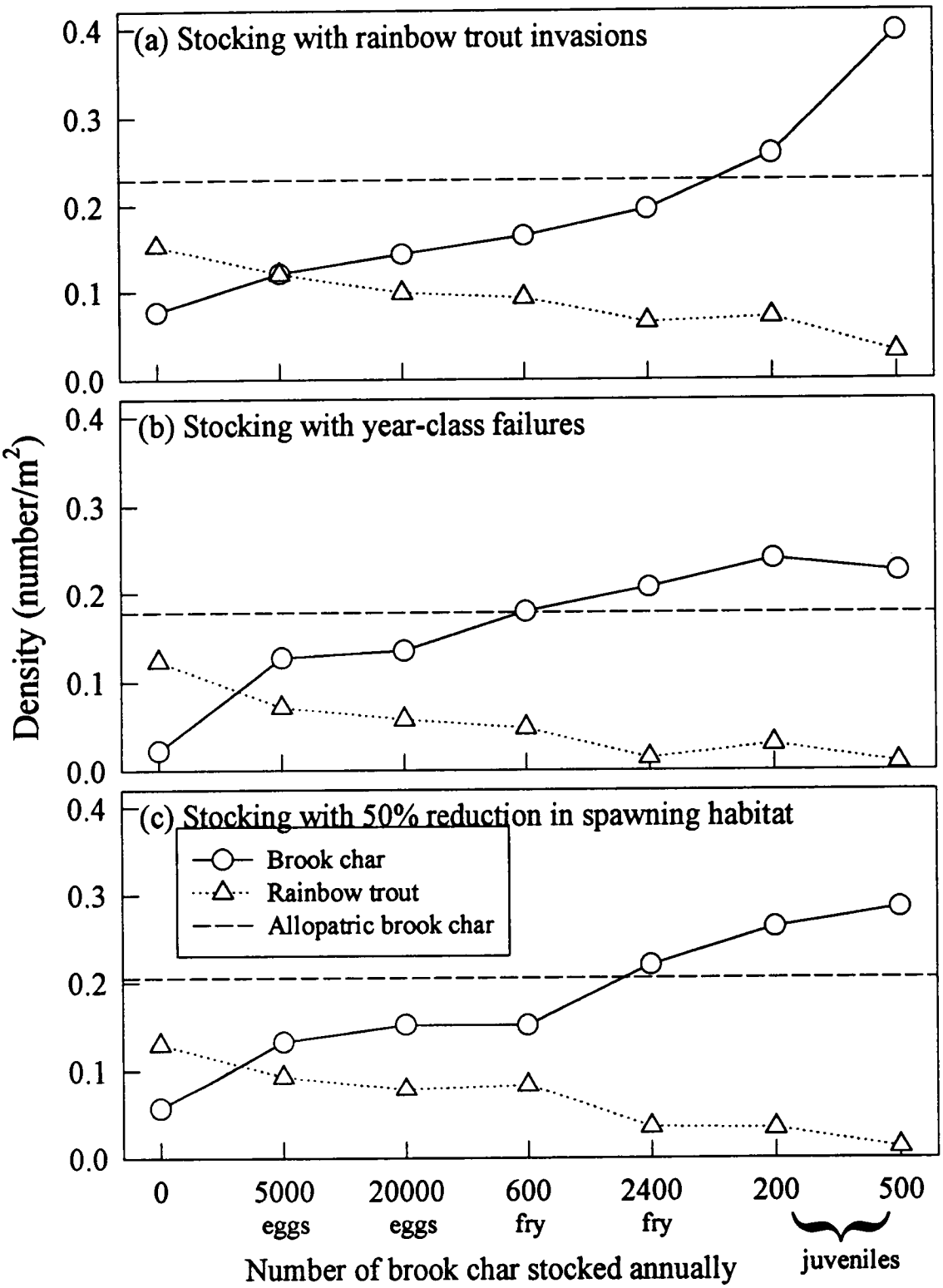

Figure 13: Mean annual brook char and rainbow trout post-fry densities for brook char stocking under (a) invasion by adult rainbow trout, (b) year-class failures every 5 years, and (c) 50% reduction in spawning habitat. Mean annual allopatric densities of brook char are included on each figure.

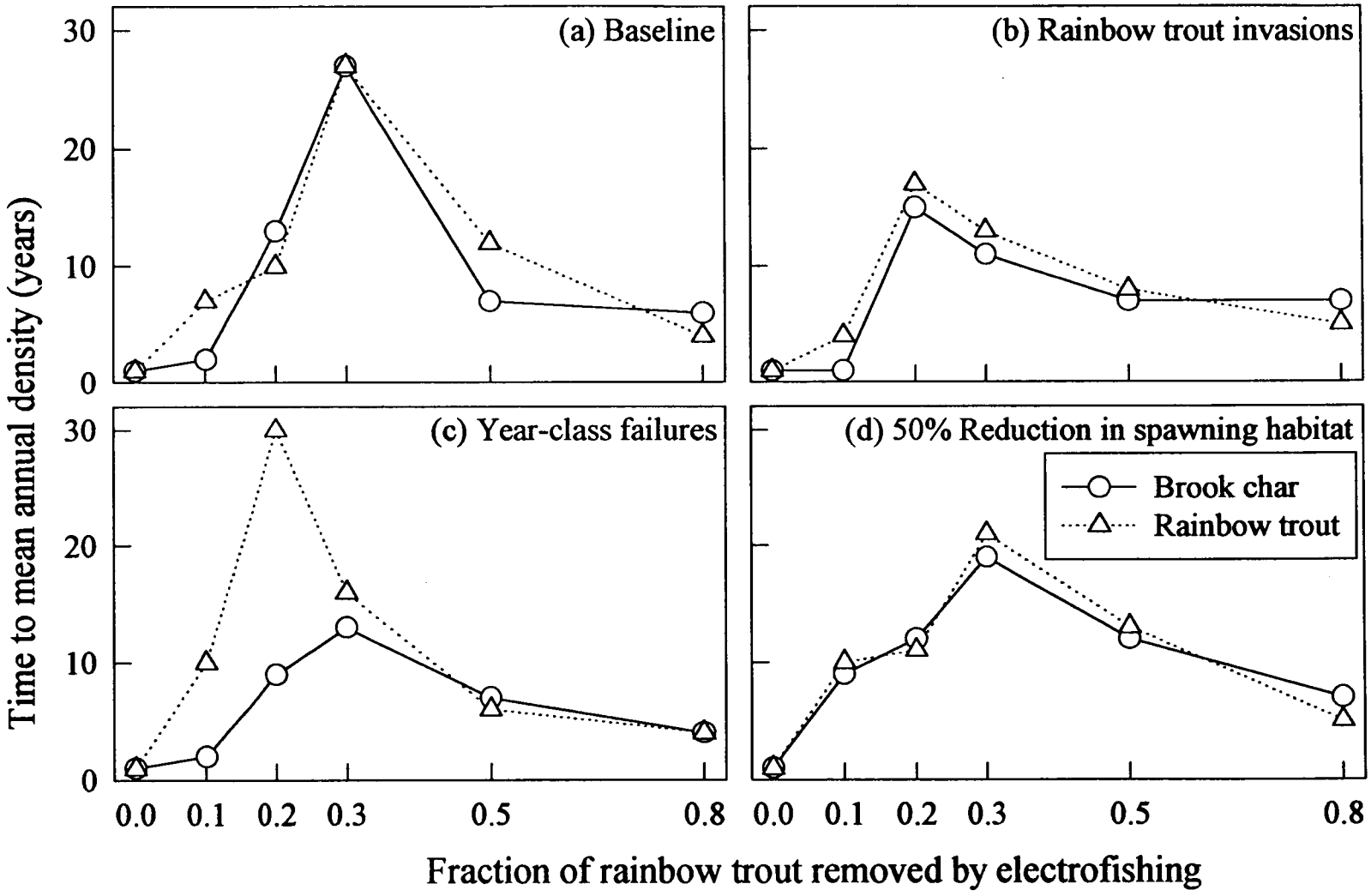

Figure 14: Time to equilibrium for brook char and rainbow trout for increasing fractions of electrofishing removal of rainbow trout under: (a) baseline, (b) rainbow trout invasion, (c) year-class failures every 5 years, and (d) 50% reduction in spawning habitat.

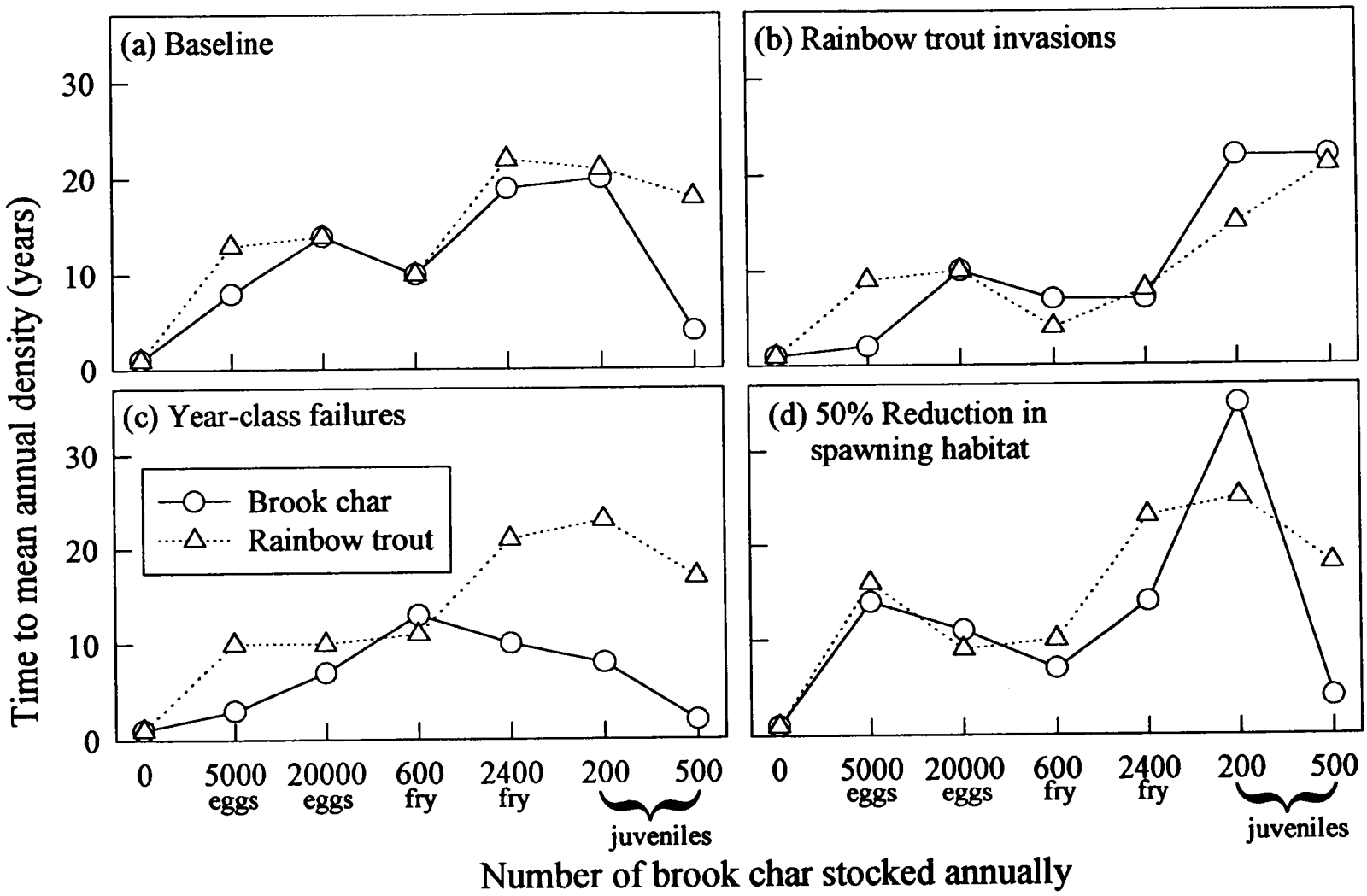

Figure 14: Time to equilibrium for brook char and rainbow trout for various combinations of brook char stocking under: (a) baseline, (b) rainbow trout invasion, (c) year-class failures every 5 years, and (d) 50% reduction in spawning habitat.

Part 5

General Summary

Objectives

The objectives of this study were to use a spatially-explicit, full life cycle model of brook char and rainbow trout in southern Appalahcian streams to examine potential factors controlling interspecific competition and to evaluate management actions for enhancing brook char populations. A better understanding of brook char population dynamics and competition with rainbow trout is essential to the future health of brook char stocks. In southern Appalachian streams, native brook char populations continue to decline, despite studies of their habitat requirements, diet, behavior and interaction with introduced rainbow trout.

The brook char - rainbow trout model simulates daily growth, mortality, movement, and spawning over the full life cycle of each species for 100 years in a compartmentalized, hypothetical stream typical of those in the southern Appalachians. The models stream is comprised of a linear series of connected cells. Water temperature, flow, and prey density are uniform throughout the stream and vary daily. Water velocity, depth, and stream width are calculated from flow, and vary from cell to cell and over time. Egg and alevin development is temperature-dependent with mortality having constant, spatial, and temperature-dependent components. Daily growth of fry, juveniles, and adults is based on bioenergetics and consumption of drift prey. Mortality rate of fry through adults decreases with length. Brook char and rainbow trout are treated identically in the model except for their metabolic rates, fecundities, spawning seasons, egg and alevin incubation times, and length-weight relationships. Model predictions include densities, survival, growth rates, size at age, and habitat use. Average values were generally

computed over years 6 to 100 to eliminate effects due to initial conditions.

Model corroboration was achieved by comparing model predictions of population densities, growth rates, size structure, and habitat use with information reported in the literature for southern Appalachain trout streams. Simulations under sympatric (both species) and allopatric (single-species) conditions provided information on the relative impacts of interspecific competition. The importance of inter-specific competition during the fry stage was demonstrated using simulations with contracted and protracted spawning seasons. Spawning season duration directly affects the degree of fry crowding.

Model simulations were performed to evaluate the effects of five factors often cited to explain dominance of rainbow trout over brook char in southern Appalachian streams. The five factors examined were: rainbow trout aggressiveness, latitude, episodic year-class failures, increased brook char fecundity, and reduced spawning habitat. Increased aggressiveness of rainbow trout was simulated by increasing the lengths of juvenile and adult rainbow trout as perceived by brook char. Latitude effects were examined by imposing water temperatures, flows, and daylengths typical of streams at northern latitudes of the Appalachians (38°N latitude). Brook char dominate over rainbow trout in Appalachian streams at northern latitudes. Temperature, flow, and daylength were imposed singly and all together. Episodic (year-class) mortalities were simulated by removing all eggs and fry of both species at regular intervals. Fecundity (number of eggs per mm) of brook char was increased to levels typical of northern Appalachian populations. Spawning habitat was reduced by eliminating fixed percentages of cells with water depths and velocities appropriate for redd construction. Model results were

combined with field-based evidence to determine the likelihood (possible and likely, possible but unlikely, highly unlikely) that each of the factors was the cause for rainbow trout dominance over brook char.

The effectiveness of four management actions designed to enhance brook char populations was determined using model simulations. The four management actions were: electrofishing removal of rainbow trout, stocking of brook char, habitat alteration, and angler harvest of rainbow trout. These actions are frequently used for the management of trout streams. Electrofishing was simulated by removing fry, juvenile, and adult rainbow trout once per year at fixed probability of capture levels. Stocking was simulated by annually adding brook char eggs, fry, or juveniles. Habitat alteration was represented by changing the mean length of pools in the model stream. Angler harvest of rainbow trout was modeled by probabilistically removing rainbow trout throughout the year that were longer than a creel size. Management actions that resulted in densities similar to allopatric brook char densities were considered successful, and were further evaluated for their robustness and response times. Robustness was established by determining whether the management actions were also successful under conditions that favor rainbow trout (invasion of rainbow trout spawners, recurring year-class failures, and limited spawning habitat). Response times were the number of years required for management actions to result in long-term mean densities. Model predictions of the success of the management actions were compared and contrasted with past field attempts in southern Appalachian streams.

Summary of Results

Baseline Dynamics and Model Corroboration

Baseline simulations generated realistic dynamics for brook char and rainbow trout population densities, growth rates, and survival compared to values reported for southern Appalachian streams. Baseline model simulations yielded higher mean densities of rainbow trout (0.13 rainbow trout/m^2) compared to brook char (0.10 brook char/m^2), and both were similar to reported densities for sympatric populations in southern Appalachian streams (Whitworth 1980; Habera 1987; Ensign et al. 1989). In agreement with Larson and Moore (1985) and Habera (1987), predicted brook char densities were negatively correlated to rainbow trout densities. Model predictions of growth rates, mean lengths at age, length frequency distributions, population age and size structure, and movement distances were also similar to values reported in the literature. Brook char were more affected by interspecific competition than rainbow trout. Under allopatric conditions, average brook char densities increased 130% over baseline (from 0.10 to 0.23 brook char/m^2), while average rainbow trout densities increased only 31% (from 0.13 to 0.17 rainbow trout/m^2). Density-dependent growth and survival were strongest in the fry stage and moderate in the juvenile stage; there was little density-dependent growth and survival in the other life stages. A contracted spawning season increased crowding among fry and favored rainbow trout, while a protracted spawning season decreased fry densities and favored brook char.

Factors Affecting Competition

Frequent year-class failures and low brook char fecundity offered possible and likely explanations for the dominance of rainbow trout over brook char in southern Appalachian streams. Year-class failures recurring every five years caused brook char extinction, and increasing brook char fecundity to levels reported for northern latitude populations resulted in near-allopatric brook char densities. Model results, combined with literature evidence of higher episodic mortalities in lower latitude Appalachian streams (Lennon 1967; Harshbarger 1975) and possible gradients in water quality (Lennon 1967) (potentially causing gradients in fecundity - McFadden 1961), suggested frequent year-class failures and low fecundity of brook char were likely explanations for dominance of rainbow trout in southern Appalachian streams.

Warmer temperatures in the southern latitudes and reduced spawning habitat were deemed to be possible but unlikely explanations for rainbow trout dominance in southern Appalachian streams. Simulations with 38°N temperatures generated higher brook char densities (0.16 brook char/m^2) and lower rainbow trout densities (0.11 rainbow trout/m^2) than baseline conditions (0.10 brook char/m^2; 0.13 rainbow trout/m^2) due to colder temperature affecting egg and alevin development and resultant mortality rates. However, the magnitude of differences between temperatures of 35°N latitude (baseline) and 38°N latitude streams were too small (United States Geological Survey 1993a,b) for temperature to be the cause of rainbow trout dominance. In simulations with an 80% reduction in spawning habitat, rainbow trout outcompeted brook char and approached allopatric densities. However, there was no empirical evidence that spawning habitat was

limiting in southern Appalachian streams (Lennon 1967; Kelly et al. 1980; Dechant and West 1985).

Greater aggressiveness of rainbow trout is a highly unlikely explanation for rainbow trout dominance. Simulations in which perceived lengths of rainbow trout juveniles and adults were increased had little effect on predicted brook char and rainbow trout densities. Field evidence also suggests that rainbow trout juveniles and adults do not outcompete brook char for food or space (Fausch 1988, 1989; Ensign et al. 1989; Lohr and West 1992).

Management Strategies

Electrofishing removal of rainbow trout and stocking of juvenile brook char were successful, and habitat alteration and angler harvest of rainbow trout were unsuccessful, in increasing brook char densities to allopatric levels. Simulations with electrofishing capture probabilities equal to or greater than 0.3 produced allopatric brook char densities. Field studies of electrofishing removal of rainbow trout in southern Appalachian streams typically report high capture probabilities (greater than 0.4). Stocking of brook char juveniles (or very large numbers of fry) also produced allopatric brook char densities; stocking of eggs or moderate numbers of fry were unsuccessful. However, field attempts at stocking brook char in southern Appalachian streams have been unsuccessful in significantly increasing brook char densities (King 1942; Lennon and Parker 1959; Kelly et al. 1980). Possible explanations for model success and field failure of stocking include the model assumption that naturally reproduced and stocked individuals are identical,

variation in factors affecting year-class strength in the field overwhelming stocking effects, and stocking for too few years in the field. Increasing pool size did not enhance predicted brook char populations. Riley and Fausch (1995) found no long term changes in Colorado trout populations when pool sizes were increased, but Burgess and Bider (1980) reported increased survival and growth of trout with increased pool habitat. Angler harvest of adult rainbow trout also did not increase brook char populations to allopatric levels, even at the highest rates of harvest. Most field evidence also suggests that fishing pressure in southern Appalachian streams is too low to greatly affect rainbow trout - brook char interactions (Whitworth and Strange 1983; Larson and Moore 1985).

Electrofishing removal of rainbow trout and stocking of juvenile brook char were robust. Similar brook char and rainbow trout densities were predicted with electrofishing and stocking imposed under baseline conditions as compared to conditions favoring rainbow trout (rainbow trout invasions, frequent year-class failures, and reduced spawning habitat). Response times of electrofishing and stocking were also similar (< 10 years for electrofishing; 10 to 20 years for stocking) for baseline, invasion, year-class failure, and reduced spawning habitat conditions. Response times were typically longest at intermediate levels of management actions. Low levels only caused small changes in density; high levels resulted in rapid changes in densities.

Concluding Remarks

Model results indicated that early life stages were the most critical to predicting brook char and rainbow trout population dynamics and interactions. Competition and

density-dependent growth and survival were strongest in the fry stage, and weaker but still significant in the juvenile stage. Factors that affected young-of-the-year densities (e.g., year-class failures, increased brook char fecundity) produced the greatest responses. Similarly, management actions that reduced rainbow trout fry and juvenile densities (electrofishing) or enabled brook char to bypass competition in the fry stage (stocking of juveniles) were the most successful in enhancing brook char densities.

A crucial model assumption largely responsible for the strong density-dependent growth and survival during the fry stage is that prey are divided equally among fry in a stream cell. This assumption is yet to be proven, though there is some evidence for its validity (Caron and Beaugrand 1988). The early life stages have been conspicuously lacking in studies of southern Appalachian trout populations. Model results demonstrating the potential importance of the growth and survival during young-of-the-year life stages, coupled with evidence of only limited differences in diet, habitat use, and behavior among adults, underscores the need to focus attention on the dynamics during the early life stages. A comparison of survival and growth from egg through the fry or juvenile stage between brook char populations in the southern Appalachian streams of varying rainbow trout dominance, or between northern and southern Appalachian streams, could pinpoint the factors responsible for rainbow trout dominance. This study should involve simultaneous measurements of growth and survival with environmental variables such as flow, temperature, and water quality. Young-of-the-year dynamics may be the key to understanding trout competition in southern Appalachian streams and to providing the information needed to effectively manage and preserve brook char populations.

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Vita

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