

# **Population Modeling for Batten Kill Trout**

**Kristian S. Omland**

Vermont Cooperative Fish and Wildlife Research Unit  
Rubenstein School of Environment and Natural Resources  
University of Vermont

and

**Donna L. Parrish**

U.S. Geological Survey  
Vermont Cooperative Fish and Wildlife Research Unit  
Rubenstein School of Environment and Natural Resources  
University of Vermont

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## Executive Summary

The Batten Kill Study Team enlisted support from the Vermont Cooperative Fish and Wildlife Research Unit for modeling trout populations beginning in 2002. That is the primary component of work covered in this report. Preliminary analysis focused attention on a possible survival bottleneck among mid-sized (6-10"; i.e., ~150-250 mm) trout. Therefore, in 2003, we initiated an effort to use mark-recapture techniques to measure survival rates among various size classes of trout. Furthermore, the most prominent hypothesis for size-selective mortality effecting mid-sized trout was predation. Therefore, in 2004, we initiated an effort to study the predatory habits of common mergansers and large brown trout.

As a prerequisite to modeling population dynamics, we modeled individual trout growth based on length-at-age data that had been collected from Batten Kill trout between 1984 and 2003. For both brook trout and brown trout, the data strongly supported the von Bertalanffy growth function over a simple linear growth model. For both species, the data supported models with uniform asymptotic length but growth rate differing among stations. For both species, estimated growth rate was greatest at a downstream station (West Mountain) and slowest at the upstream stations (East Dorset and Manchester).

Having quantitatively described the relationship between age and size among populations of the two species in the Batten Kill, we analyzed changes in abundance over the period 1984-2005 in the framework of structured population models. We were able to estimate growth and fecundity parameters from the length-at-age analysis as well as published values, therefore our model-fitting work entailed estimating survival parameters as well as parameters describing plasticity of growth, density-dependence, and trends over time in survival parameters. Candidate models included three broad classes: stationary models (Leslie and Lefkovitch matrix models), density-dependence models (both Beverton-Holt and Ricker), and trend models in which one or more survival parameters was allowed to change monotonically over time.

The dominant inference from our analysis was that, even though overall the population is declining, survival of eggs and fry is compensating for the decline to some degree. In other words, survival of eggs and fry has improved as the abundance of spawners has declined. We estimated the rate of decline to be approximately 9% per year for both brook trout and brown trout. As experienced by anglers and reported widely in the news, 1) abundance of "catchable" brown trout has declined dramatically over the years of the surveys reported here. However, 2) abundance of young-of-year (YOY) brown trout has not declined nearly as noticeably. The models incorporating compensatory survival of eggs and fry represent that pair of observations very well and were better supported by the data than a variety of other models.

Given that survival of trout in the early life history stages appears to have improved as abundance of spawners has declined, we can discount factors affecting those stages as root causes of the decline. Specifically, pollution, disease, siltation, and fertility changes are not likely to be causing the decline. Furthermore, since the population has

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not recovered as fishery managers have imposed stricter fishing regulations, overfishing is not likely to be causing the decline. Based on our population modeling work, the most likely hypotheses to account for the decline are: a) predators are selectively preying on mid-size trout, b) dearth of cover suitable for mid-size trout equates with lower carrying capacity in the stream, and c) recreational activity is increasing stress, thereby decreasing growth and survival. Those three effects may be acting synergistically.

From a conventional mark-recapture analysis, we found that apparent survival did not vary with trout size. However, the analysis probably had little power to detect differences due to small sample size and an overwhelming difference in survival among the periods of the study. Resorting to an ad hoc analysis that accounted for the growth of individuals (as inferred from the subsample that we recaptured at least once during the study), we showed that mortality probably was greater for YOY trout than larger trout, and that most mortality occurred early in the summer.

Common merganser abundance has increased in recent decades in a broad region including the Batten Kill and other Vermont trout streams. Abundance of other avian and mammalian fish predators may have increased as well. However, common mergansers were not more abundant overall on the Batten Kill than they were on other Vermont trout streams. Again, the sample may have been too small to yield the statistical power to detect differences. Suggestively, density of females with broods and recruitment of common mergansers were marginally higher on the Batten Kill than on other streams.

We collected 26 common mergansers to describe their diet. Half of the mergansers we collected had identifiable fish parts in their upper digestive tract, while slightly more than half of the specimens contained identifiable items that were not fish. We also sampled the gut contents of 38 large brown trout and found evidence of piscivory in nearly half of those individuals. For comparison to those two samples, we quantitatively described the forage fish community in the Batten Kill and other streams. Trout made up a higher proportion of fish in common merganser stomachs than in any of the community samples. On the other hand, the proportion of trout among the fish in the stomachs of large trout was well within the observed range of relative abundance of trout in forage fish communities. Our observations suggest that common mergansers selectively prey on trout but that large brown trout do not.

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## 1. Introduction

### 1.1. Trout decline and formation of Batten Kill Study Team

The Batten Kill flows out of the Green and Taconic mountains in southern Vermont and is a tributary of the Hudson River. It is a highly regarded trout stream with populations of native brook trout (*Salvelinus fontinalis*) and naturalized brown trout (*Salmo trutta*; native to Atlantic watersheds of Eurasia). Prior to 1976, both brook trout and brown trout as well as rainbow trout (*Oncorhynchus mykiss*; native to Pacific watersheds of western North America) were stocked in the Batten Kill as part of management of the trout fishery. Beginning around 1970, the Vermont Department of Fish and Wildlife (VTFW) steered toward managing the Batten Kill as a wild trout stream. Over the subsequent twenty years, wild populations of brook and brown trout sustained themselves at levels that permitted satisfactory fishing experience and maintenance of the Batten Kill's reputation as a great trout stream.

However, in the mid-1990s, anglers began reporting unsatisfactory fishing experiences and VTFW monitoring began to detect declines in the numbers of catchable trout, which was particularly noticeable among brown trout. VTFW responded with a series of special regulations including, beginning in 2000, a catch-and-release rule. In addition, they also convened an inter-agency Batten Kill Study Team involving members from VTFW, the U. S. Forest Service (USFS), and the Vermont Department of Environmental Conservation (VTDEC) and enlisted the collaboration of partners from other agencies and academic institutions.

At the outset, the Batten Kill Study Team identified a list of possible factors and causes for the decline of the trout fishery:

- Fish habitat (cover, spawning)
- Water quality and chemistry
- Pollution and contaminants (e.g., pesticides, fertilizers, runoff)
- Water temperature
- Stream flows (seasonal runoff patterns, flood and drought events)
- Nutrient enrichment or de-enrichment and associated biological productivity
- Disease
- Predation (e.g., mergansers, otters, mink)
- Forage base (invertebrate and fish)
- Land use and development impacts
- Other recreational uses (e.g., paddling, tubing, swimming)

Members of the Team as well as their collaborators gathered existing data and collected new data looking either for changes in the Batten Kill over time or differences between the Batten Kill and comparable trout streams where trout populations were not declining.

### 1.2. Population modeling and ensuing field studies

In 2002, the Team enlisted support from the Vermont Cooperative Fish and Wildlife Research Unit (the Coop Unit) for modeling trout populations, which is the primary component of work covered in this report. Population modeling offered a useful

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approach to investigating the cause of the trout decline by enabling us 1) to quantify the decline in biologically meaningful terms, i.e., birth, death, and growth rates, or changes in those parameters (Hilborn and Mangel 1997; Turchin 2003), 2) to weigh the relative support for each among a set of competing hypotheses (Burnham and Anderson 2002; Hilborn and Mangel 1997), and 3) to identify critical gaps in our knowledge, which would help us to focus further field work. Data-driven population modeling was enabled by the high quality population monitoring effort that had been sustained by VTFW for approximately 20 years.

Preliminary analysis of the VTFW monitoring data focused attention on a possible survival bottleneck among mid-sized (6-10";~150-250 mm) trout. Therefore, in 2003, the Coop Unit initiated an effort to use mark-recapture techniques to measure survival rates among various size classes of trout. Furthermore, the most prominent hypothesis for size-selective mortality effecting mid-sized trout was predation. Therefore, in 2004, the Coop Unit initiated an effort to study the predatory habits of common mergansers and large brown trout.

## 2. Methods

### 2.1. Study sites

Most studies reported here either used data collected by VTFW at their survey stations along the Batten Kill or data we collected at the same sites. The four primary stations were East Dorset 7A, Manchester 11 & 30, West Mountain, and Cemetery Run (Figure 2.1). Sampling at other locations is described in subsections, below.

### 2.2. Sampling fish

Fish were sampled by electrofishing using gasoline generators borne in aluminum canoes (where flow was sufficient) or placed on the streambank (near the headwaters). One to six wands were employed with as many as ten workers manning nets and buckets to aid in the handling of fish. In a few cases, Coop Unit personnel used a battery powered backpack electrofishing unit to sample the forage fish community outside of VTFW electrofishing efforts. Typical workup included measuring length and weight for individual trout (batches of 2-12 YOY). Sampling methods have been consistent since 1984 at two of the primary stations and since 1988 at the other two.

#### 2.2.1. Sampling trout

Each year, scales were retained from a haphazardly selected subsample of trout representing a range of sizes. Fish total length was recorded to the nearest millimeter, and weight to the nearest gram. Totals of 891 brook trout and 1,988 brown trout were represented. One individual (K. Cox, VTFW) estimated the age of each individual represented by the scales in the sample. Scales were inspected under a light microscope as well as a microfiche reader in some cases. Individuals for which all scales appeared to have been regenerated, for which scales were uninterpretable for other reasons, or which were deemed to have been escaped hatchery fish (judging by wear on fins as well as other indications) were excluded. That left 791 brook trout and 1,745 brown trout. Age of the

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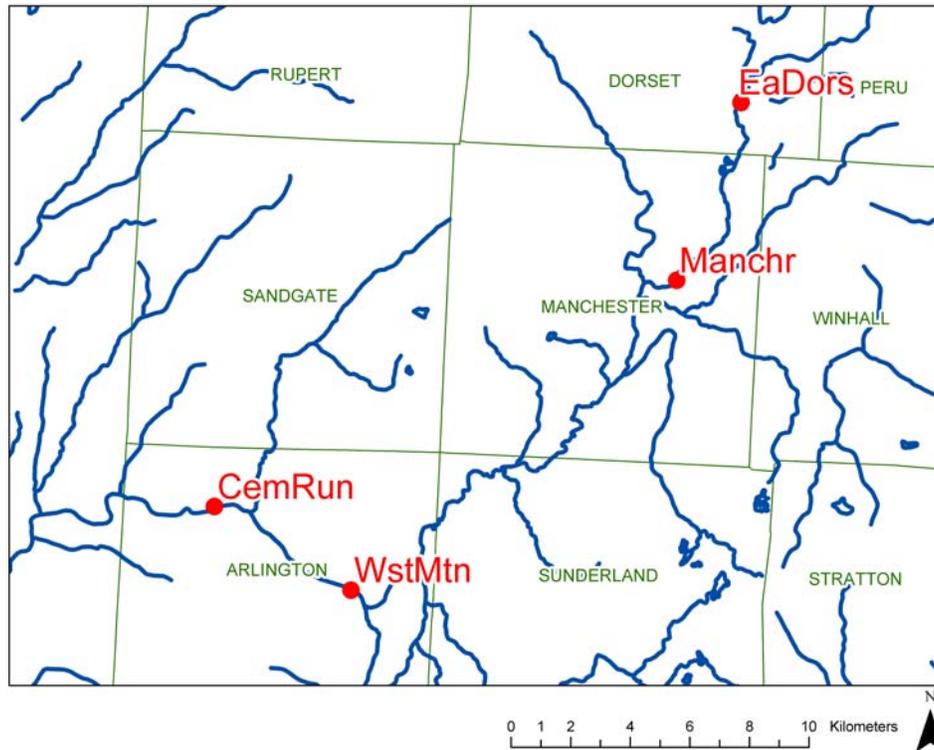


Figure 2.1. Four main study sites along the Batten Kill in southwestern Vermont. EaDors=East Dorset 7A, Manchr=Manchester 11 & 30, WstMtn=West Mountain, and CemRun=Cemetery Run

trout at the time the scale sample was taken was recorded in discrete age classes (1, 2, ...). In fitting the growth models, we assumed that each fish had hatched in late April.

In 2003, we conducted a mark–recapture study of 4 to 12" (100–300 mm) trout to obtain directly measured estimates of the survival rates of brown trout in the Batten Kill. Fish were marked with PIT tags. We initially marked trout around midsummer, then returned on three other occasions at five-week intervals to recapture marked fish. We set out to mark a large batch of trout in each of four size classes at each of three sites; size classes for the study were to have been 100–150 mm (approx. 4–6"), 150–200 mm (6–8"), 200–250 mm (8–10"), and 250–300 mm (10–12"). We were not able to tag as many trout as we wanted, particularly in the 200–200 mm ranges, but we analyzed the smaller data set using an ad hoc size classification created after the initial marking effort.

We analyzed the encounter histories of our sample of marked trout in Program MARK (White and Burnham 1999). We used model selection (§2.4) to infer whether size was a useful explanatory covariate accounting for apparent survival of trout and, if so, whether apparent survival of mid-size trout was less than that of smaller and larger trout. In addition, we were interested in whether directly measured survival probabilities

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squared with those estimated by fitting projection matrix models to annual census data (§3.3).

In 2004, we sampled stomach contents from some large brown trout using gastric lavage (UVM IACUC 04-203; Baker and Fraser 1976). Regurgitated gut contents were collected in cloth bags fitted under a large funnel. We took care to rinse the funnel well so that all contents were washed into the cloth bag. The cloth bag was then inserted into a roll-pack bag and placed on dry ice for flash-freezing. In the lab, we thawed the bag, turned it inside out over a white invertebrate tray, and reverse-rinsed it to ensure that all fragments were removed. The identity of recognizable fragments was recorded and their size estimated.

### 2.2.2. Sampling forage fish

Also in 2004, we sampled the forage fish community for comparison with what we would find in the guts of predators. We took the samples either during regular trout electrofishing or in separate electrofishing efforts. In either case, during community sampling, we netted every fish over 50 mm until we had collected approximately 100 fish.

### 2.3. Sampling mergansers

We estimated common merganser density on the Batten Kill and a number of other streams by floating approximately 10 km stretches of each river in canoes and kayaks. These included three stretches of the Batten Kill. Other streams were the Mettawee, Poultney, Castleton, and Dog rivers; in addition, since it was convenient to combine trips on the Stevens Branch and Winooski River with trips on the Dog River, we also surveyed those streams. We were able to make such trips in early June, while females were presumably incubating eggs, in July, when broods of young ducks were on the water, and in August when hatch-year birds were nearly fully grown and partially capable of flight. We recorded sightings of all waterfowl, other avian fish predators (e.g., belted kingfishers (*Ceryle alcyon*), herons (Ardeidae), osprey (*Pandion haliaetus*); Steinmetz et al. 2003), other noteworthy wildlife (rarely including mink, *Mustella vison*), and anglers as we floated downstream. We avoided double counting to the best of our ability by not counting individual birds or groups that appeared to be the same (i.e., same species, same number in group, same age and sex makeup of groups).

We collected common mergansers (*Mergus merganser*) using shotguns (UVM IACUC 04-203). Ducks were retrieved as soon as possible after being killed, and were immediately dissected to remove the entire upper digestive tract from the gullet to the beginning of the intestine. Those organs were placed in a roll-pack bag and placed among blocks of dry ice for flash-freezing. We also collected feather and blood samples to be sent to another lab for mercury contamination analysis, and heart tissue for DNA extraction for molecular systematics studies. In the lab, merganser stomachs were thawed and immediately cut open. The identity of recognizable fragments was recorded and their size estimated.

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### 2.4. Statistical data analysis using model selection

We used the statistical approach of model selection (Burnham and Anderson 2002; Johnson and Omland 2004) throughout our analyses. Model selection is a process in which various mathematical models, each one representing a scientific hypothesis, are fit to a set of data, and scored according to a criterion that accounts for both fit and complexity. Ideally, the selected model exhibits both predictive accuracy (technically, lack of bias) and precision. Too simple a model likely gives biased predictions, while too complex a model likely gives imprecise predictions. Akaike's Information Criterion (AIC) is widely used in model selection. Some scientists believe using AIC leads to selection of excessively complex models (Johnson and Omland 2004), and for that reason, we also report Schwarz' Criterion (SC), which incorporates a stronger penalty for complexity, as well as the results of likelihood ratio tests (LRT), which both have a longer history and tend to lead to selection of simpler models. Finally, an essential but oft-overlooked step in model selection is to address whether estimated parameter values are plausible and satisfactorily precise (Motulsky and Christopoulos 2004).

### 3. Analysis of annual survey data (1984-2005)

#### 3.1. Trout growth

##### 3.1.1. Importance of individual growth and framework for analysis

Growth of individuals in a population constitutes one of the basic processes of population dynamics together with survival and recruitment, particularly in the context of size-structured population models commonly used in fisheries (Quinn and Deriso 1999). Growth is also a fundamental measure of fitness (Niva and Jokela 2000) and it is a focal variable of life history evolution studies (Olsen and Vollestad 2003).

The state of the art of analyzing size-at-age data in terms of between-population comparisons is characterized by a reliance on likelihood ratio tests (LRT) to compare von Bertalanffy growth functions (VBGF) for two populations (Kimura 1980; Cerrato 1990; Villamor et al. 2004). Here we incorporate modern model selection using AIC into that basic approach to make inferences about differences in growth among locations for both brook trout and brown trout in the Batten Kill.

We entertained a set of candidate models for trout growth as follows. First, it was conceivable that the size of trout in our sample did not represent plateauing growth (e.g., trout in the study population may not live long enough to approach asymptotic length); in that case, trout length could be modeled as a linear function of age. For consistency with the VBGF function, we depicted that function in terms of a slope,  $k$ , and an  $x$ -intercept,  $t_0$ :

$$Length = k(Age - t_0) \tag{Equation 1}$$

On the other hand, growth may have slowed in the older fish in our sample, in which case the VBGF model would be a suitable model of length as a function of age:

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$$Length = L_{\infty} \left( 1 - \exp(-k(Age - t_0)) \right) \quad \text{Equation 2}$$

where  $L_{\infty}$  is asymptotic length (Quinn and Deriso 1999).

For each of the families depicted in equations 1 and 2,  $t_0$  should be negative (or, equivalently, the  $y$ -intercept should be positive). To permit  $t_0$  to be positive would imply a negative  $y$ -intercept, i.e., positing that trout begin life with negative length. We constrained the fitting of all models such that  $t_0$  was negative by using a logarithm link function, i.e., by substituting  $t_0'$  in place of  $t_0$  in equations 1 and 2 with  $t_0' = \ln(-t_0)$ . Ultimately we backtransformed  $t_0'$  [ $t_0 = -\exp(t_0')$ ], which led to asymmetrical confidence intervals. Considering that variation in length at the beginning of life should be negligible compared to variation in length of older fish, we did not permit  $t_0$  to vary by station in the model fitting.

On the other hand,  $k$  and  $L_{\infty}$  might vary among populations related to prey availability, environmental conditions, or local genetic adaptations. Therefore, we included in the set of candidate models variations in which  $k$ ,  $L_{\infty}$ , or both parameters were permitted to vary by station. We gave greater credence to the hypothesis that developmental plasticity would be reflected in variation in  $k$  among populations than the hypothesis that there would be variation in  $L_{\infty}$  (indeed it is unclear whether variation in  $L_{\infty}$  without variation in  $k$  is biologically tenable), but we left both models in the candidate set to permit the data to guide our thinking in that regard. That yielded a set of six basic candidate models (Tables 3.1a, 3.2a.)

Finally, by analogy with analysis of variance, we adopted an approach of first asking whether growth was heterogeneous among stations, then, if the data did support heterogeneity among stations, we would ask “Where are the differences?” We chose this hierarchical approach rather than attempting to include all plausible candidate models at the outset to avoid fitting too large a number of models to the data, which may lead to spurious inference (Burnham and Anderson 2002; Johnson and Omland 2004). For four stations along a stream continuum, there are six contrasts that entail adjacent stream sections (Table 3.1b):

- contrast a.     A vs. B-C-D
- contrast b.     A-B vs. C-D
- contrast c.     A-B-C vs. D
- contrast d.     A vs. B vs. C-D
- contrast e.     A vs. B-C vs. D
- contrast f.     A-B vs. C vs. D

Knowing that stations A (EaDors) and B (Manchr) are small, second-order stream reaches while stations C (WstMtn) and D (CemRun) are wide, third-order reaches,

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contrasts (c) and (e) were viewed as unlikely variations on the selected model, however, we left them in the candidate set to test the procedure's capacity for identifying realistic patterns.

Each candidate model was fit to the data using nonlinear least squares regression in S-Plus (Insightful 2002). We arrived at starting values for the nonlinear regression routine by inspecting Ford plots (Quinn and Deriso 1999). We considered AIC, SC, LRT, the plausibility of parameter estimates, and the precision of parameter estimates (quantified as a coefficient of variation, standard error/estimate; Motulsky and Christopoulos 2004) to select a model (or set of models if there was substantial model selection uncertainty) of trout growth in the Batten Kill.

### 3.1.2. Inference about trout growth

#### 3.1.2.1. Patterns common to both species

Size-at-age data for both species of trout in the Batten Kill strongly support the VBGF function over the linear function, and they indicate significant differences in growth among stations (Figure 3.1, Tables 3.1a, 3.2a). Among the six general models, the data support models with  $k$  varying among stations or both  $L_\infty$  and  $k$  varying among stations. The models with uniform  $k$  but different  $L_\infty$  for each station garnered little support (brook trout:  $\Delta\text{AIC} = 5.1$ ,  $\Delta\text{SC} = 9.5$ ; brown trout:  $\Delta\text{AIC} = 27$ ,  $\Delta\text{SC} = 24$ ).

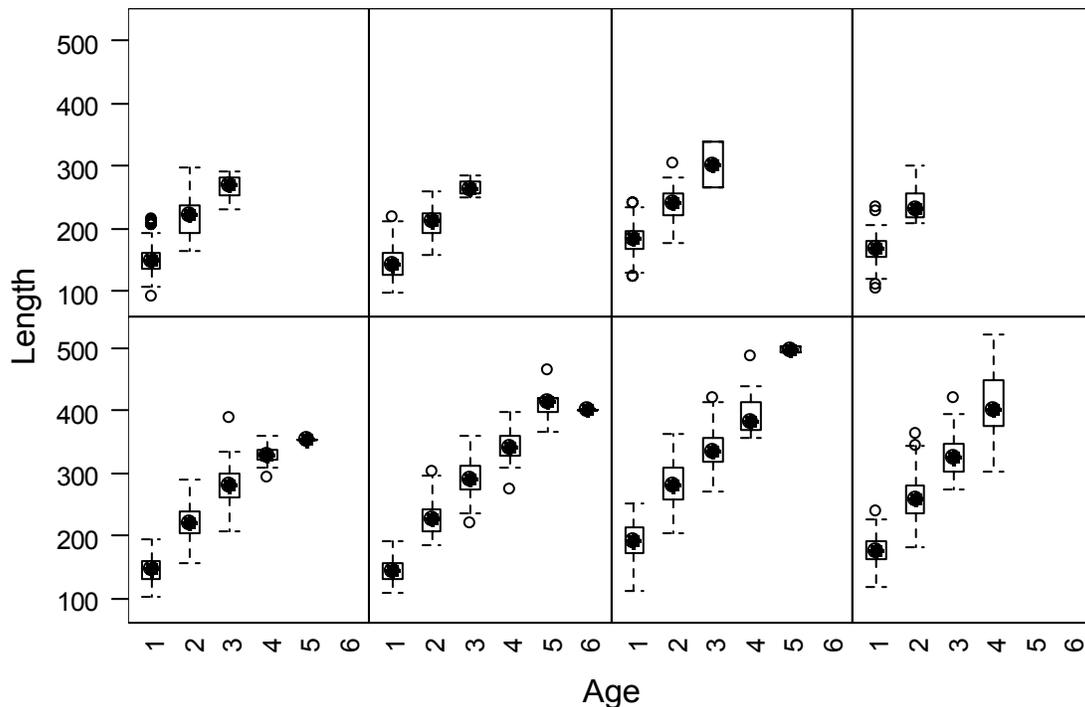


Figure 3.1. Box-and-whisker plots of length-at-age for brook trout (top row) and brown trout (bottom) at four stations (left to right: EaDors, Manchr, WstMtn, CemRun). Filled circles are medians, boxes extend to the first and third quartiles, whiskers extend  $1\frac{1}{2}$  interquartile ranges from the medians, and open circles are outliers.

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Table 3.1. Model selection for brook trout growth. (a) Six basic models, (b) the best among the basic models with the six corresponding models with stations grouped. Models are numbered from simplest to most complex but sorted by Schwartz' criterion (SC; actually  $\Delta SC$ , the difference between each model's SC and the lowest SC among all models). The two characters of the model name represent the structure of the two parameters of the VBGF growth model,  $L_\infty$  and  $k$ : – signifies that  $L_\infty$  does not appear in the model; • signifies that the parameter is uniform among stations;  $s$  signifies that the parameter is heterogeneous among stations; letters in (b) correspond to contrasts described in text.

a)	Model Number	Model Name	$p$	$-\log L$	$\Delta AIC$	$\Delta SC$
	4	• s	7	-435.31	0.00	0.00
	5	s •	7	-432.76	5.11	5.11
	2	– s	6	-428.31	12.00	7.33
	6	s s	10	-437.67	1.29	15.31
	1	– •	3	-299.05	264.53	245.84
	3	• •	4	-302.25	260.12	246.10

b)	Model Number	Model Name	$p$	$-\log L$	$\Delta AIC$	$\Delta SC$
	12	• f	6	-434.15	0.33	0.00
	4	• s	7	-435.31	0.00	4.34
	8	• b	5	-426.14	14.34	9.34
	10	• d	6	-427.27	14.08	13.75
	7	• a	5	-319.32	227.99	222.99
	11	• e	6	-321.10	226.42	226.09
	9	• c	5	-306.52	253.58	248.57

For both species, considering the six possible contrasts of either just  $k$  or both  $L_\infty$  and  $k$ , the data supported contrast (f), i.e., similar growth between the two upstream stations but different growth among those two and each of the downstream stations (Tables 3.1b, 3.2b). All other contrasts, including grouping the two downstream stations in addition to grouping the two upstream stations (contrast b), scored poorly in the model selection process, whether based on SC, AIC, or LRT.

### 3.1.2.2. Model of individual brook trout growth

For brook trout, model 4 ( $L_\infty$  uniform,  $k$  structured by stations) and model 12 ( $L_\infty$  uniform,  $k$  structured according to contrast f) rank the highest by either AIC or SC (Table 3.1b). The negative log-likelihood of model 4 is only 1.16 lower than that of model 12, which is not a significant improvement when judged by an LRT ( $\chi^2 = 2.33$ , d.f. = 1,  $p > 0.1$ ). We selected model “f” as the best model of brook trout growth (Table 3.3a, Figure 3.2).

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Table 3.2. Model selection for brown trout growth. (a) Six basic models, (b) the best two among the basic models the twelve corresponding models with stations grouped. Organization as in Table 3.1.

a)	Model Number	Model Name	$p$	$-\log L$	$\Delta AIC$	$\Delta SC$
	4	• s	7	-1153.96	2.60	0.00
	6	s s	10	-1158.26	0.00	13.80
	5	s •	7	-1141.81	26.91	24.31
	2	– s	6	-969.20	370.12	362.06
	3	• •	4	-689.17	926.18	907.20
	1	– •	3	-569.62	1163.28	1138.82

b)	Model Number	Model Name	$p$	$-\log L$	$\Delta AIC$	$\Delta SC$
	17	• f	6	-1152.08	4.37	0.00
	4	• s	7	-1153.96	2.60	3.69
	18	f f	8	-1153.95	4.61	11.17
	6	s s	10	-1158.26	0.00	17.49
	9	• b	5	-1115.73	75.07	65.24
	13	• d	6	-1117.52	73.48	69.11
	10	b b	6	-1117.40	73.73	69.36
	14	d d	8	-1121.52	69.49	76.05
	7	• a	5	-871.66	563.19	553.36
	15	• e	6	-875.05	558.41	554.05
	8	a a	6	-871.67	565.19	560.82
	16	e e	8	-875.67	561.18	567.74
	11	• c	5	-729.04	848.44	838.61
	12	c c	6	-729.53	849.47	845.10

( $\chi^2 = 8.60$ , d.f. = 3,  $p > 0.03$ ). Furthermore, model 17, which is a simplification of model 4 in which growth at the two upstream stations is modeled with the same growth constant,  $k$ , comes in only 1.77 AIC units behind model 4, it beats model 4 by 3.69 SC units, and it would be accepted under an LRT ( $\chi^2 = 3.77$ , d.f. = 1,  $p > 0.05$ ). Thus we also selected model “f” as the best model of brown trout growth (Table 3.3b, Figure 3.2).

### 3.1.2.3. Model of individual brown trout growth

For brown trout, model 6, which includes station-specific parameter estimates for both  $L_\infty$  and  $k$ , has the lowest AIC, but we suspected that the model was overparameterized, and that the estimates of  $L_\infty$  under that model were biologically implausible. In particular, we were skeptical that brown trout at West Mountain (station C) would have a lower  $L_\infty$  than the two upstream stations where pools are much shallower. Model 4, which posits a uniform  $L_\infty$  among stations, is only 2.6 AIC units behind model 6, it scores better by Schwarz’ criterion, and it would be only tentatively rejected by an LRT

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### 3.1.3. Summary of analysis of trout growth

We identified heterogeneity in the growth of two species of trout among four stations along the Batten Kill. We determined that growth was similar for both species at the two upstream stations, A (EaDors) and B (Manchr), but different among that pair of stations, station C (WstMtn), and station D (CemRun). It was remarkable that our approach led us to the same model being selected for both brook trout and brown trout, i.e., similar growth at the two upstream stations but different growth among the two upstream stations and each of the downstream stations. It was even more remarkable that the relative pattern of estimated  $k$  was the same between the two species, with fastest growth at station C, slowest growth at stations A-B, and intermediate growth at station D. Brook trout generally thrive relative to brown trout in headwaters sections, but that generalization was not reflected in the pattern of growth rates depicted in Figure 3.2.

Table 3.3. Parameter estimates for model “• f” for (a) brook trout and (b) brown trout.

a)	Parameter	Estimate	SE	CV	LCL	UCL
	$L_{\infty}$	350	68	19%	217	483
	$k_{A \& B}$	0.38	0.17	44%	0.05	0.71
	$k_C$	0.50	0.24	47%	0.04	0.97
	$k_D$	0.45	0.21	46%	0.05	0.86
	$\ln(-t_0)$	-2.44	3.05	125%	-8.41	3.54
	$t_0$	-0.09			-34	0.00

b)	Parameter	Estimate	SE	CV	LCL	UCL
	$L_{\infty}$	542	39	7%	466	618
	$k_{A \& B}$	0.22	0.03	12%	0.17	0.27
	$k_C$	0.30	0.04	13%	0.22	0.38
	$k_D$	0.27	0.04	13%	0.20	0.34
	$\ln(-t_0)$	-2.64	0.85	32%	-4.31	-0.96
	$t_0$	-0.07			-0.38	-0.01

### 3.2. Re-classification of size

We found it problematic to apply statistical analyses to the annual survey data based on the size classification used by VTFW, primarily because having zeroes in the data set caused problems with model fitting. In particular, a) the *length* <6" size class frequently was not represented by any trout in a sample, and b) the largest size classes ( $10" \leq \textit{length} < 12"$  and  $12" \leq \textit{length}$ ) typically did not include any brook trout. Based on the results of our analysis of trout growth, we sought to define more appropriate length classes for our statistical analyses. From an ecological point of view, we wanted to define the length classes such that individuals predominantly graduated from one size class to the next on an annual basis. Furthermore, from a statistical point of view, we wanted to minimize the occurrence of zeroes in the data set. We used the fitted von Bertalanffy growth parameters, described above, to set appropriate boundaries between size classes to approximate, but not necessarily act as surrogate for age classes (see below).

## Batten Kill trout population modeling

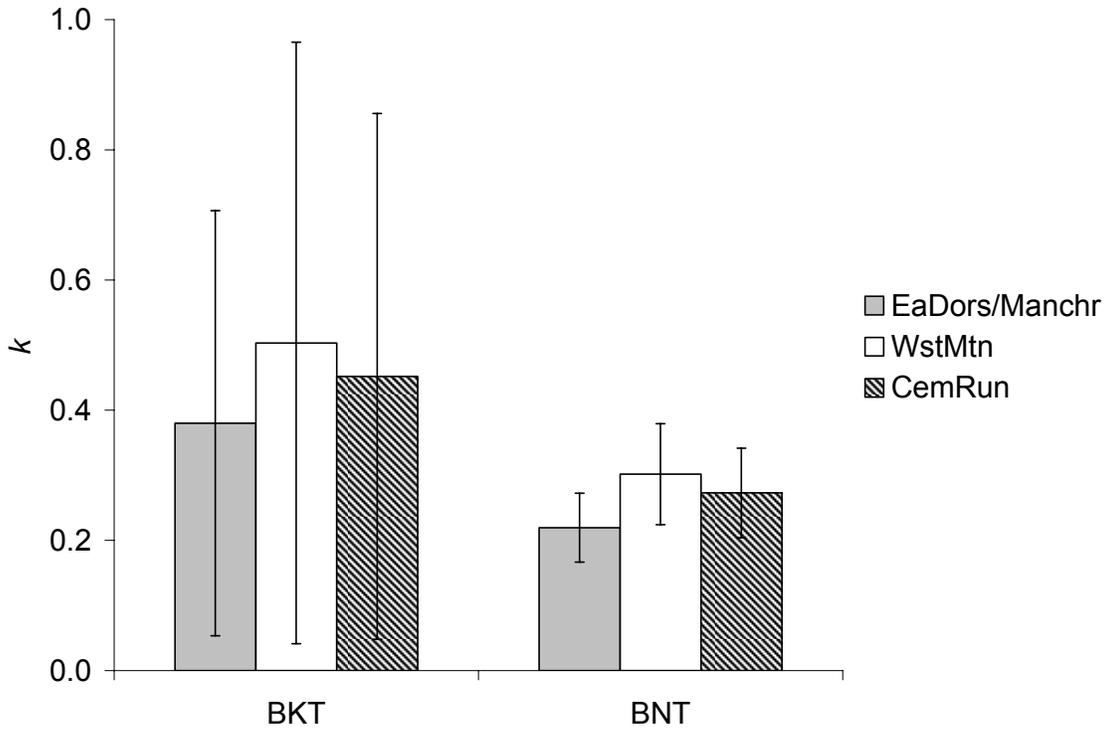


Figure 3.2. Estimated growth parameter,  $k$ , from the VBGF at three stations for both brook and brown trout. Error bars depict 95% confidence intervals about the estimates.

We computed the length (to the nearest mm) at which the probability that a fish would be misclassified was minimized. For example, given the von Bertalanffy parameters for the two upstream stations, approximately 9% of yearling brook trout are expected to be  $> 177$  mm, while approximately 9% of second-year brook trout are expected to be  $\leq 177$  mm; choosing 177 mm as the ceiling for length class II minimized the expected probability of misclassifying the age of brook trout at that station. The ceilings that we selected using that algorithm closely matched the empirical distribution of size at age. For example, 39 of 362 (11%) yearling brook trout from the upper two stations were  $> 177$  mm, while 9 of 96 (9%) second-year brook trout were  $\leq 177$  mm. Having found that the growth coefficient differed among stations, length classes were defined differently among stations (Table 3.4). We allowed for flexibility in the ceiling for YOY to reflect the determination of YOY status that had been made by VTFW biologists in the field each year.

In addition to the removal estimates, we obtained raw data on individual fish from VTFW and classified each trout according to the newly defined length classes. We performed removal sample estimation using Program MARK (White and Burnham 1999) using the simple closed population estimation model with the recapture probability constrained to equal 0. For each set of data, we entertained a set of 4 candidate models for initial capture probability,  $p$ :

## Batten Kill trout population modeling

1.  $p(\cdot)$  – capture probability uniform among all trout (the simplest model)
2.  $p(\text{Sp} \times \text{Size})$  – capture probability differing by both size class and species (the most complex model)
3.  $p(\text{YOY})$  – capture probability different for young-of-year trout (YOY) than for older trout (regardless of species)
4.  $p(\text{Sp})$  – capture probability different for brook trout than brown trout (regardless of size)

Model selection was based on  $AIC_c$  with post-hoc assessment of plausibility. For each station, where the highest ranking model by  $AIC_c$  included one or more estimates of  $p$  outside of the interquartile range of  $p$  over the years from the  $p(\cdot)$  model (frequently that entailed putative capture probabilities of 0 or 1), we deemed the estimate implausible and the fitted model pathological, thereby rejecting it. We then looked at the next ranking  $AIC_c$  model (invariably a simpler model), evaluated the plausibility of its parameter estimates in the same fashion, and iteratively arrived at a selected removal sample model for that year at that station. Estimates of  $N$  for each size class in each species from the selected model were then taken as estimated abundance for that year at that station (Figure 3.4). In general, 90% confidence intervals for the vector of  $N$  were tight, i.e., the estimates of abundance were precise. On that basis, as we proceeded to model changes in abundance, we assumed that observation error was negligible compared to process noise.

### 3.3. Population modeling

#### 3.3.1. Model framework

Structured populations are modeled using projection matrices. Assuming a stochastic process with negligible observation error, the predicted vector of abundance next year is equal to the projection matrix,  $\mathbf{A}$ , times the realized vector of abundance this year:

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t \quad \text{Equation 3}$$

The projection matrix,  $\mathbf{A}$ , can be decomposed into three components corresponding to recruitment, graduation (or growth), and survival (Quinn and Deriso 1999):

$$\mathbf{A} = \mathbf{R} + \mathbf{GS} \quad \text{Equation 4}$$

Table 3.4. Ceilings (in mm) for size classes by species and station.

station	brook trout		brown trout		
	YOY	II	YOY	II	III
EaDors & Manchr	97	177	92	182	253
WstMtn	121	211	121	231	313
CemRun	111	198	111	215	293

# Batten Kill trout population modeling

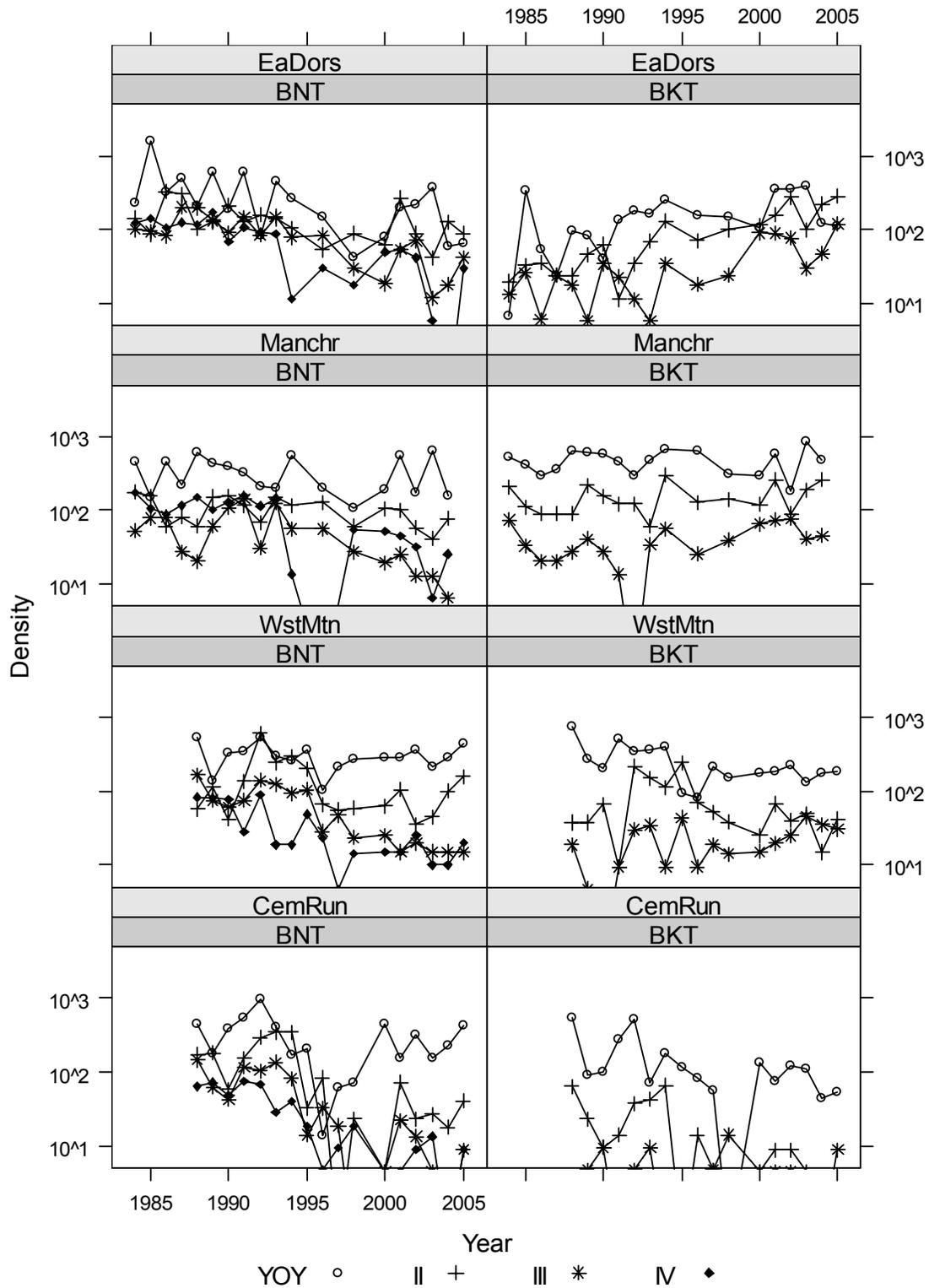


Figure 3.4. Time series plots of trout density ( $N/km$ ) in revised size classes (Table 3.4) at the four Batten Kill stations.

## Batten Kill trout population modeling

In the conventional taxonomy of matrix population models, age-structured and stage-structured populations are treated separately with  $\mathbf{A}$  called the Leslie matrix and the Lefkovitch matrix, respectively (Caswell 2001). In catch-at-size analysis (Sullivan et al. 1990), however, the graduation matrix,  $\mathbf{G}$ , is modeled as a realization of a stochastic growth process following a gamma distribution, which has a scale parameter,  $\beta$ , quantifying the degree of stochasticity in growth. With  $\beta$  relatively large, the resulting population projection matrix,  $\mathbf{A}$ , is a Lefkovitch matrix. If  $\beta$  is sufficiently small, however, individuals within the population grow in lock-step and, provided the size classes have been defined appropriately to approximate age classes,  $\mathbf{A}$  is effectively a Leslie matrix. Therefore, part of our analysis entailed optionally constraining  $\beta$  to be small (0.001; the gamma distribution does not permit the scale parameter to be 0) or estimating it from the data. This, in effect, was a contest between two hypotheses:

$H_A$ : the size classes we defined served as an adequate surrogate for age classes so that population growth may be modeled with a Leslie matrix

$H_B$ : the degree of stochasticity in the growth of individuals is sufficiently large to require that population growth be modeled with a Lefkovitch matrix

Note that the playing field for this contest is flat: while, in general, a Lefkovitch matrix appears to be considerably more complex than a Leslie matrix, in catch-at-size analysis it requires only one additional free parameter,  $\beta$ .

Other parameters in the graduation matrix,  $\mathbf{G}$ , were estimated from our length-at-age analysis (above).

We garnered estimates of the parameters of the recruitment matrix,  $\mathbf{R}$ , from published literature supplemented with empirical information from our population. We assumed that sex ratio was 1:1 having found no published information to the contrary for brook trout or brown trout. For brook trout our classification included only one reproductive size class, therefore it was unnecessary to consider size-specific maturity or fecundity. For brown trout, on the other hand, reproductively mature individuals appeared in two size classes. Avery (1985) had studied a similar naturalized brown trout population in Michigan and reported the proportion of mature individuals in a range of size classes. We fit a logistic regression model to his data, then predicted the proportion of mature individuals in each of our size classes. In effect that amounted to predicting the proportion of brown trout in size class III that were mature since, for all populations, the predicted proportions were 0 for size class II and 1 for size class IV. We assembled a collection of thirteen studies in addition to Avery's (1985) in which the authors had reported a length-fecundity regression (Brown and Kemp 1941; Allen 1951; Nicholls 1958; Buss and McCreary 1960; Taube 1976; Sadler 1983; Elliott 1984; Papageorgiou et al. 1985; Garcia and Brana 1988; Hegge et al. 1991; Bembo et al. 1995; Lobon-Cervia et al. 1997; Olofsson and Mosegaard 1999). These included a total of 18 distinct brown trout populations. For each of the 18 regression equations, we computed the predicted fecundity of fish at 10 mm intervals within the range of lengths included in that study, averaged the predicted fecundity across studies, and estimated the parameters of the power function that best fit those averages. Finally, we computed the expected fecundity

## Batten Kill trout population modeling

of fish in each of the reproductive size classes based on the empirical median length of trout in each size class at each station (Table 3.5).

The remaining component of the projection matrix,  $\mathbf{A}$ , is the vector of survival probabilities. There are  $a + 1$  survival probabilities for  $a$  size classes, the additional survival probability being that for early life history stages. It was that vector of survival probabilities that was optimized in the model fitting described below, as well as variance and, optionally,  $\beta$ , the scale parameter for growth increment.

The survival probability for early life history stages (eggs, fry, parr),  $s_0$ , gets incorporated into the recruitment matrix,  $\mathbf{R}$ , as follows. Population surveys take place in late summer each year, while spawning occurs about two months after that, therefore recruitment accounts for both the probability that an adult spawner survives for two months and the probability that its offspring survives the ten months required to get from being an egg in the fall to being a YOY at the next survey date. Thus the top row of the recruitment matrix,  $\mathbf{R}$ , is given by:

$$\mathbf{R}_{1,j} = s_j^{2/12} \times \rho \times m_j \times F_j \times N_j \times s_0^{10/12} \quad \text{Equation 5}$$

(with  $j$  indexing columns;  $\rho$  = proportion of females = 0.5;  $m$  = proportion of females that are reproductively mature,  $F$  = predicted fecundity). Other rows of  $\mathbf{R}$  comprise zeroes.

Density-dependent recruitment is common in fish populations, particularly among juveniles (Milner et al. 2003), and we incorporated density dependence into Eq. 5 as one

Table 3.5. Elements of the projection matrix estimated outside of the model-fitting accounted for in this section.  $L_\infty$  = the asymptotic length of fish;  $\kappa$  = the growth rate coefficient in the VBGF;  $m_{III}$  = the proportion of brown trout in size class III that are reproductively mature;  $F$  = the predicted fecundity (number of eggs produced per female) for brown trout in size classes III and IV based on  $F = 0.0008 L^{2.4}$ .

station	parameter	brook trout	brown trout	
all	$L_\infty$	365	560	
EaDors & Manchr	$\kappa$	0.35	0.21	
WstMtn		0.46	0.28	
CemRun		0.41	0.26	
EaDors & Manchr	$m_{III}$		0.6	
WstMtn			0.9	
CemRun			0.8	
			size class III	size class IV
EaDors	$F$		540	670
Manchr			540	740
WstMtn			640	800
CemRun			610	780

## Batten Kill trout population modeling

of the possible elaborations in our candidate set of models. Egg production was directly proportional to density of spawners,  $N_j$ , in all models:

$$\text{eggs}_j = s_j^{2/12} \times \rho \times m_j \times F_j \times N_j \quad \text{Equation 6}$$

In the models with density dependence, survival rate after hatching ( $s_0$  in Eq. 5), i.e., survival rate of fish in the early free-swimming stages, was a function of the density of those individuals. We included a compensatory Beverton-Holt (Eq. 7) and an overcompensatory Ricker (Eq. 8) function:

$$s_0 = \frac{\alpha}{1 + \beta \times \text{eggs}} \quad \text{Equation 7}$$

$$s_0 = \exp(\alpha - \beta \times \text{eggs}) \quad \text{Equation 8}$$

While there may also be density-dependent survival in later stages, we did not include models of that in our candidate set.

Survival probabilities for each of the size classes are the diagonal elements of the survival matrix,  $\mathbf{S}$ , with the remaining elements being zeroes.

In summary, we constrained much of the overall population projection matrix,  $\mathbf{A}$ , based on published values or ancillary data from our study population. The remaining elements of  $\mathbf{A}$ , which we estimated by numerical optimization, comprise a vector of survival probabilities, optionally one parameter for stochastic growth, optionally one parameter for density-dependence, and a variance parameter.

### 3.3.2. Candidate models

VTFW and U.S. Forest Service (USFS) biologists took input from experts and convened a series of public meetings from which they had generated a list of factors that may relate to the declining trout population (§1.1; also Table 3.6, left column). In communication with other experts on the Batten Kill study team, we articulated a set of specific hypotheses corresponding to that list of factors (middle column). Some of the factors manifolded into more than one specific hypothesis, while other factors, on their face, would seem to have no distinct impact. In simple terms, each hypothesis can be represented, perhaps inadequately, by an anticipated effect on one or more survival parameters (right column).

As far as our analysis went, we were concerned with detecting either a survival parameter being lower than expected or a negative trend in a survival parameter over time. We incorporated the possibility that a survival parameter changed over time by using a four-parameter logistic function as a submodel of that parameter:

$$s_a = s_{a,end} + \frac{s_{a,base} - s_{a,end}}{1 + \exp\left(-s_{a,slope} \times (t - s_{a,inflection})\right)} \quad \text{Equation 9}$$

## Batten Kill trout population modeling

Table 3.6. Factors put forward that may contribute to trout population decline, together with specific hypotheses pertaining to each factor and the affected parameter.

Factor	Hypothesis	Affected parameter
Temperature	Higher summertime temperatures are impacting growth and survival	
Ecosystem productivity	Lessened productivity in the stream is leading to decreased fecundity and decreased survival	$S_{all}$
Recreational use	Recreational activity is increasing stress, thereby decreasing growth and survival	
Disease	Disease is impinging on survival of all age classes Disease impinges on early survival	
Pesticide pollution	Pesticide or other pollution interferes with trout early development	$S_0$
Other pollution		
Siltation	Siltation is reducing habitat quality for eggs, alevins, and fry	
Fertility	Fewer eggs are laid, or fewer of them develop	
Predation	Predators are selecting mid-size trout	
Cover	Dearth of cover suitable for mid-size trout equates with lower carrying capacity in the stream	$S_{I, II}$
Habitat quality		
Fishing pressure	Fishing pressure is diminishing the survival of large trout	$S_{IV}$

where  $t$  measures the survey year. In effect, this represented the generic hypothesis that survival was at some baseline ( $s_{a,base}$ ) in the 1980s (or earlier) and changed over time to reach (or at least approach) an asymptotic level currently ( $s_{a,end}$ ). The four-parameter logistic function has the flexibility to represent a continuum from slow, continuing change (with a shallow slope parameter,  $s_{a,slope}$ ) to sudden change (with a steep slope parameter; if the slope parameter is high enough, the logistic function is indistinguishable from a step function in terms of annual intervals). Slow, continuing change could be represented with two parameters (i.e., a line instead of a logistic function), but that would carry the pathological implication that survival was greater than 1 at some point in the past and would become less than 0 at some point in the future. Sudden change could be

## Batten Kill trout population modeling

represented with three parameters (a step function entailing baseline survival probability, terminal survival probability, and year of shift), but could not encompass more gradual change. Finally, the fourth parameter,  $s_{a,inflection}$ , permitted the inflection point of the shift from baseline to asymptotic level to occur early or late in the study period.

We were realistic about the level of inference approachable through this analysis. Through the process of model fitting and model selection, we anticipated enhancing or diminishing the credence of the various hypotheses. We anticipated prescribing additional field studies to further distinguish among those hypotheses that would have enhanced credence following this analysis (and incorporation of other new information).

### 3.3.3. Maximum likelihood fitting and model selection

We modeled abundance as a lognormally distributed random variable assuming that stochasticity in survival and recruitment overwhelmed observation error. We fit each population model to the data by minimizing the negative log-likelihood of the model over its free parameters given the data. In particular, we used the software package, S-Plus (Insightful 2002) and the `optim()` function from the MASS library (Venables and Ripley 1999). We defined the negative log-likelihood with the simple command,

```
nLL <- sum(log(dlnorm(data, prediction, shape)))
```

where “`dlnorm`” is the density function of the lognormal distribution, “`data`” is the matrix of abundances with size classes in columns and years in rows, “`prediction`” is the matrix of predicted abundances with the same rows and columns as the data, and “`shape`” is the shape parameter of the lognormal distribution. Predictions were one-step-ahead predictions from the preceding year’s data, thus there were no predictions for year one. Also, for years following missed surveys, predictions were two-steps-ahead predictions from the data of two years earlier. We only supplied one shape parameter in the call to `optim()`, which was tantamount to assuming uniform stochasticity across size classes and years. For simplicity, all observations were weighted equally.

Survival parameters were fitted through a logit link function to ensure that they remained within  $(0, 1)$ ;  $\alpha$  in the Beverton-Holt function was handled similarly. We ensured that a number of parameters remained positive by fitting them through a log link function. This applied to the shape parameter of the lognormal distribution, the shape parameter controlling stochasticity of individual growth, and the density dependence parameters in both the Beverton-Holt and Ricker function.

We fed a vector of plausible initial parameter values to the optimization for the simplest model, then used fitted values for simpler models coupled with plausible additional parameters as the initial values in optimizing more complex models. In the script calling `optim()`, we iterated the optimization a minimum of three times to ensure that the routine arrived at global minima. In cases where the routine had not converged after the second call, the script automatically iterated the call to `optim()` until it had converged before calling it one last time; in some cases that required more than 10 iterations, but never more than about 15. We reviewed the S-Plus objects produced by `optim()` verifying that the ultimate fitted model had converged. We also verified that

## Batten Kill trout population modeling

each model with the additional free parameter,  $\beta$ , (i.e., the Lefkovitch version of the model) had a lower negative log-likelihood than its counterpart with  $\beta$  constrained to be 0.001 (i.e., the Leslie version of the model) to ensure that the fitting routine had not converged on a local minimum with low  $\beta$ . Similarly, we verified that each density-dependent model had a lower negative log-likelihood than its density independent counterpart.

We implemented model selection primarily using  $AIC_c$  but supplementing that criterion with evaluating the plausibility of estimated parameter values as well as their lack of precision (as measured by their standard errors, which we obtained by inverting the Hessian matrix; Motulsky and Christopoulos 2004).

### 3.3.4. Inference about population dynamics

#### 3.3.4.1. Leslie versus Lefkovitch

On the whole, the data did not support including the one additional parameter required to make the population projection matrix into a Lefkovitch matrix (Table 3.7). This was unambiguously the case for both species at the upstream stations, and for brook trout at the third station. More interesting is the case of brown trout at the two downstream stations, where the data appear to require the richer projection matrix that includes some individuals persisting in a size class or leaping ahead more than one size class in a year.

For the remainder of results presented here, models included the  $\beta$  parameter for stochastic growth only for brown trout at the downstream sites (West Mountain and Cemetery Run).

#### 3.3.4.2. Best stationary projection matrices

Estimated survival through the early life history stages was approximately 0.06 for brook trout and 0.01 for brown trout. Estimated survival for trout of both species upon reaching YOY status was approximately 0.3 with no strong patterns relative to species, size, or location (Figure 3.5). For highly ranked models (Table 3.8), precision of the estimates was good with most ratios of maximum likelihood estimate to standard error ( $t$  ratios; computed on the parameters as fitted, i.e., through the logit link) substantially larger than 2. The least precise estimates were for size III brook trout at Manchester

Table 3.7. Scores in the contest between Leslie and Lefkovitch models where pairs of models were identical except that the Lefkovitch model included one additional parameter for stochastic growth of individuals. The “winner” had a lower  $AIC_c$  than its counterpart.

station	brook trout		brown trout	
	Leslie	Lefkovitch	Leslie	Lefkovitch
EaDors	16	0	34	2
Manchr	16	0	36	0
WstMtn	14	2	5	31
CemRun		NA	1	35

## Batten Kill trout population modeling

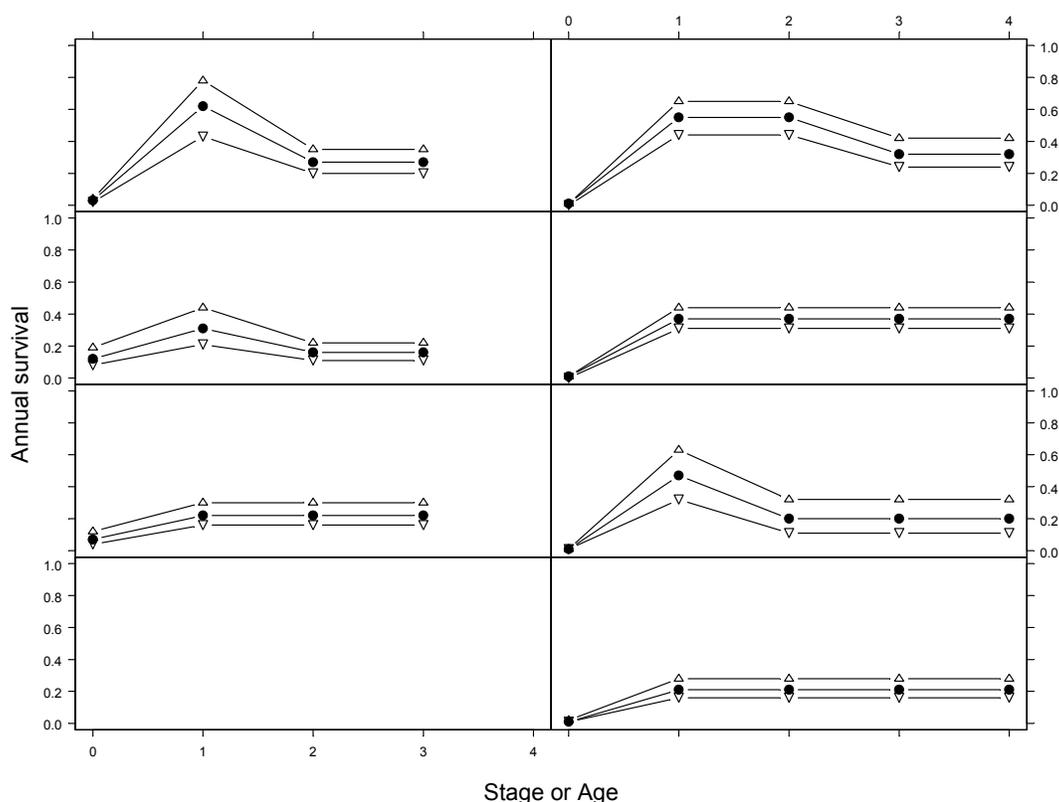


Figure 3.5. Estimated annual survival with 95% confidence intervals under the best plausible stationary models. Columns – left: brook trout; right: brown trout. Rows – top to bottom EaDors, Manchr, WstMtn, CemRun.

11/30 and size I brown trout at West Mountain; in both cases, even though the 90% confidence interval about that parameter was large, it did not overlap the confidence interval of adjacent size classes.

There were some subtle patterns in the survival of subadult and adult trout (Figure 3.5). The best supported plausible stationary model for several data subsets featured higher survival probability for size class II (yearlings) than for larger fish. There was also an indication that survival is lower in the wide, downstream reaches, particularly for size classes II and III. Finally, it appeared that survival probability of brook trout was lower than that of brown trout for some size-location combinations.

Finite rate of increase ( $\lambda$ ) was less than 1, indicating a declining population for all top-ranked stationary models fit to subsets of the data except for brook trout at East Dorset 7A. We computed a diffusion approximation estimate of  $\lambda$  (Dennis et al. 1991) for YOY brook trout at Cemetery Run (where we avoided fitting structured models owing to zeroes in the data set for larger size classes), which yielded an estimate of  $\lambda = 0.89$ . Overall, both brook trout and brown trout populations have been declining by approximately 9% each year.

## Batten Kill trout population modeling

Table 3.8a. Model selection for brook trout population dynamics. Models were classified in three classes (stationary, density-dependent, or trend in survival over time). Within stationary models, form was either Leslie or Lefkovitch; within density-dependent models, form was either Beverton-Holt or Ricker; within trend models, the trend affected eggs and fry, YOY, Adults, or both YOY & Adults. Finally, for each model, survival rate for adults either was constrained to be equal to survival rate for YOY ( $s_A = s_Y$ ) or was an additional free parameter ( $s_A \neq s_Y$ ). Number of parameters,  $p$ , measures model complexity, likelihood ratio measures lack of model fit compared to the best-fitting model,  $\Delta AIC_c$  and  $\Delta SC$  measure support for the model balancing complexity and fit.

	Class	Form	Structure	$p$	L ratio	$\Delta AIC_c$	$\Delta SC$
EaDors	density-dependent	Beverton-Holt	$s_A \neq s_Y$	5	0.00	0.00	0.00
	stationary	Lefkovitch	$s_A \neq s_Y$	5	0.34	0.67	0.67
	density-dependent	Ricker	$s_A \neq s_Y$	5	1.14	2.28	2.28
	stationary	Lefkovitch	$s_A = s_Y$	4	2.62	2.83	1.19
	stationary	Leslie	$s_A \neq s_Y$	4	3.03	3.65	2.01
	density-dependent	Beverton-Holt	$s_A = s_Y$	4	4.35	6.30	4.67
	trend	eggs and fry	$s_A \neq s_Y$	7	1.06	7.22	10.20
	trend	YOY	$s_A \neq s_Y$	7	1.28	7.67	10.64
	trend	Adults	$s_A \neq s_Y$	7	1.51	8.13	11.10
	density-dependent	Ricker	$s_A = s_Y$	4	5.32	8.24	6.60
	trend	YOY & Adults	$s_A = s_Y$	6	4.13	10.76	12.30
	stationary	Leslie	$s_A = s_Y$	3	7.78	10.84	7.47
	trend	eggs and fry	$s_A = s_Y$	6	6.16	14.82	16.36
	Manchr	density-dependent	Beverton-Holt	$s_A \neq s_Y$	5	0.00	0.00
density-dependent		Beverton-Holt	$s_A = s_Y$	4	2.30	2.17	0.62
density-dependent		Ricker	$s_A \neq s_Y$	5	2.39	4.77	4.77
density-dependent		Ricker	$s_A = s_Y$	4	4.57	6.70	5.15
stationary		Lefkovitch	$s_A = s_Y$	4	8.39	14.34	12.78
stationary		Lefkovitch	$s_A \neq s_Y$	5	8.04	16.08	16.08
stationary		Leslie	$s_A \neq s_Y$	4	9.52	16.60	15.04
stationary		Leslie	$s_A = s_Y$	3	11.39	18.01	14.80
trend		eggs and fry	$s_A \neq s_Y$	7	8.79	22.76	25.55
trend		Adults	$s_A \neq s_Y$	7	9.01	23.21	26.01
trend		YOY	$s_A \neq s_Y$	7	9.07	23.32	26.11
trend		YOY & Adults	$s_A = s_Y$	6	10.51	23.57	25.02
trend		eggs and fry	$s_A = s_Y$	6	10.70	23.94	25.39
WstMtn		density-dependent	Beverton-Holt	$s_A = s_Y$	4	0.14	0.00
	density-dependent	Beverton-Holt	$s_A \neq s_Y$	5	0.00	2.19	3.65
	density-dependent	Ricker	$s_A = s_Y$	4	2.18	4.09	4.09
	density-dependent	Ricker	$s_A \neq s_Y$	5	2.07	6.32	7.79
	trend	eggs and fry	$s_A = s_Y$	6	2.90	10.02	15.10
	trend	eggs and fry	$s_A \neq s_Y$	7	2.76	12.24	19.05
	stationary	Lefkovitch	$s_A = s_Y$	4	7.15	14.02	14.02
	stationary	Lefkovitch	$s_A \neq s_Y$	5	6.07	14.32	15.79
	trend	YOY & Adults	$s_A = s_Y$	6	5.70	15.64	20.72
	stationary	Leslie	$s_A = s_Y$	3	9.23	15.83	14.26
	stationary	Leslie	$s_A \neq s_Y$	4	9.13	17.99	17.99
	trend	YOY	$s_A \neq s_Y$	7	7.42	21.55	28.36
	trend	Adults	$s_A \neq s_Y$	7	7.43	21.59	28.40

## Batten Kill trout population modeling

Table 3.8b. Model selection for brown trout population dynamics. Classes, forms, and model selection statistics as described for Table 3.8a. Structure for the survival among the four size classes was either 1) all constrained to be equal ( $s_{IV} = s_{III} = s_{II} = s_Y$ ), or 2) adult survival differing from juvenile survival with the adult survival rate applying to a) size classes III and IV ( $s_{IV} = s_{III} \neq s_{II} \neq s_Y$ ) or b) only size class IV ( $s_{IV} \neq s_{III} = s_{II} \neq s_Y$ ).  
(continued on next page)

	Class	Form	Structure	$\rho$	L ratio	$\Delta AIC_c$	$\Delta SC$
EaDors	density-dependent	Ricker	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	5	0.00	0.00	0.61
	density-dependent	Beverton-Holt	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	5	0.08	0.16	0.76
	stationary	Leslie	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	4	1.86	1.43	0.00
	stationary	Lefkovitch	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	5	1.68	3.37	3.98
	density-dependent	Beverton-Holt	$s_{IV} = s_{III} = s_{II} = s_Y$	4	2.92	3.55	2.12
	density-dependent	Ricker	$s_{IV} = s_{III} = s_{II} = s_Y$	4	2.93	3.57	2.14
	density-dependent	Ricker	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	5	2.50	4.99	5.60
	density-dependent	Beverton-Holt	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	5	2.52	5.03	5.64
	stationary	Leslie	$s_{IV} = s_{III} = s_{II} = s_Y$	3	4.87	5.22	1.69
	trend	eggs and fry	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	7	0.55	5.88	10.36
	stationary	Lefkovitch	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	5	2.96	5.93	6.54
	trend	YOY	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	7	0.60	6.00	10.47
	stationary	Leslie	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	4	4.26	6.23	4.80
	stationary	Lefkovitch	$s_{IV} = s_{III} = s_{II} = s_Y$	4	4.44	6.59	5.16
	trend	Adults	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	7	1.80	8.39	12.86
	trend	Adults	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	7	2.29	9.38	13.86
	trend	eggs and fry	$s_{IV} = s_{III} = s_{II} = s_Y$	6	3.66	9.69	12.27
	trend	eggs and fry	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	7	3.01	10.81	15.28
	trend	YOY & Adults	$s_{IV} = s_{III} = s_{II} = s_Y$	6	4.45	11.27	13.84
	trend	YOY	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	7	3.45	11.70	16.18
Manchr	density-dependent	Ricker	$s_{IV} = s_{III} = s_{II} = s_Y$	4	0.34	0.00	0.00
	density-dependent	Beverton-Holt	$s_{IV} = s_{III} = s_{II} = s_Y$	4	0.38	0.07	0.07
	density-dependent	Beverton-Holt	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	5	0.00	1.62	3.59
	density-dependent	Ricker	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	5	0.02	1.67	3.63
	density-dependent	Beverton-Holt	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	5	0.18	1.98	3.95
	density-dependent	Ricker	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	5	0.19	2.00	3.97
	stationary	Leslie	$s_{IV} = s_{III} = s_{II} = s_Y$	3	6.56	10.20	8.16
	stationary	Lefkovitch	$s_{IV} = s_{III} = s_{II} = s_Y$	4	5.56	10.42	10.42
	stationary	Lefkovitch	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	5	4.92	11.46	13.43
	stationary	Leslie	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	4	6.46	12.23	12.23
	stationary	Leslie	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	4	6.47	12.24	12.24
	stationary	Lefkovitch	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	5	5.38	12.38	14.34
	trend	Adults	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	7	3.02	12.50	18.17
	trend	Adults	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	7	3.17	12.81	18.49
	trend	YOY & Adults	$s_{IV} = s_{III} = s_{II} = s_Y$	6	6.05	16.11	19.97
	trend	eggs and fry	$s_{IV} = s_{III} = s_{II} = s_Y$	6	6.56	17.14	20.99
	trend	YOY	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	7	5.38	17.22	22.89
	trend	YOY	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	7	6.15	18.76	24.44
	trend	eggs and fry	$s_{IV} = s_{III} \neq s_{II} \neq s_Y$	7	6.46	19.38	25.06
	trend	eggs and fry	$s_{IV} \neq s_{III} = s_{II} \neq s_Y$	7	6.47	19.40	25.07

Batten Kill trout population modeling

Table 3.8b (cont.)

	Class	Form	Structure	$p$	L ratio	$\Delta AIC_c$	$\Delta SC$
WstMtn	density-dependent	Ricker	$S_{IV} = S_{III} = S_{II} = S_Y$	4	0.62	0.00	0.00
	density-dependent	Beverton-Holt	$S_{IV} = S_{III} = S_{II} = S_Y$	4	1.05	0.86	0.86
	density-dependent	Ricker	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	5	0.00	1.09	2.98
	density-dependent	Beverton-Holt	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	5	0.41	1.91	3.80
	density-dependent	Ricker	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	5	0.59	2.28	4.17
	density-dependent	Beverton-Holt	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	5	1.01	3.12	5.00
	stationary	Lefkovitch	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	5	8.28	17.66	19.54
	stationary	Lefkovitch	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	5	8.72	18.53	20.42
	stationary	Lefkovitch	$S_{IV} = S_{III} = S_{II} = S_Y$	4	10.53	19.81	19.81
	stationary	Leslie	$S_{IV} = S_{III} = S_{II} = S_Y$	3	11.84	20.18	18.22
	stationary	Leslie	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	4	11.37	21.51	21.51
	trend	YOY & Adults	$S_{IV} = S_{III} = S_{II} = S_Y$	6	9.42	22.35	26.05
	stationary	Leslie	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	4	11.80	22.37	22.37
	trend	YOY	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	7	8.47	22.92	28.35
	trend	Adults	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	7	8.47	22.94	28.36
	trend	Adults	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	7	9.15	24.29	29.72
	trend	YOY	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	7	10.40	26.79	32.22
	trend	eggs and fry	$S_{IV} = S_{III} = S_{II} = S_Y$	6	11.84	27.18	30.88
	trend	eggs and fry	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	7	11.37	28.74	34.16
	trend	eggs and fry	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	7	11.80	29.60	35.02
CemRun	density-dependent	Beverton-Holt	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	5	0.00	0.00	1.67
	density-dependent	Beverton-Holt	$S_{IV} = S_{III} = S_{II} = S_Y$	4	1.28	0.22	0.00
	density-dependent	Beverton-Holt	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	5	0.94	1.88	3.55
	stationary	Lefkovitch	$S_{IV} = S_{III} = S_{II} = S_Y$	4	5.02	7.70	7.48
	stationary	Lefkovitch	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	5	4.87	9.74	11.40
	stationary	Lefkovitch	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	5	5.00	10.01	11.68
	density-dependent	Ricker	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	5	5.25	10.50	12.17
	density-dependent	Ricker	$S_{IV} = S_{III} = S_{II} = S_Y$	4	6.49	10.65	10.43
	density-dependent	Ricker	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	5	6.13	12.27	13.94
	stationary	Leslie	$S_{IV} = S_{III} = S_{II} = S_Y$	3	9.02	13.46	11.28
	stationary	Leslie	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	4	7.90	13.47	13.25
	stationary	Leslie	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	4	8.67	15.01	14.79
	trend	YOY	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	7	5.71	16.32	21.53
	trend	YOY & Adults	$S_{IV} = S_{III} = S_{II} = S_Y$	6	8.21	18.83	22.31
	trend	Adults	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	7	7.09	19.09	24.30
	trend	YOY	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	7	7.64	20.17	25.38
	trend	Adults	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	7	7.64	20.18	25.38
	trend	eggs and fry	$S_{IV} = S_{III} = S_{II} = S_Y$	6	9.02	20.46	23.94
	trend	eggs and fry	$S_{IV} \neq S_{III} = S_{II} \neq S_Y$	7	7.90	20.70	25.91
	trend	eggs and fry	$S_{IV} = S_{III} \neq S_{II} \neq S_Y$	7	8.67	22.24	27.45

## Batten Kill trout population modeling

Table 3.9. Elasticity matrices for the best plausible stationary models for brook trout (BKT) on left and brown trout (BNT) on right. Elasticities quantify the expected effect on population growth in response to a small proportional change in each of the vital rates, e.g., a 1% increase in each parameter. Values of 0 were omitted for clarity.

	BKT				BNT				
		YOY	II	III		YOY	II	III	IV
EaDors	YOY			0.300	YOY			0.099	0.155
	II	0.300			II	0.254			
	III		0.300	0.100	III		0.254		
					IV			0.155	0.084
Manchr	YOY			0.219	YOY			0.062	0.170
	II	0.219			II	0.232			
	III		0.219	0.343	III		0.232		
					IV			0.170	0.134
WstMtn	YOY			0.165	YOY			0.188	0.180
	II	0.165			II	0.121	0.007		
	III		0.165	0.504	III	0.180	0.078	0.017	
					IV	0.067	0.043	0.070	0.050
CemRun					YOY			0.146	0.185
					II	0.137	0.008		
					III	0.154	0.094	0.017	
					IV	0.039	0.043	0.102	0.074

Elasticity analysis of the best stationary models for brook trout revealed no clear pattern at EaDors and Manchr. However, at WstMtn, population growth responds more strongly to adult survival than to juvenile survival or recruitment (Table 3.9). For brown trout, elasticity was high for YOY and yearling survival at the two upstream stations and for transitions from YOY to size classes II and III as well as recruitment at the two downstream stations.

### 3.3.4.3. Density-dependence

Every subset of the data (i.e., species-station combination) supported models incorporating density dependence. Density-independent counterparts to the leading density dependent models lagged more than 10  $AIC_c$  units back at both Manchester 11/30 and West Mountain, and over 7 units back for brown trout at Cemetery Run. Density dependent and density independent models were essentially tied for both species at East Dorset 7A. For brook trout, all three subsets of the data quite unambiguously supported the compensatory Beverton-Holt model over the overcompensatory Ricker model;  $\Delta AIC_c$  for the Ricker model corresponding to the leading Beverton-Holt model ranged from 2.3 to 4.8. For brown trout, Beverton-Holt and Ricker forms were equally well supported except at Cemetery Run where the Beverton-Holt form outcompeted the Ricker form by over 10  $AIC_c$  units.

The model with uniform survival among size classes performed as well as or better than more complex models for brown trout at Manchester 11/30, West Mountain,

## Batten Kill trout population modeling

and Cemetery Run; at East Dorset 7A, model selection supported modeling YOY and yearlings as having a higher survival rate than brown trout 2 years old and older. Similarly, for brook trout at both East Dorset 7A and Manchester 11/30, model selection supported modeling YOY as having higher survival than larger trout, while, at West Mountain, the model with uniform survival of trout having once attained YOY status provided nearly as good a fit to the data as the more complex model.

### 3.3.4.4. Trend in vital rate(s)

No model incorporating a trend in survival was well supported by the data; this was true for both species at all stations. In every case, models with recruitment being a function of density provided a better fit to the data than models with recruitment changing over time; furthermore, that was accomplished with simpler models (one additional parameter in Eq. 7 or 8 rather than three additional parameters to model a trend). Moreover, those trend models that appeared to be well-supported by the data upon inspection were generally revealed to have been unduly influenced by outliers, e.g., ordinary recruitment of YOY in a year following anomalously low observed density of spawners.

### 3.3.5. Summary of population modeling

The dominant inference from our analysis was that density-dependent survival of eggs and fry best accounts for the observed changes in abundance among the candidate models we considered. As experienced by anglers and reported widely in the news, abundance of “catchable” brown trout has declined dramatically over the years of the surveys reported here. However, abundance of YOY brown trout has not declined nearly as noticeably. Models incorporating compensatory density-dependent recruitment represent that pair of observations very well and, in the process of model selection, outcompeted a variety of other models including those intended to represent the hypotheses depicted in Table 3.6. Regardless of the factor(s) causing the overall population decline, recruitment of YOY trout is compensating to some degree.

Given that survival of trout in the early life history stages appears to have improved as abundance of spawners has declined, we can discount factors affecting those stages as root causes of the decline. Pollution, disease, siltation, and fertility changes are not likely to be causing the decline. Furthermore, since the population has not recovered as fishery managers have imposed stricter fishing regulations, overfishing is not likely to be causing the decline.

The remaining hypotheses to account for the decline are:

- a) Recreational activity is increasing stress, thereby decreasing growth and survival.
- b) Predators are selecting mid-size trout.
- c) Dearth of cover suitable for mid-size trout equates with lower carrying capacity in the stream.

## Batten Kill trout population modeling

Table 4.1. Sample sizes in intended size ranges and ad hoc size ranges delimited after the first sample of trout had been taken.

intended		ad hoc	
Length range (cm)	<i>N</i>	Length range (cm)	<i>N</i>
100-150	81	100-125	35
150-200	35	125-150	46
200-250	9	150-200	35
250-300	2	200+	38

Our population modeling analysis per se sheds little light on which among those is most tenable. All three hypotheses may be true, and there may be synergistic effects among them. For example, in addition to stress from recreational activity, recreationalists may be removing logs from the stream. Between removal of logs by recreationalists and other causes for dearth of cover, trout of a size favored by common mergansers, river otters (*Lontra canadensis*), and other predators may be more exposed to predation.

#### 4. Brown trout mark-recapture study (2003)

We set out to mark a large batch of trout (minimum of 50, goal of 100) in each of four size classes at each of three sites, i.e., a grand total of 600-1200 fish. Size classes for the study were to have been 100-150 mm (approx. 4-6"), 150-200 mm (6-8"), 200-250 mm (8-10"), and 250-300 mm (10-12"). Unfortunately, we were only able to tag 153 trout, and they were not well distributed among the planned size classes (Table 4.1). We resorted to analyzing the smaller data set using an ad hoc size classification that partitioned the sample into four roughly equal classes.

##### 4.1. Survival

We found that apparent survival did not vary with size. Models with size as a covariate ranked below those that did not include size as a covariate (Table 4.2). Furthermore, maximum likelihood estimates of size-specific survival rates varied little (Figure 4.1). The best-supported model allowed for different survival over the three periods, with maximum likelihood estimates of survival 0.29 (95% CI 0.20-0.40) between the June and July electrofishing occasions and 1.00 (with virtually no uncertainty) over the other two periods of our study. Implausible though it may be to have 100% survival from late July through early October (especially when estimated survival in early summer was much lower), the data at least suggested that mortality was greater early in the summer. Furthermore, in fitting population models to the annual survey data, we had estimated that annual survival of trout was about 0.3; taken together, our analyses suggest that most mortality occurs in early summer.

##### 4.2. Growth

We were able to analyze individual growth patterns from the 34 records of brown trout measured and tagged in June and subsequently measured at least one more time. Multiple regression analysis supported a model of growth with the independent variables length-in-June and station. Trout that started the summer at a larger size grew less rapidly, consistent with plateauing growth as depicted by the von Bertalanffy growth function. Furthermore, for a given initial size, trout at West Mountain and Manchester 11&30

## Batten Kill trout population modeling

Table 4.2. Model selection table for brown trout marked with PIT tags, summer 2003. Models are identified by their apparent survival parameter,  $\phi$ , and their recapture probability,  $p$ .  $\cdot$  indicates common parameter values,  $t$  variability related to time, and  $size$  variability related to (ad hoc) size group. Number of parameters is a measure of model complexity, deviance a measure of model (lack of) fit.  $\Delta AIC_c$ , measuring the difference between each model's  $AIC_c$  and the lowest  $AIC_c$  among all of the models, provides a simple scoring of distance from best;  $w_i$  is a transformation of  $\Delta AIC_c$  that can be interpreted as weight of evidence in support of a given model. Cumulative  $w_i$  reveals that 93% of the weight in the data supports apparent survival differing among sampling occasions.

Model	$p$	Deviance	$\Delta AIC_c$	$w_i$	cum( $w_i$ )
Phi(t) p( $\cdot$ )	4	31.76	0.00	0.64	0.64
Phi(t) p(t)	5	31.18	1.53	0.30	0.93
Phi( $\cdot$ ) p(t)	4	36.97	5.22	0.05	0.98
Phi(size*t) p(t)	15	14.74	7.58	0.01	0.99
Phi(size) p(t)	7	34.60	9.26	0.01	1.00
Phi(size*t) p( $\cdot$ )	13	24.50	12.64	0.00	1.00
Phi( $\cdot$ ) p( $\cdot$ )	2	53.80	17.89	0.00	1.00
Phi(size) p( $\cdot$ )	5	50.08	20.43	0.00	1.00

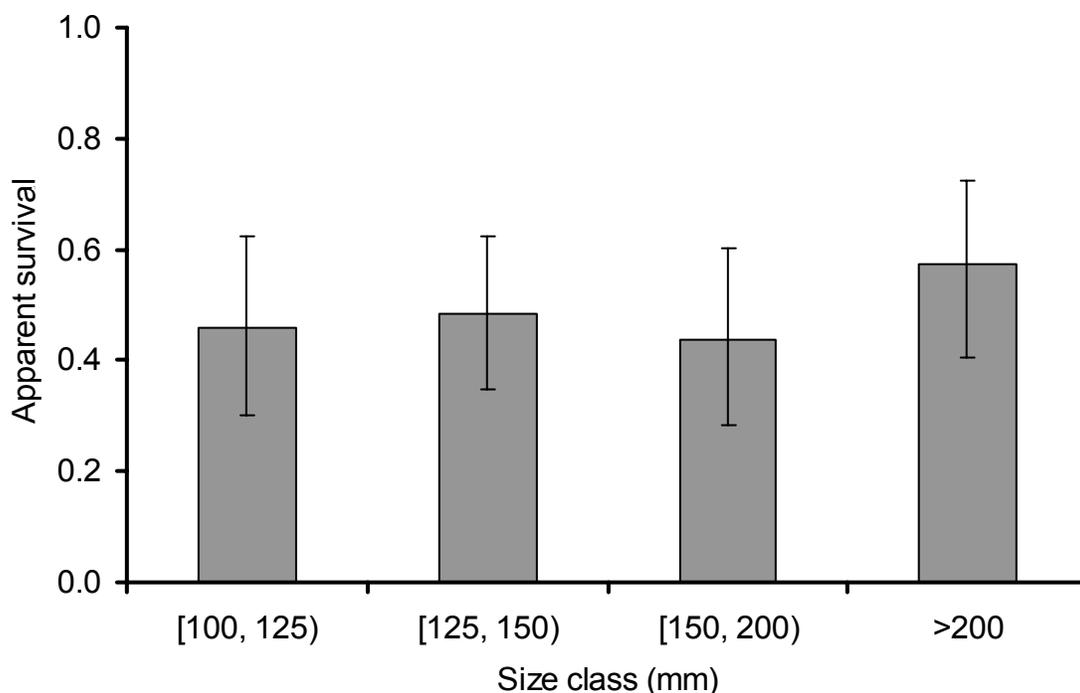


Figure 4.1. Estimated apparent survival from the model Phi(size) p(t), which was the best model that included size-specific survival. Maximum likelihood estimates with 95% confidence intervals.

## Batten Kill trout population modeling

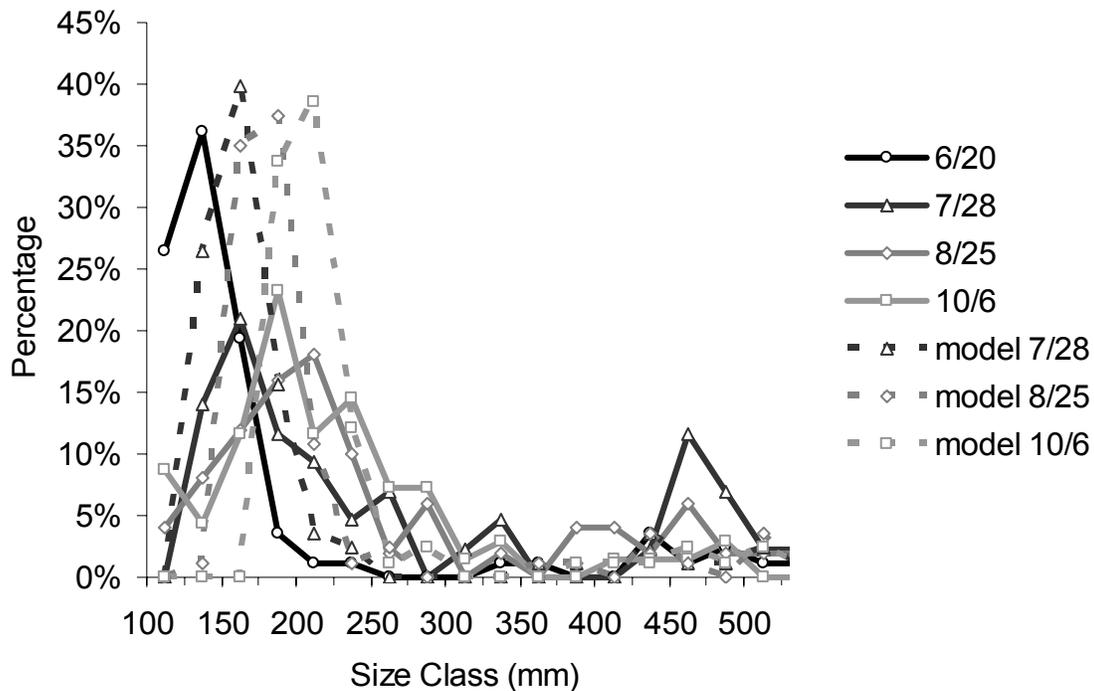


Figure 4.2. Contrast between observed (solid lines) and modeled (dashed lines) size distribution assuming growth with uniform or random mortality across sizes.

appeared to grow faster than those at 313 Bridge with those at East Dorset 7A growing slowest. That was largely consistent with our analysis of the size-at-age data.

### 4.3. Growth and survival together

With a model of individual growth based on the same 34 trout described in the preceding section, we returned to the issue of size-specific survival. We plotted the empirical distribution of trout lengths from each of the electrofishing efforts, then superimposed distributions assuming uniform mortality across sizes, i.e., changing distribution due to growth only (Figure 4.2). The graph shows a large bolus of YOY trout in June, and it shows that bolus shifting to the right as the trout grew over the course of the summer consistent with the growth-only model. However, it also shows that bolus making up a smaller percentage of the population in the July and subsequent samples indicating that mortality was greater for YOY than larger trout. Furthermore, the percentage contribution of YOY to the whole sample remained quite consistent from July onward, indicating that there was high mortality among YOY early in the summer, then quite uniform survival across the sizes later in the summer.

## Batten Kill trout population modeling

### 5. Predator studies (2004)

#### 5.1. Common merganser abundance

##### 5.1.1. BBS

Ducks are relatively infrequently recorded in the USGS Breeding Bird Survey (BBS), yet the BBS data are the only widely available data about duck abundance. We retrieved BBS data from 1966-2004 for the northeastern states and provinces, and analyzed them as presence-absence data. We found that Common Mergansers have been detected in a greater proportion of Vermont routes in recent years (Figure 5.1). Prior to 1990, Common Mergansers went undetected on any route in 19 of 24 years; since 1990, they were detected in 14 of 15 years. Furthermore, they were detected on an increasing proportion of routes over years. We performed a multiple logistic regression analysis of Common Merganser detection with state/ province as a covariate, and plotted the logistic coefficients on a map of the region (Figure 5.2, left). Common Mergansers have been detected with increasing frequency particularly in Vermont, the southern New England states, and New Jersey/ Pennsylvania. That observation is consistent with BBS summary data (Figure 5.2, right), which are given with caveats for infrequently detected species, such as ducks.

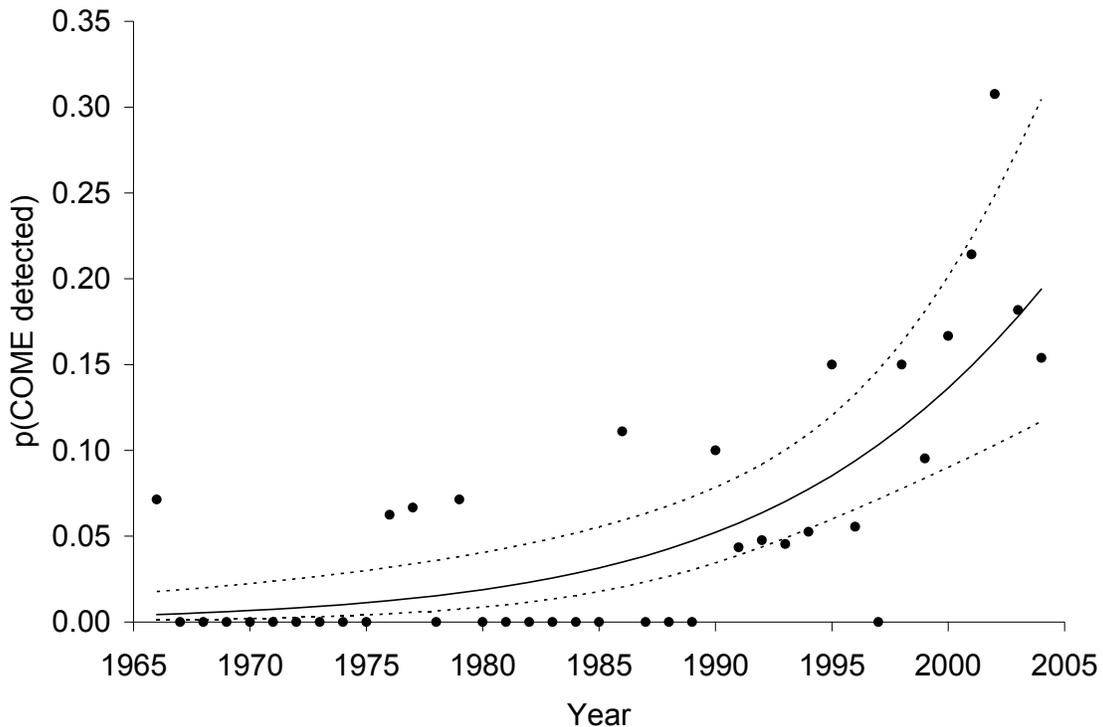


Figure 5.1. Incidence of common mergansers in Vermont BBS routes over the last 39 years. Data plotted on the y-axis are proportion of routes surveyed in a given year on which common mergansers were detected. Curves are fitted logistic regression model (solid) with its 95% confidence interval (dashed).

## Batten Kill trout population modeling

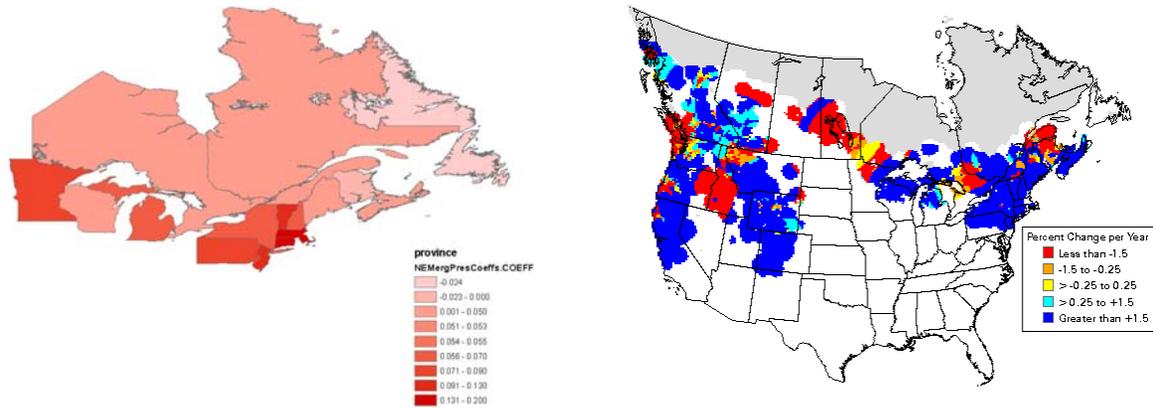


Figure 5.2. Logistic slope parameters estimated for each state or province as in Fig. 4.1 (left) together with BBS-reported trends in common merganser abundance (right).

In summary, BBS data suggest that Common Mergansers have been increasing in incidence in Vermont and across the southern tier of their range.

### 5.1.2. Vermont trout streams

We recorded the presence of common mergansers and belted kingfishers on nearly all of our trips (26 of 30 trips for common mergansers, 28 of 30 for belted kingfishers). Great blue herons (14 of 30), green herons (10 of 30), and hooded mergansers (7 of 30) were the other avian fish predators commonly seen. We recorded

one individual of each of the following species: little blue heron, cattle egret, and osprey. In terms of total numbers, we recorded a grand total of 449 common mergansers, 181 belted kingfishers, and 30-40 great blue herons, green herons, and hooded mergansers.

Average density of common mergansers was 0.39 ind/km (individuals per kilometer) of stream (geometric mean of all 30 counts; includes both adults and hatch-year birds; 95% CI 0.15—1.01) while the same statistic for belted kingfishers was 0.28 ind/km (0.15—0.54). Density of belted kingfishers generally increased monotonically over the course of the summer, i.e., there were more in July than in June and more in August than July (true for 6 of 10 stream stretches; geometric mean density across all stretches June: 0.063 ind/km, July 0.51 ind/km, August 0.72 ind/km; Figure 5.3a). There was no such regular pattern over time in the density of common mergansers (Figure 5.3b).

Mean density of common mergansers did not differ significantly between the Batten Kill and the other streams (Batten Kill: geometric mean 0.67 ind/km, 95% CI 0.12—3.85; other streams: 0.31 ind/km, 0.10—0.98;  $F_{1,8} = 0.56$ ,  $p = 0.48$ ; Table 5.1 and Figure 5.4a). Post-hoc (i.e., unplanned) comparisons based on region (southern: Batten Kill, Mettawee, Poultney, and Castleton rivers; northern: Stevens Branch, Dog, and Winooski rivers; Figure 5.4b) and river size (large: Sunderland and Arlington sections of Batten Kill plus both sections of Winooski River; small: Manchester section of Batten Kill, Mettawee, Poultney, Castleton, Dog rivers, Stevens Branch; Figure 5.4c) did not yield significant differences in total common merganser density, either.

Batten Kill trout population modeling

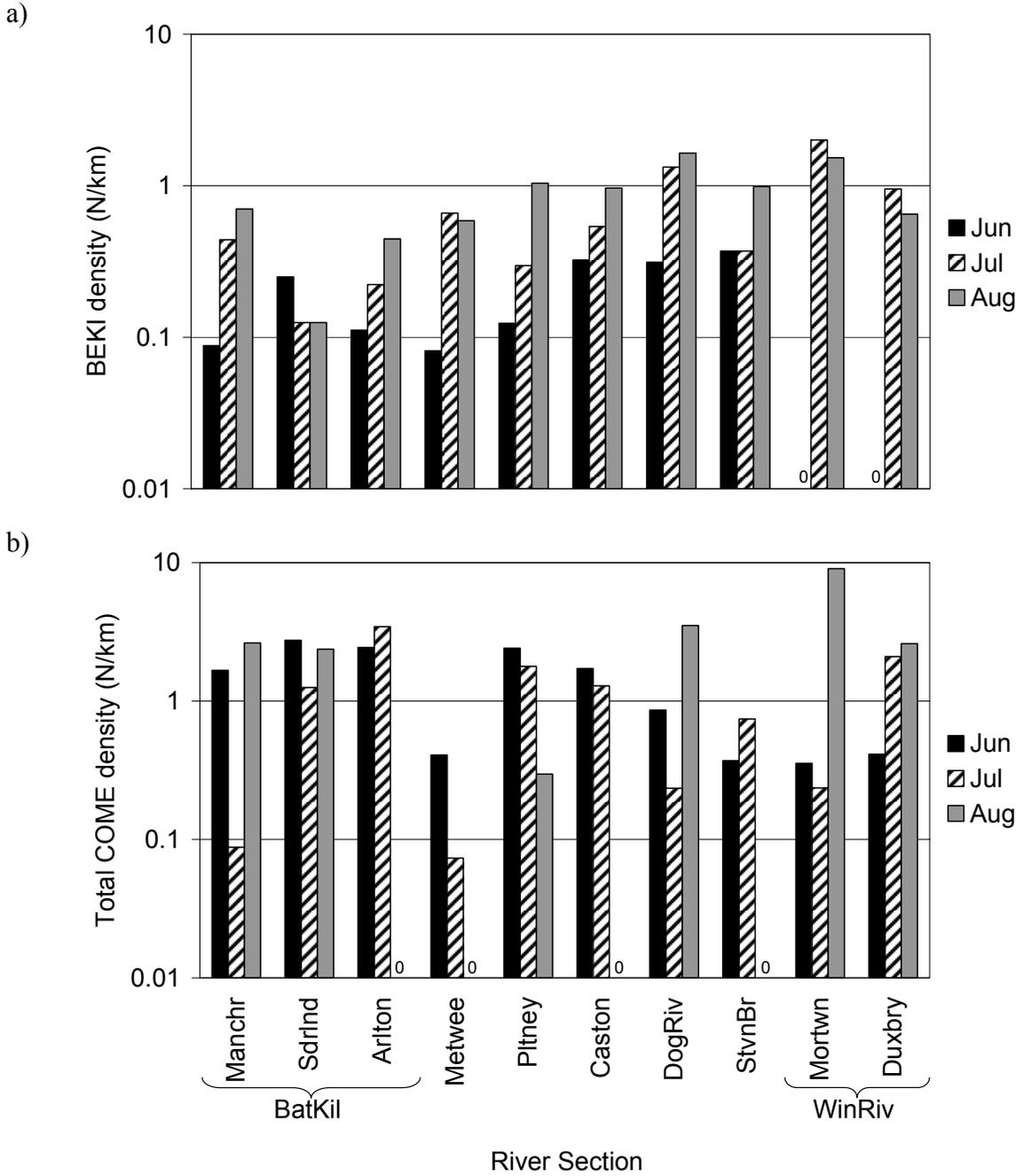


Figure 5.3. Total density of a) belted kingfishers and b) common mergansers on ten stream sections in Vermont, summer 2004; note the logarithmic scale of the y-axis.

## Batten Kill trout population modeling

Table 5.1. Repeated measures analysis of variance for total merganser density. Factor was river (Batten Kill vs. other); response variable was total merganser density (log scale) in each of three months.

Error: Section					
	df	Sum of Sq	Mean Sq	F Value	Pr(F)
River	1	3.6	3.6	0.56	0.48
Residuals	8	51.2	6.4		
Error: Within					
	df	Sum of Sq	Mean Sq	F Value	Pr(F)
Month	2	27.8	13.9	1.88	0.19
River : Month	2	0.8	0.4	0.06	0.95
Residuals	16	118.4	7.4		

Density of females with broods may have been significantly greater on the Batten Kill than on other streams (geometric means with 95% CIs – Batten Kill: 0.061 (0.013-0.29), others: 0.0064 (0.0027-0.015); repeated measures ANOVA:  $F_{1,8} = 5.58$ ,  $p = 0.046$ ; Figure 5.5a). Similarly, the number of recruits to the common merganser population may have been significantly greater on the Batten Kill than on other streams (Figure 5.5b), although for that data set half of the observations yielded a count of zero (we saw no merganser ducklings on 3 of 10 sections in June, 4 sections in July, and 8 sections in August when hatch-year birds were difficult to distinguish from older ducks).

## 5.2. Predator diet

### 5.2.1. Diet of common mergansers

We collected 22 common mergansers from the Batten Kill and the Dog River in July and August (Table 5.2). In addition, a duck hunter who resides on the Dog River collected 4 specimens for us during hunting season in October. To the best of our ability to discern (based on color of the skin on the legs, syrinx development, flight feathers, leg size, and beak size), our sample included 11 hatch-year (HY) and 15 older (AHY, for after hatch-year) ducks.

Among those 26 specimens, we found food items that were identifiable to some degree in all but 4. We found evidence of fish-eating in 13 (50%) of the mergansers, while 14 (54%) had eaten some non-fish food items (5 individuals had both fish and non-fish food items in their stomachs). There were three clearly recognizable trout among the fish we recovered from the mergansers' stomachs: a yearling brown trout and a second-year brook trout from the Batten Kill, and a yearling rainbow trout from the Dog River. There were two other well-digested fish that, judging from the jaw and other parts, appeared to be trout. In nine of the thirteen cases where we found evidence that a merganser had eaten any fish, we only found evidence that it had eaten one fish; another case was a merganser in whose stomach we found a piece of fishing tackle (but no fish

### Batten Kill trout population modeling

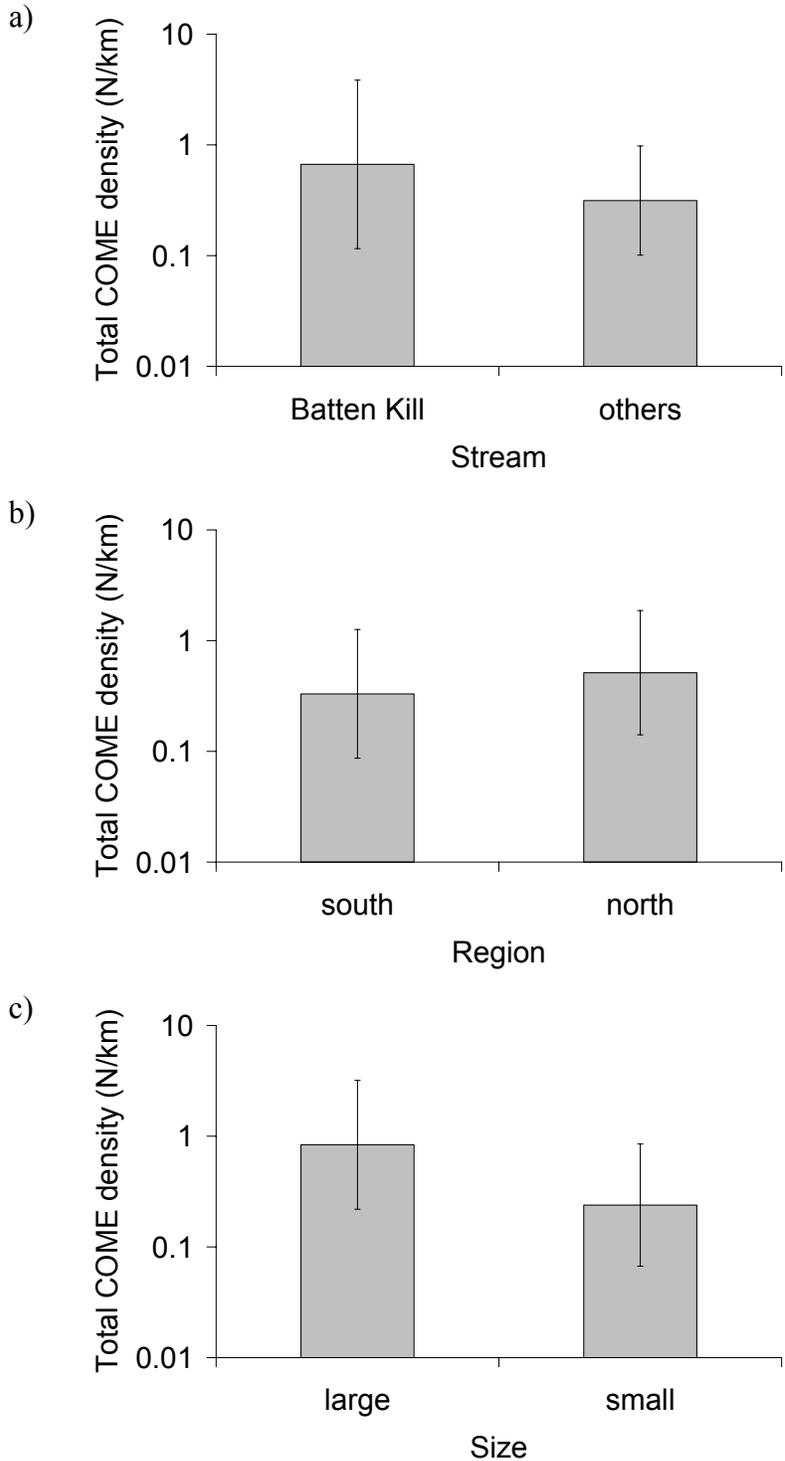


Figure 5.4. Mean density of common mergansers on the study reaches; plotted are geometric mean density of all individuals, i.e., adults and hatch-year ducks. Error bars depict 1.96\*standard error. a) Batten Kill compared to all other streams. b) Southern streams compared to northern streams. c) Large sections compared to small sections.

### Batten Kill trout population modeling

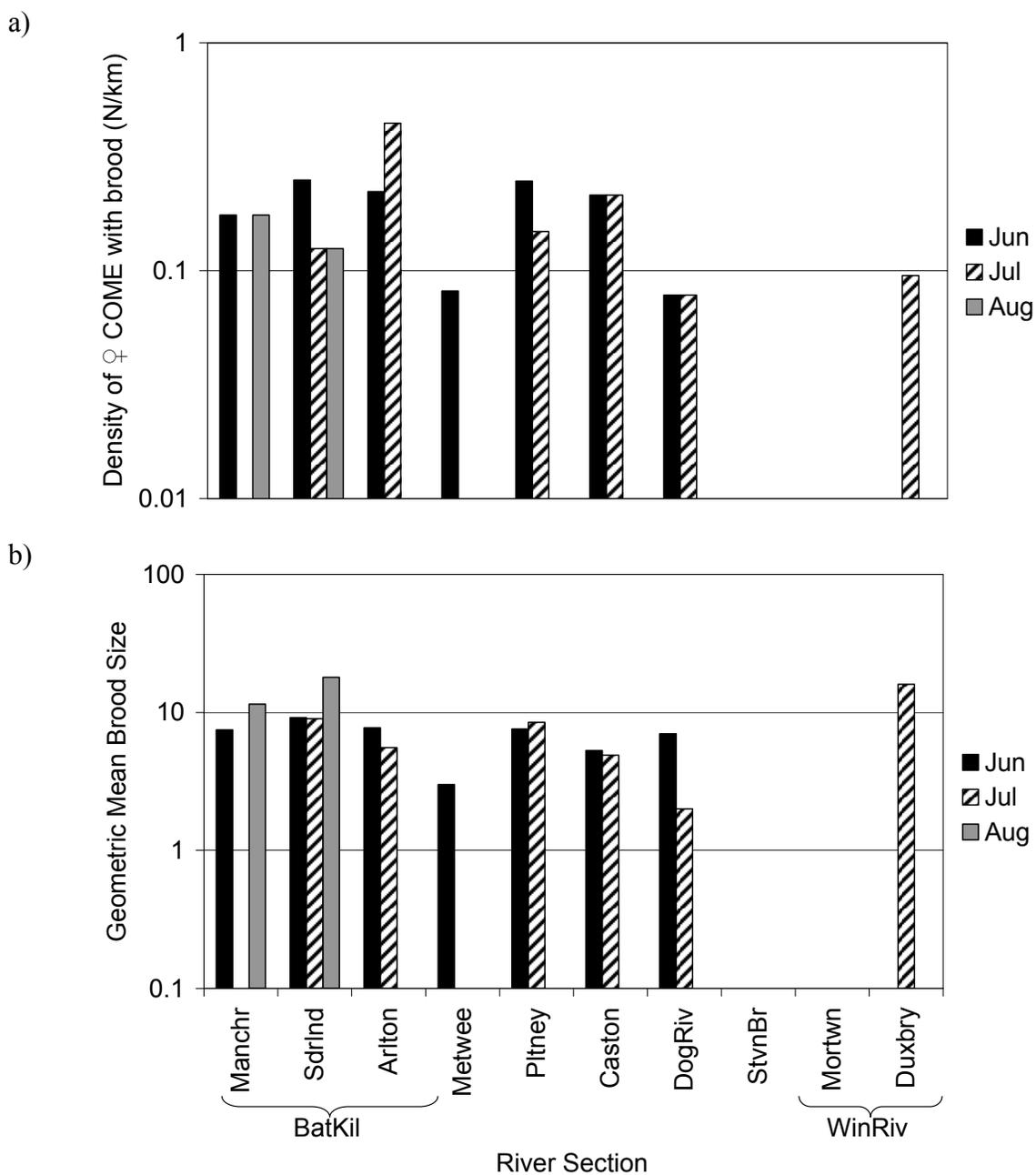


Figure 5.5. Similar data and presentation as Fig. 5.3. a) Density of common mergansers with broods. b) Geometric mean size of broods.

## Batten Kill trout population modeling

Table 5.2. Summary of merganser collecting effort.

Date	Stream	Shotgun-hours	<i>N</i> collected
9 July	Batten Kill	16	6
15 July	Dog River	16	0
20 July	Dog River	18	2
23 July	Batten Kill	8	4
25 August	Batten Kill	16	10
27 August	Dog River	8	0
Total		82	22

bones or flesh). The three other cases involved 2 to 6 small fish (dace and sculpins). Other items recovered from mergansers stomachs included insects (both aquatic and flying, 9 ducks), seeds (6 ducks), crayfish (3 ducks), and amphibians (2 ducks).

HY were just as likely as AHY ducks to have eaten fish (5 of 11 compared to 8 of 15 samples), and they were also just as likely to have eaten trout (2 of 5 compared to 3 of 8 cases). They seemed, however, more likely to have eaten insects or other animals (6 of 11 compared to 4 of 15 samples) and seeds (5 of 11 compared to 2 of 15 samples) than AHY ducks.

A simple estimate, then, is that 38% (5/13) of the fish in merganser's diet is trout. It is noteworthy, also, that the three trout for which we were able to directly estimate size were all in the 6-8" size range about which we had been concerned.

### 5.2.2. Diet of large brown trout

We sampled the stomach contents of 38 large brown trout from the Batten Kill, including its tributary, the Green River, as well as three reference streams (Table 5.3). Our sampling was opportunistic over the course of the summer, including two efforts specifically intended to acquire stomach samples and seven efforts that were piggybacked on other electrofishing efforts under the auspices of VTFW. The general criterion for inclusion in the sample was length  $\geq 300$  mm, but we included two that were just shy of that criterion (298 mm).

We found evidence of piscivory in 17 of the 38 sampled fish. There was clearly no relationship between size and the probability of finding evidence of piscivory (Figure 5.6a;  $F_{1,36} = 0.33$ ,  $p = 0.57$ ;  $\Delta$ AIC for logistic regression model (2 parameters) compared to simple mean model (1 parameter) 1.65). If there was any pattern, it was a slight tendency for larger fish to produce no material following gastric lavage, but that relationship was not significant (Figure 5.6b;  $F_{1,36} = 1.37$ ,  $p = 0.25$ ;  $\Delta$ AIC for logistic model compared to mean model 0.54). We found trout in two samples, a 403-mm brown trout from the Castleton (prey recognized based on jaw morphology, brown trout versus brook trout undetermined, total length estimated 50 mm) and a 518-mm brown trout from the Batten Kill (prey was brown trout recognized based on skin, total length 50 mm; Figure 5.7).

## Batten Kill trout population modeling

Table 5.3. Summary of trout stomach sampling effort.

Date	Stream	Station	Trout sampled*
23 Jun	Batten Kill	Scales	3
		Wilbur Bridge	1 <sup>†</sup>
2 Jul	Mettawee River	Rosenbauer	3
22 Jul	Batten Kill	313 Bridge	5
4 Aug	Castleton River	Upper	7 <sup>‡</sup>
12 Aug	Mettawee River	above Buttermilk Falls	1
24 Aug	Batten Kill	Manchester 11/30	1
26 Aug	Batten Kill	Cemetery Run	4
		West Mountain	2
15 Sep	Dog River	Northfield wellfields	4
27 Oct	Green River	pullout	6
	Batten Kill	Union St	1
Total			38

\* General criterion: length  $\geq$  300 mm  
<sup>†</sup> Length 298 mm  
<sup>‡</sup> One 298 mm; also one 308 mm brook trout sampled but not included in tally

### 5.2.3. Comparison with the community of forage fish

We sampled the forage fish community opportunistically throughout the course of the summer. Detailed data have been submitted to the Vermont Nongame & Natural Heritage Program according to the conditions of our scientific collecting permit. For purposes of the question at hand, the relevant variable is essentially the relative abundance of young-of-year and yearling trout in the communities. Trout generally make up less than 15% of the forage fish community (Table 5.4.) The most abundant species were blacknose dace (*Rhynchichthys atratulus*), longnose dace (*R. cataractae*), and slimy sculpin (*Cottus cognatus*).

Our data about the diet of common mergansers indicated that trout were relatively more abundant in the predators' stomachs than in the stream. Trout made up a higher proportion of fish in common merganser stomachs (5 of 13, or 38%) than in any of our 11 electrofishing samples (maximum 28 of 87, or 32%). That suggests that mergansers preferentially feed on trout. On the other hand, of the 17 large brown trout where we found evidence of piscivory, only 2 (12%) had eaten trout, well within the observed range of relative abundance of trout in forage fish communities. That observation does not constitute evidence of cannibalism being a preferred foraging strategy on the part of large brown trout.

### Batten Kill trout population modeling

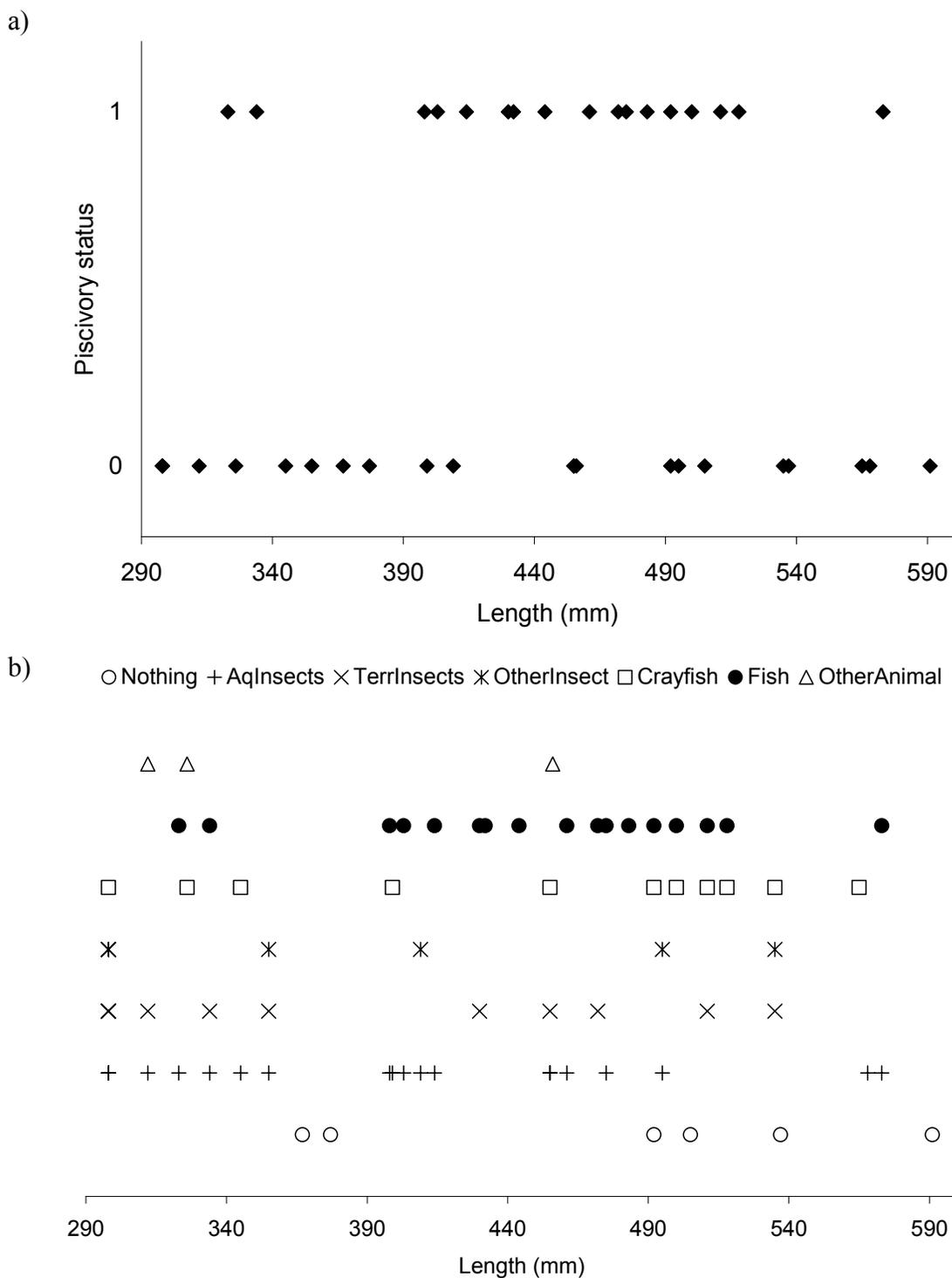


Figure 5.6. a) Piscivory status (1 = fish or fish parts found in stomach contents, 0 = no evidence of piscivory found) for 38 brown trout sampled summer 2004. b) Summary of diet items by size of brown trout. AqInsects = aquatic insect, TerrInsects = terrestrial insects, OtherInsects = parts not identifiable to order, e.g., just a flight wing; OtherAnimal included two-lined salamander, snails, a leech, and a millipede.

## Batten Kill trout population modeling

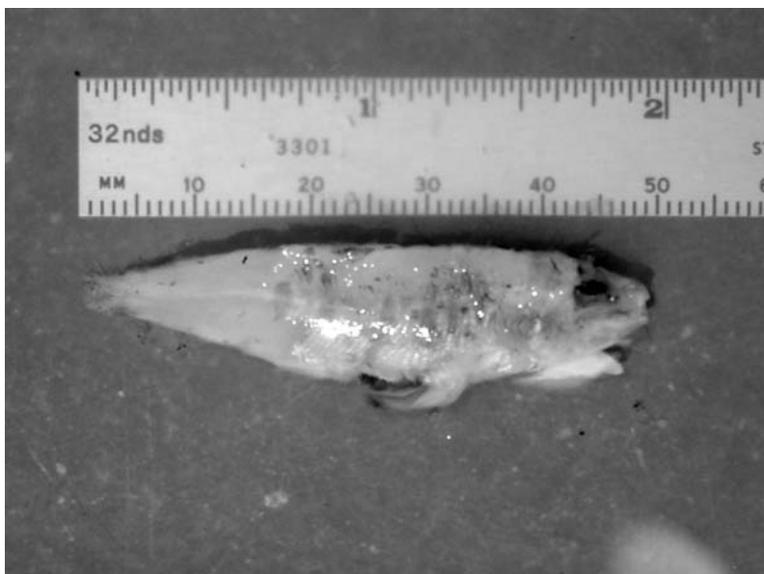


Figure. 5.7. Young-of-year brown trout from stomach contents of larger brown trout (518 mm) removed by gastric lavage, 24 August 2004, Batten Kill, Manchester 11/30 station.

Table 5.4. Summary of forage fish community sampling, 2004. Efforts grouped by stream and arranged from upstream to downstream.  $N$  is the total number of fish in the sample. For each of the three species of trout as well as the three species cumulatively, the table shows counts and proportions of total ( $p$ ).

Date	Stream	Station	$N$	BNT ( $p$ )	BKT ( $p$ )	RBT ( $p$ )	all trout ( $p$ )
24-Aug	Batten Kill	East Dorset 7A	165	10 (0.06)	16 (0.10)	0 (0.00)	26 (0.16)
23-Jul	Batten Kill	above 313 Bridge	122	4 (0.03)	2 (0.02)	0 (0.00)	6 (0.05)
16-Jun	Batten Kill	West Mountain	182	0 (0.00)	2 (0.01)	0 (0.00)	2 (0.01)
26-Aug	Batten Kill	West Mountain	170	11 (0.06)	10 (0.06)	0 (0.00)	21 (0.12)
26-Aug	Batten Kill	Cemetery Run	87	18 (0.21)	10 (0.11)	0 (0.00)	28 (0.32)
2-Jul	Metawee River	Rosenbauer property	45	1 (0.02)	0 (0.00)	1 (0.02)	2 (0.04)
12-Aug	Metawee River	Above Buttermilk Falls	123	15 (0.12)	0 (0.00)	19 (0.15)	34 (0.28)
3-Aug	Poultney River	East Poultney	239	27 (0.11)	0 (0.00)	0 (0.00)	27 (0.11)
14-Sep	Dog River	Station 555	151	2 (0.01)	0 (0.00)	9 (0.06)	11 (0.07)
15-Sep	Dog River	Below Lusher's	105	3 (0.03)	0 (0.00)	2 (0.02)	5 (0.05)
30-Jun	Dog River	Powerline below Rte 12 br	163	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)

## Batten Kill trout population modeling

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