

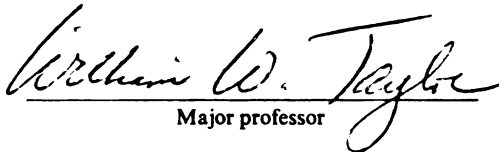
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Reproduction, Early Life History,
and Recruitment of Rainbow Smelt
in St. Martin Bay, Lake Huron
presented by

Russell W. Brown

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of the requirements for

Ph.D. degree in Fisheries


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**REPRODUCTION, EARLY LIFE HISTORY, AND RECRUITMENT OF
RAINBOW SMELT IN ST. MARTIN BAY, LAKE HURON**

By

Russell W. Brown

A DISSERTATION

**Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of**

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

1994

ABSTRACT

REPRODUCTION, EARLY LIFE HISTORY, AND RECRUITMENT OF RAINBOW SMELT IN ST. MARTIN BAY, LAKE HURON

By

Russell W. Brown

Rainbow smelt (*Osmerus mordax*) provide an important source of forage for introduced salmonines, and are considered to be an important competitor and predator of native Great Lakes species. Historical records reflect unstable levels of rainbow smelt abundance in the upper Great Lakes, with much of this instability in population abundance due to highly variable year class formation and recruitment. Spawning rainbow smelt were sampled in four tributaries to St. Martin Bay, Lake Huron to measure population characteristics of spawning populations and to estimate egg deposition and larval outmigration. Age composition of tributary spawning rainbow smelt from 1991-1993 was significantly younger than age compositions reported in the 1970's. Diel patterns of larval outmigration were consistent between tributaries with greater than 90% of larval outmigration occurring between 2100 and 0600 hours. Of the four study tributaries, the Carp River dominated larval production, producing 72.8%, 74.8%, and 96.4% of the total larval output from 1991 to 1993, respectively. The four tributary streams produced a total of 46 million larvae in 1991, 13 million larvae

in 1992, and 32 million larvae in 1993, with annual differences due to variable levels of egg deposition and survival between years.

Larval and juvenile stages of rainbow smelt were sampled in St. Martin Bay, Lake Huron from 1991 to 1993 to estimate relative abundance and growth and survival rates. In 1991, high tributary larval production and high degree of spatial overlap between larvae and zooplankton prey resources resulted in production of a strong year class comprised mainly of tributary produced progeny. In 1992, low tributary production of larvae, low densities of zooplankton prey resources, and poor spatial overlap between larval populations and prey resources resulted in relatively poor year class comprised mainly of lake spawned larvae. In 1993, intermediate levels of tributary larval production and a high degree of spatial overlap with moderate densities of zooplankton prey resources resulted in production of a moderate year class, with approximately 65% of recruits hatching during tributary outmigration. Interannual variation in year class strength of rainbow smelt in St. Martin Bay resulted primarily from variable contributions of tributary spawned larvae between years.

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Dissertation Introduction

Rainbow smelt (*Osmerus mordax*) were first introduced into Lake Michigan through a single stocking in Crystal Lake, Michigan in 1912 and spread throughout the Great Lakes by the mid 1930's (Van Oosten 1937). In the upper Great Lakes, rainbow smelt rapidly became an important component of the recreational and commercial fisheries. During the late 1930's, the recreational and commercial fisheries harvested 2.5 and 1.8 million kilograms annually in the Michigan waters of the Great Lakes (Van Oosten 1947). Currently, rainbow smelt support a popular recreational dip net fishery during spring spawning runs (Raab and Steinnes 1979), although the commercial fishery in the Michigan waters of the Great Lakes has declined significantly from historical levels. In 1993, commercial harvest of rainbow smelt from the Michigan waters of Lakes Superior, Michigan, Huron and Erie represented less than 5% of the total commercial fishery by weight and approximately 1% by value (Kinnunen 1994).

Currently, rainbow smelt provide an important source of forage for introduced salmonines (chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), and pink (*O. gorbuscha*) salmon, brown trout (*Salmo trutta*) and steelhead (*O. mykiss*) and native predators (lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*)) in the upper Great Lakes (Stewart et al. 1981, Hatch et al. 1981, Johnson et al. 1994). Growth and survival rates of introduced salmonines have declined during the 1980's (Eck and Wells 1983), resulting in concerns over the possible depletion of the forage base in the Great Lakes (Stewart et al. 1981, Johnson et al. 1994).

In addition to its role as a prey species, the rainbow smelt is also considered to be a competitor and predator of native Great Lakes species (Crowder 1980). Rainbow smelt have the potential to compete with native coregonines because of broad overlaps in distribution and diet with lake herring *Coregonus artedii* (Anderson and Smith 1971), deepwater ciscos (*C. sp.*), and lake whitefish (*C. clupeaformis*). Although rainbow smelt in the Great Lakes feed mainly on invertebrates (Gordon 1961, Foltz and Norden 1977, Anderson and Smith 1971), their diet also includes larval and juvenile fishes (Hale 1960, Price 1963). Predation by adult smelt has been documented for age 0+ alewives (*Alosa pseudoharengus*, O'Gorman 1974), lake herring (Selgeby et al. 1978, Loftus and Hulsman 1986), bloaters (*C. hoyi*, Stedman and Argyle 1985), slimy sculpin (*Cottus cognatus*, Brandt and Madon 1986), and lake whitefish (Loftus and Hulsman 1986). Predation by rainbow smelt and alewife has been hypothesized to be a major mechanism for the collapse of native coregonines in the upper Great Lakes (Crowder 1980) and inland waters (Evans and Loftus 1987).

Historical records reflect unstable levels of rainbow smelt abundance in the upper Great Lakes over the past sixty years with periods of marked increases followed by precipitous declines (Baldwin et al. 1979). Standardized bottom trawl surveys by the National Biological Survey (Argyle 1994) indicate that lake-wide indices of adult rainbow smelt abundance have experienced two major peaks (1981 and 1987) since 1973 (Figure 1). Indices of age 0+ rainbow smelt indicate variable levels of recruitment have occurred, with strong year classes (Catch per Unit Effort (CPUE) > 800 fish/tow) occurring in 1980, 1981, 1982, and 1986

(Figure 1). Recently, the species composition of prey biomass in Lakes Michigan and Huron has shifted from exotic alewife and rainbow smelt to native bloaters (*Coregonus hoyi*; Argyle 1994).

Fluctuations in the abundance of rainbow smelt have been attributed to cannibalism (Regier et al. 1969), disease (Van Oosten 1947), parasitism (Nepszy et al. 1978), and climatic factors during spawning including wave action and water temperatures (Rothschild 1961; Rupp 1965). An annual cycle of alternating year-class dominance in Lake Erie between 1963 and 1974 has been attributed to cannibalism by yearling rainbow smelt on age 0+ larvae and juveniles (Henderson and Nepszy 1989). The role of rainbow smelt as a key forage species, predator, and competitor of other Great Lakes fishes underscores the importance of identifying and understanding variability in abundance and factors influencing their recruitment.

Variability in year class strength of many pelagic and demersal fish species in large aquatic systems is primarily caused by variation in growth and survival during the early life stages (Houde 1987, Fritz et al. 1990). Relatively small changes in growth and survival rates of these early stages can translate into large annual fluctuations in resulting year-class strength (Houde 1987). My hypothesis is that a combination of abiotic and biotic factors occurring between spawning and the demersal juvenile stage is important in controlling the year class strength of rainbow smelt in the upper Great Lakes. The goal of this project was to measure important parameters during the early life history stages to allow for the

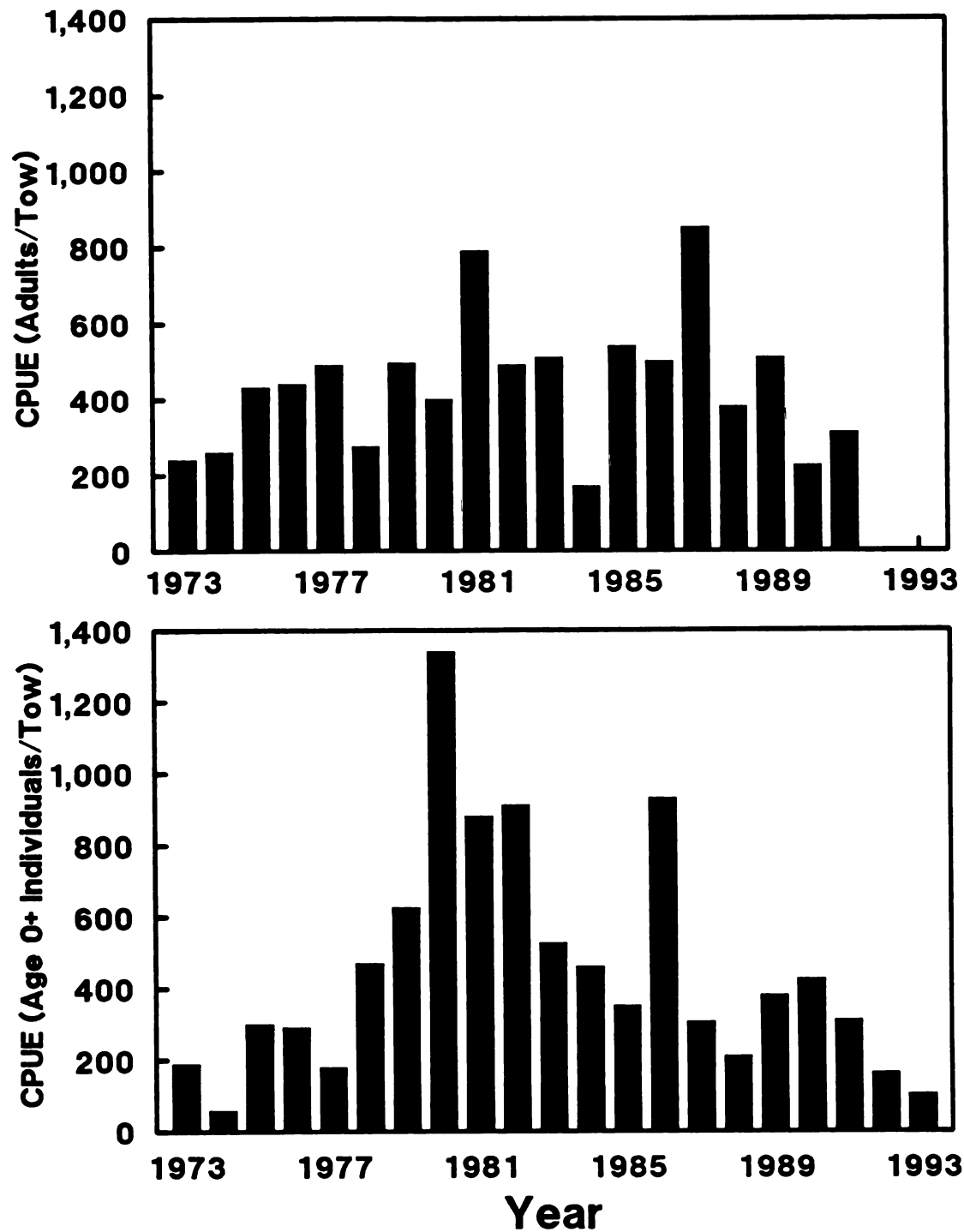


Figure 1. Catch per unit effort index of adult (Panel A) and age 0+ rainbow smelt (Panel B) indexed by the National Biological Survey standardized trawl survey program at five sites on Lake Huron.

identification of causal mechanisms controlling year class formation in rainbow smelt. My specific objectives are to:

1. Measure vital statistics of tributary spawning rainbow smelt populations including size and age composition, length-weight relationships, and sex ratios.
2. Estimate seasonal patterns in egg deposition and larval outmigration from tributary streams.
3. Measure diel, spatial, and seasonal patterns in abundance, growth and survival of larval rainbow smelt in Lake Huron.
4. Describe patterns of larval distribution in relation to distributional patterns of larval zooplankton prey resources.
5. Estimate the relative contribution of tributary vs. lake spawned larvae to overall recruitment.

Study Area

I selected the St. Martin Bay area of northern Lake Huron as a study area based on estimated strong production of rainbow smelt in this region of Lake Huron (Argyle 1982), historically consistent spawning in area tributaries, and reported high densities of larval rainbow smelt (O’Gorman 1983). St. Martin Bay is located in the northwest region of Lake Huron along the southern shore of Michigan’s upper peninsula (Figure 2). This oligotrophic bay has an average depth of 8-m with gradually increasing depths to a maximum of 30-m. Water circulates in a clockwise direction which is driven by an offshoot eddy from the Straits of Mackinac. The bay generally is ice-covered from January to March (Assel et al. 1983). Surface water temperature ranges from 12 C to 20 C during the summer, and thermal stratification is rare due to wind and current patterns.

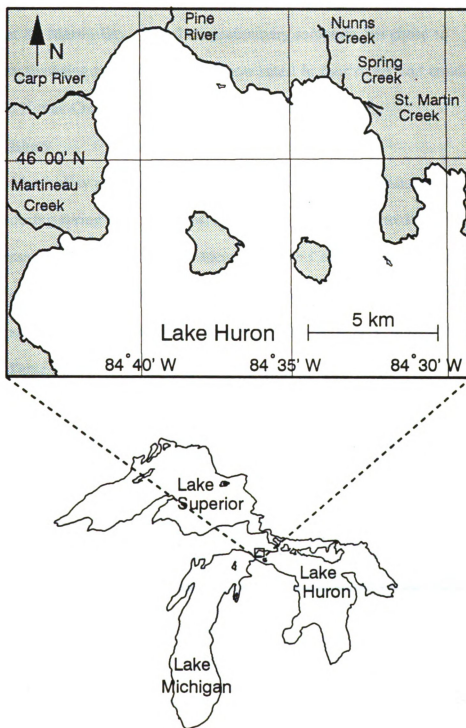


Figure 2. Map showing the location of the study area in St. Martin Bay, Lake Huron.

Three large (3rd and 4th order) and several smaller (1st and 2nd order) tributaries enter St. Martin Bay. Based on preliminary sampling, we chose to sample tributary spawning populations of rainbow smelt in four rivers and creeks, the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek.

Recreational Fishery

The St. Martin Bay area hosts a recreational dip net fishery that targets rainbow smelt during spring spawning runs. During my study (1991 to 1993), the majority of recreational fishing effort was focused on the Carp River, where up to 1000 people participated in the fishery on peak weekend nights. The Carp River supported a seasonal average of 16,542 hours of recreational fishery activity from 1991 to 1993 (Table 1).

Table 1. Available stream length and area, peak nightly participation, and average total seasonal effort of recreational anglers pursuing rainbow smelt on four study tributaries.

Tributary	Stream Length Available to Fishery (m)	Stream Area Available to Fishery (m ²)	Peak Participation (people)	Average Seasonal Total Effort (hours)
Carp River	> 2000.0	> 10,000.0	1043	16,542
Nunns Creek	59.5	757.1	221	4,876
Spring Creek	98.0	227.0	34	532
St. Martin Creek	149.3	720.1	47	957

Nunns Creek is a second popular dipping area in the bay, although the fishery is limited to the lake area and a stream length of approximately 60-m due to private property. Nunns Creek supported a seasonal average of 4,876 hours of fishery effort from 1991 to 1993 with up to 221 people participating in the fishery on peak weekend nights. Most of the smaller tributaries in the bay receive at least token pressure from the recreational fishery. Recreational fishers participating in the fishery are highly mobile and move between stream locations until they are able to locate spawning runs of rainbow smelt. I frequently encountered anglers who had checked streams between Detour and Naubinway, Michigan, a distance in excess of 150 km, in a single night.

Dissertation Overview

The purpose of this study was to follow three annual cohorts of rainbow smelt (1991 to 1993 year classes) from spawning and outmigration from tributaries through the pelagic larval stage until the cohort had become demersal juveniles in St. Martin Bay. There were three main areas of research effort: 1. measurement of vital statistics for tributary spawning stocks; 2. estimation of spawner abundance, egg deposition, and larval outmigration; and 3. estimation of larval abundance, growth and survival; and juvenile recruitment in St. Martin Bay. I have organized this dissertation into three chapters to focus on each of these research areas.

In Chapter 1, I summarize findings regarding vital statistics of tributary spawning populations including size composition, age composition, length-weight relationships, and sex ratios. These data provided information on the status of

adult populations in the St. Martin Bay region that could be compared to other regions in the Great Lakes for the same time period and for other time periods in Lake Huron.

In Chapter 2, I report on findings regarding spawner abundance, egg deposition, larval outmigration, and egg to outmigrant survival. During three spawning seasons (1991 to 1993), I indexed the relative abundance of spawners and measured egg deposition in four representative tributaries in St. Martin Bay. Because the recreational fishery appeared to have a significant impact on the density of eggs deposited, I also quantified the effect that the fishery had on egg densities. I also describe diel and seasonal patterns in larval outmigration from each of the four study tributaries, which allowed for estimation of total larval outmigration from each tributary and egg to hatching estimates of survival.

In Chapter 3, I describe spatial patterns in the distribution of larval rainbow smelt and their zooplankton prey resources during the pelagic larval period. Once age 0+ rainbow smelt had become demersal (August-September), I indexed the relative strengths of annual cohorts through a standardized bottom trawl survey. One of the focuses of Chapter 3 was to identify unique characteristics of recruited juvenile rainbow smelt. Lake spawning populations were assumed to spawn later and incubate longer due to colder lake temperatures, creating temporal segregation in the hatch dates of tributary and lake spawned larvae. By analyzing sagittal otolith microstructure, I was able to determine the hatch date distribution of recruited juveniles. I was able to distinguish between early and late hatching larval cohorts because I had accurate

measurements of the timing of spawning and larval outmigration of tributary spawning rainbow smelt (Chapter 2). Finally, I describe interannual patterns in larval growth, larval survival, and relative contributions of tributary and lake spawned larvae, and relate these to juvenile recruitment.

**CHAPTER 1: VITAL STATISTICS OF RAINBOW SMELT SPAWNING IN
FOUR TRIBUTARIES OF ST. MARTIN BAY, LAKE
HURON**

Abstract

Spawning rainbow smelt were sampled in four tributaries to St. Martin Bay, Lake Huron to estimate population characteristics including size distribution, age composition, length-weight relationships and sex ratio. Spawners were collected twice nightly with dip nets from the Carp River, Nunns Creek, Spring Creek and St. Martin Creek throughout the spawning season from 1991 to 1993. Rainbow smelt were aged by examining prepared cross-sections of pectoral fin rays. Age data were used to construct age-length keys to partition the entire sample of fish into age classes based on length. Length-frequency distributions were not significantly different ($P > 0.05$) between the Carp River and Nunns Creek. Length-frequency distributions of fish sampled from Spring and St. Martin Creeks were significantly ($P < 0.05$) larger than those from the Carp River and Nunns Creek due to the presence of larger, older spawning fish. The slope of length-weight regression equations decline annually from 1991 to 1993, indicating a decline in the average condition factor of spawners. Samples of spawning fish were dominated by males, but the percentage females increased in larger size and older age classes. Age composition of rainbow smelt from 1991 to 1993 was significantly younger than age compositions reported in the 1970's. Because only two age classes (2+ and 3+) of rainbow smelt contain greater than 90% of the

adult population, production of several consecutive weak year classes could result in substantial declines in the population abundance of rainbow smelt.

Introduction

The rainbow smelt is an important forage and recreationally-sought species in Lake Huron. Over the past two decades, the absolute biomass and the biomass of rainbow smelt relative to other forage species have both declined. From 1975 to 1984, rainbow smelt represented approximately 60% of the total biomass of forage fish in Lake Huron (Argyle 1994). Since 1986, the relative biomass of rainbow smelt has declined steadily from 60% to less than 20% of the total forage biomass in Lake Huron (Argyle 1994). These trends are due to a series of relatively weak year classes of rainbow smelt since 1986 (Figure 1) causing a decline in total biomass, and increases in the total biomass of bloaters (Argyle 1994).

Declines in rainbow smelt populations have been attributed to a number of factors including predation by stocked salmonines, disease (Van Oosten 1947), parasitism (Schaefer et al. 1982, Henderson and Nepszy 1989), poor recruitment associated with environmental conditions, and exploitation by recreational fisheries. Salmonine stocking levels have increased significantly during the past two decades, resulting in increased forage consumption (Johnson et al. 1994). A disease outbreak is thought to have resulted in a dramatic die-off of rainbow smelt in 1943 to 1944 (Van Oosten 1947), while parasitic fungi are thought to

cause significant mortality in adult rainbow smelt in Lake Superior (Schaefer et al. 1982) and Lake Erie (Henderson and Nepzy 1989). Exploitation by recreational dip net fisheries has been demonstrated to have significant effects on the population dynamics of exploited rainbow smelt populations in localized areas. Frie and Spangler (1985) examined vital statistics of rainbow smelt in South Bay, Lake Huron during a period of intensive fishing (1948 to 1957) and after exploitation had ceased (1958 to 1970). They found that the modal ages of spawning rainbow smelt shifted from 2 to 3 during intensive exploitation to 3 to 4 after exploitation had ended. Total annual mortality decreased from 90% during a period of exploitation to 67% after exploitation ceased, and relative stock sizes increased sharply after 1957.

Population dynamics of rainbow smelt in the Great Lakes have been assessed from spring spawning runs, when concentrations of sexually mature fish can be sampled using a variety of sampling gears (Luey and Adelman 1984, Frie and Spangler 1985, Gebhardt 1993). Sampling during this time period allows for representative sampling of the sexually mature portions of tributary spawning populations. Estimates of vital statistics including size and age compositions, sex ratios, and length-weight relationships can serve as a measure of the current status of spawning populations. Comparison of current estimates with estimates from other areas of the Great Lakes during the same time period and estimates obtained during different time periods provides information about the current status of spawning populations. Estimates of the age composition allow for

assessment of the sensitivity of adult stocks to variation in year class strength and recruitment.

The goal of this study was to estimate vital statistics of populations of rainbow smelt spawning in tributaries to St. Martin Bay, Lake Huron. My specific objectives were to:

1. Determine the size and age distributions of spawning rainbow smelt.
2. Identify tributary, size-related, and age related patterns in the sex ratios of spawning rainbow smelt.
3. Develop length-weight relationships of rainbow smelt from four tributaries to St. Martin Bay.

Methods

Sampling of Spawning Adults

Sampling of spawning adult rainbow smelt was conducted in four tributaries to St. Martin Bay: the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek (Figure 2). In each tributary, sampling was conducted nightly to assess the vital statistics of spawning populations of rainbow smelt. Sampling was conducted from April 12 to May 1, 1991, from April 15 to May 4, 1992, and from April 14 to May 3, 1993 on all tributaries, except for 1991 when Spring Creek was not sampled. When rainbow smelt were present, samples of fish were collected using a long handled (1.3-m) smelt dip net (8-mm mesh).

Previous investigators have found that the age and size composition of spawners changes on a nightly and seasonal basis. To obtain representative

samples of spawning populations on a nightly basis, tributary samples were collected twice nightly, once between 22:00 and 01:00 hours and again between 01:00 and 04:00 hours. During each sampling period, I sampled for 45 minutes or until I had collected a timed sample of 100 fish. Length (nearest mm) and weight (nearest 0.1 g) were recorded from each fish. Because all fish sampled were in spawning condition, the sex of sampled fish was determined through extrusion of gametes.

To obtain representative samples for age determination throughout the spawning season, I collected pectoral fin samples from a maximum subsample of 50 rainbow smelt per sampling period. This allowed for sampling of bony parts to occur throughout the course of the spawning run (period ranging from 6 to 11 nights). Approximately 500 (range 481 to 504) fin samples were collected on each tributary in each year.

Fin Ray Aging

Pectoral fin ray samples were chosen for age analysis for several reasons. First, scale samples collected from spawning males were difficult to age due to the presence of nuptial tubercles. Second, some fish lost scales during handling prior to sample processing. I subsampled collected fin ray samples because of extensive time involved in the preparation and analysis of fin ray samples. I prepared and analyzed a subsample of fin rays that was weighted by the overall length and sex distribution of rainbow smelt collected throughout the spawning season. These weighted samples were produced for each sampled tributary in each year ($N =$

11). Subsample size was 160 samples and usable samples ranged from 134 to 151 samples per tributary for each year (Table 2).

Dried fin rays were placed in a plastic mold and were embedded in electron microscopy embedding resin (EmBed-812). Each fin ray was then sectioned using a low-speed radial arm saw with a wafer-thin diamond blade at the base on the fin-body margin. Each section was then polished with progressively finer wet-dry sandpaper (220-, 400-, 600-grit) with final polishing using aluminum polishing powder and a polishing cloth. Each section was examined under 10X to 50X magnification to identify annuli. Because fin samples were collected in early spring prior to significant growth, the margin of the fin ray was assumed to represent the last annuli.

Data Analysis

I used Kolmogorov-Smirnov tests (Siegel 1956, Snedecor and Cochran 1980) to detect differences in the length frequency distribution between males and females within tributaries and years, between years within tributaries (pooled sexes), and between streams within years (pooled sexes). When significant differences were found in the distributions using a two-tailed test, we used one-tailed tests to determine which distribution had a larger size distribution.

Age data determined from analysis of fin rays was used to construct age-length keys (Ricker 1975) for each tributary in each year. I tested for differences between tributaries within years using a Chi-Square contingency tables (Siegel 1956, Snedecor and Cochran 1980). Because I found no significant differences between tributaries within years, I pooled the age-length keys for all tributaries

Table 2. Subsample sizes and the number of readable fin ray samples used to estimate age composition of spawning rainbow smelt sampled from four tributaries to St. Martin Bay, Lake Huron from 1991 to 1993.

Year	Tributary	Subsample Size	Readable Samples
1991	Carp River	160	139
1991	Nunns Creek	160	137
1991	St. Martin Creek	160	143
1992	Carp River	160	137
1992	Nunns Creek	160	140
1992	Spring Creek	160	153
1992	St. Martin Creek	160	139
1993	Carp River	160	145
1993	Nunns Creek	160	140
1993	Spring Creek	160	141
1993	St. Martin Creek	160	150
Total	All Tributaries	1760	1564

within years to form a single age-length key for each year. As chi-square tests indicated significant differences in the age length keys between years, I used age-length keys specific to each year in subsequent analysis. Age-length keys were used to partition overall length frequency data into age frequency data for each year.

Length-weight relationships (Ricker 1975) were determined as follows:

$$\log_{10}(W) = a + b \log_{10}(L)$$

I used analysis of covariance (Steel and Torrie 1980) to test for significant differences between the slope and intercept of length-weight regression equations.

Results

Length-Frequency Distributions

Length-frequency distributions for the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek are shown in Figures 3 to 6, respectively. Greater than 90% of fish sampled during spawning runs were between 110 to 170 mm in total length. Female rainbow smelt had significantly larger mean lengths than males for all tributary-year combinations (Tables 3 to 5). Length frequency distributions of female fish were significantly larger than the distributions of males in 9 of 11 tributary-year combinations tested (Table 6). I found no significant

differences in length-frequency distributions between sexes for 1992 samples collected at the Carp River and St. Martin Creek.

Length-frequency distributions of rainbow smelt were significantly larger in 1991 than in 1992 or 1993 for all tributaries sampled from 1991 to 1993 (Table 7). These length-frequencies were significantly larger in 1992 than 1993 in the Carp River and St. Martin Creek, but not for fish from Nunns and Spring Creeks. There was a steady decline in the mean length of rainbow smelt on all tributaries during the three years of this study (Figure 7).

I found significant differences in the length frequencies of spawning tributaries within years (Table 8). A general pattern that emerged from these tests was that length frequency differences were as follows: Carp River < Nunns Creek < (St. Martin Creek = Spring Creek). Mean lengths within years were always smallest at the Carp River and largest at either St. Martin Creek or Spring Creek. There was an inverse relationship between recreational fishing intensity on tributaries and mean lengths of spawning rainbow smelt (i.e. tributaries with the lowest recreational fishing intensity (Spring and St. Martin Creeks) had the largest mean lengths, while tributaries with the highest recreational fishing intensity (Carp River and Nunns Creek) had the smallest mean lengths.

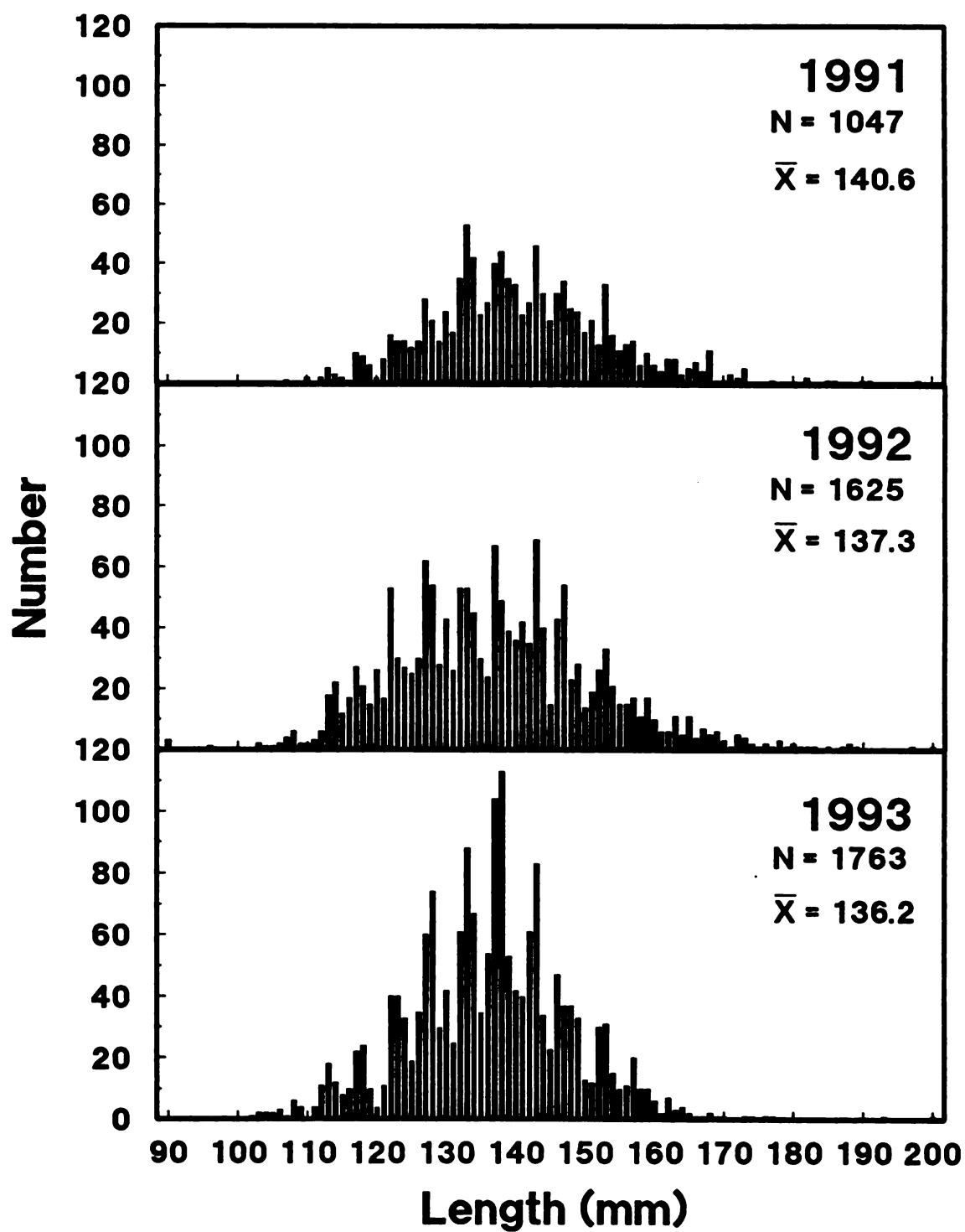


Figure 3. Length frequency distribution of spawning rainbow smelt collected from the Carp River (Mackinac County, Michigan) from 1991 to 1993.

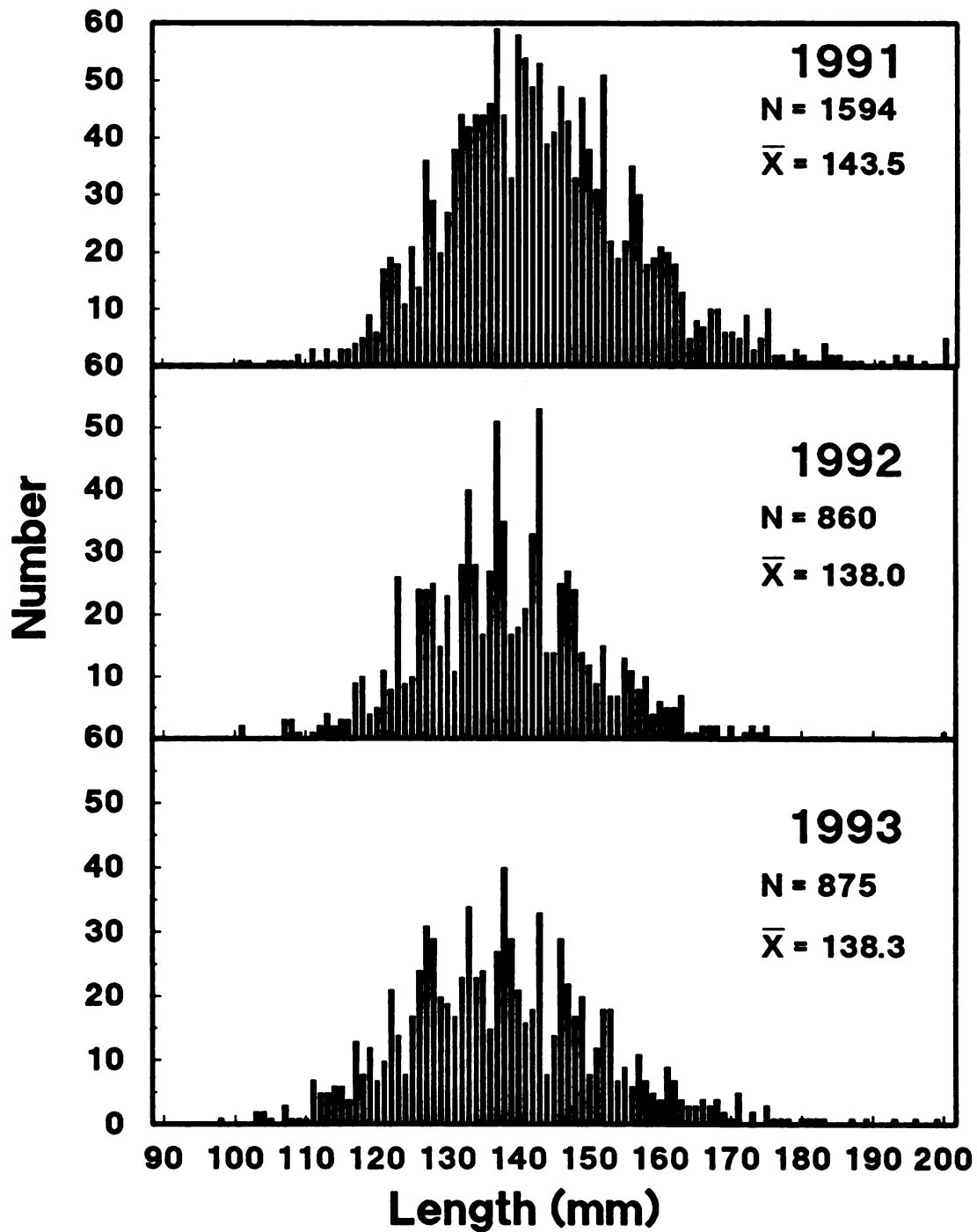


Figure 4. Length frequency distribution of spawning rainbow smelt collected in Nunns Creek (Mackinac County, Michigan) from 1991 to 1993.

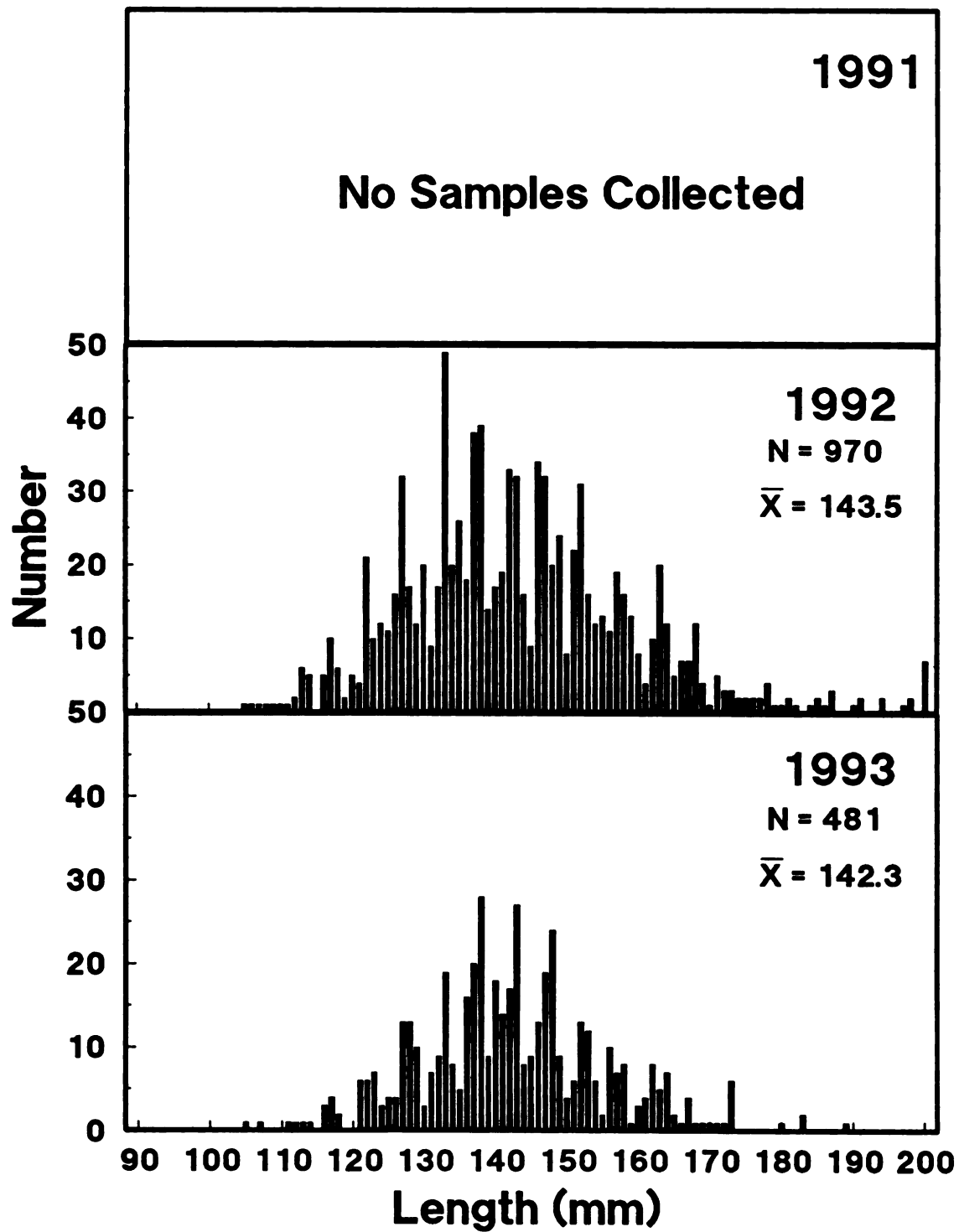


Figure 5. Length frequency distribution of spawning rainbow smelt collected in Spring Creek (Mackinac County, Michigan) from 1991 to 1993.

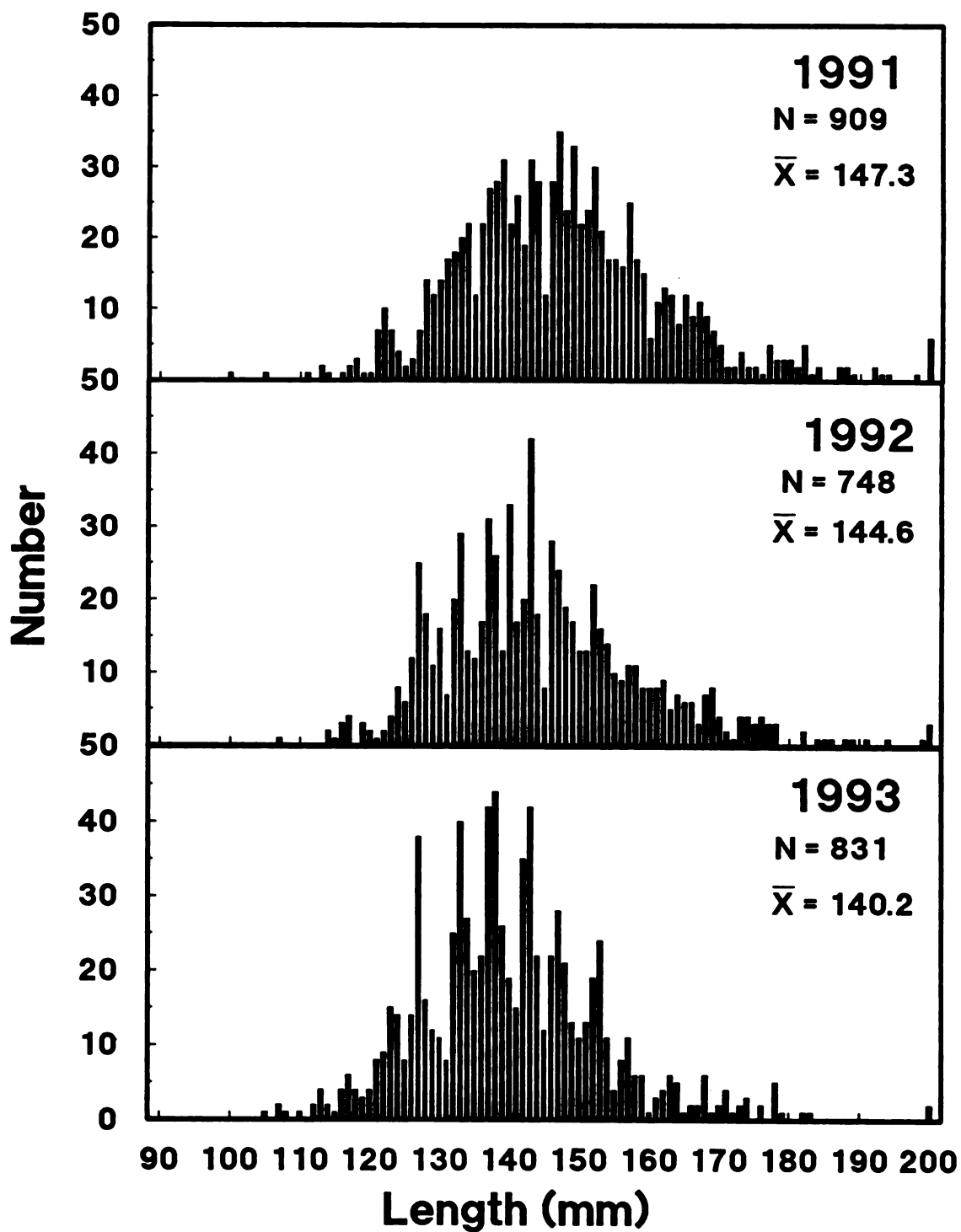


Figure 6. Length frequency distribution of spawning rainbow smelt collected in St. Martin Creek (Mackinac County, Michigan) from 1991 to 1993.

Table 3. Sample size, mean length (mm), standard errors (SE), and range in lengths of rainbow smelt sampled from four tributaries to St. Martin Bay, Lake Huron in 1991.

Year	Tributary	Sex	Sample Size	Mean Length	Standard Error	Range
1991	Carp River	Both	1047	140.63	0.392	107 - 198
1991	Carp River	Male	715	139.73	0.426	110 - 173
1991	Carp River	Female	332	142.58	0.818	107 - 198
1991	Nunns Creek	Both	1594	143.48	0.359	101 - 219
1991	Nunns Creek	Male	1000	142.38	0.404	102 - 197
1991	Nunns Creek	Female	594	145.30	0.677	101 - 219
1991	St. Martin Creek	Both	909	147.33	0.505	100 - 237
1991	St. Martin Creek	Male	581	145.67	0.572	100 - 237
1991	St. Martin Creek	Female	328	150.27	0.943	105 - 216

Table 4. Sample size, mean length (mm), standard errors (SE), and range in lengths of rainbow smelt sampled from four tributaries to St. Martin Bay, Lake Huron in 1992.

Year	Tributary	Sex	Sample Size	Mean Length	Standard Error	Range
1992	Carp River	Both	1625	137.32	0.359	96 - 210
1992	Carp River	Male	1066	136.90	0.419	96 - 185
1992	Carp River	Female	559	138.14	0.671	103 - 210
1992	Nunns Creek	Both	875	138.03	0.494	98 - 199
1992	Nunns Creek	Male	523	137.18	0.553	103 - 175
1992	Nunns Creek	Female	352	139.31	0.905	98 - 199
1992	Spring Creek	Both	970	143.50	0.528	105 - 231
1992	Spring Creek	Male	557	140.97	0.596	106 - 194
1992	Spring Creek	Female	413	146.87	0.921	105 - 231
1992	St. Martin Creek	Both	748	144.63	0.527	107 - 210
1992	St. Martin Creek	Male	413	143.77	0.615	114 - 191
1992	St. Martin Creek	Female	335	145.69	0.898	107 - 210

Table 5. Sample size, mean length (mm), standard errors (SE), and range in lengths of rainbow smelt sampled from four tributaries to St. Martin Bay, Lake Huron in 1993.

Year	Tributary	Sex	Sample Size	Mean Length	Standard Error	Range
1993	Carp River	Both	1763	136.19	0.276	102 - 203
1993	Carp River	Male	1234	135.70	0.322	102 - 203
1993	Carp River	Female	529	137.33	0.528	106 - 193
1993	Nunns Creek	Both	860	138.25	0.422	101 - 225
1993	Nunns Creek	Male	537	137.48	0.487	101 - 173
1993	Nunns Creek	Female	287	139.77	0.803	101 - 225
1993	Spring Creek	Both	481	142.26	0.591	105 - 189
1993	Spring Creek	Male	342	140.89	0.679	105 - 189
1993	Spring Creek	Female	139	145.65	1.131	117 - 183
1993	St. Martin Creek	Both	831	140.18	0.457	105 - 232
1993	St. Martin Creek	Male	522	138.85	0.501	105 - 179
1993	St. Martin Creek	Female	309	142.43	0.877	107 - 232

Table 6. Results of Kolmogorov-Smirnov tests to detect differences in the length frequency distributions between male and female rainbow smelt sampled from four St. Martin Bay tributaries from 1991 to 1993.

Year	Tributary(s)	Sample Size		Kolmogorov - Smirnov Test Results	
		Males	Females	M < > F P-Value	M > F P-Value
1991	Carp River	715	332	0.0370	0.0185
1992	Carp River	1066	559	0.2281	----
1993	Carp River	1233	529	0.0360	0.0180
1991-1993	Carp River	3014	1402	0.0006	0.0003
1991	Nunns Creek	1000	594	0.0800	0.0117
1992	Nunns Creek	523	352	0.0908	0.0454
1993	Nunns Creek	573	287	0.0805	0.0402
1991-1993	Nunns Creek	2096	1233	0.0003	0.0001
1992	Spring Creek	557	413	0.0000	0.0000
1993	Spring Creek	342	139	0.0104	0.0052
1992-1993	Spring Creek	899	552	0.0000	0.0000
1991	St. Martin	581	328	0.0011	0.0006
1992	St. Martin	413	335	0.1452	----
1993	St. Martin	520	311	0.0038	0.0019
1991-1993	St. Martin	1514	974	0.0000	0.0000
1991	All	2296	1254	0.0000	0.0000
1992	All	2559	1659	0.0000	0.0000
1993	All	2668	1266	0.0000	0.0000

Table 7. Results of Kolmogorov-Smirnov tests to detect differences between years in the length frequency distributions of rainbow smelt sampled in four St. Martin Bay tributaries from 1991 to 1993.

Year	Tributary(s)	Sample Size		Kolmogorov - Smirnov Test Results	
		Year ₁	Year ₂	Y ₁ <> Y ₂ P-Value	Y ₁ <> Y ₂ P-Value
1991,1992	Carp River	1047	1625	0.0000	0.0000
1991,1992	Nunns Creek	1594	875	0.0000	0.0000
1991,1992	St. Martin Creek	909	748	0.0010	0.0005
1991,1992	All	3550	4218	0.0000	0.0000
1991,1993	Carp River	1047	1763	0.0000	0.0000
1991,1993	Nunns Creek	1594	860	0.0000	0.0000
1991,1993	St. Martin Creek	909	831	0.0000	0.0000
1991,1993	All	3550	3935	0.0000	0.0000
1992,1992	Carp River	1625	1763	0.0003	0.0001
1992,1993	Nunns Creek	875	860	0.1630	----
1992,1993	Spring Creek	970	481	0.1315	----
1992,1993	St. Martin Creek	748	841	0.0000	0.0000
1992,1993	All	4218	3935	0.0000	0.0000

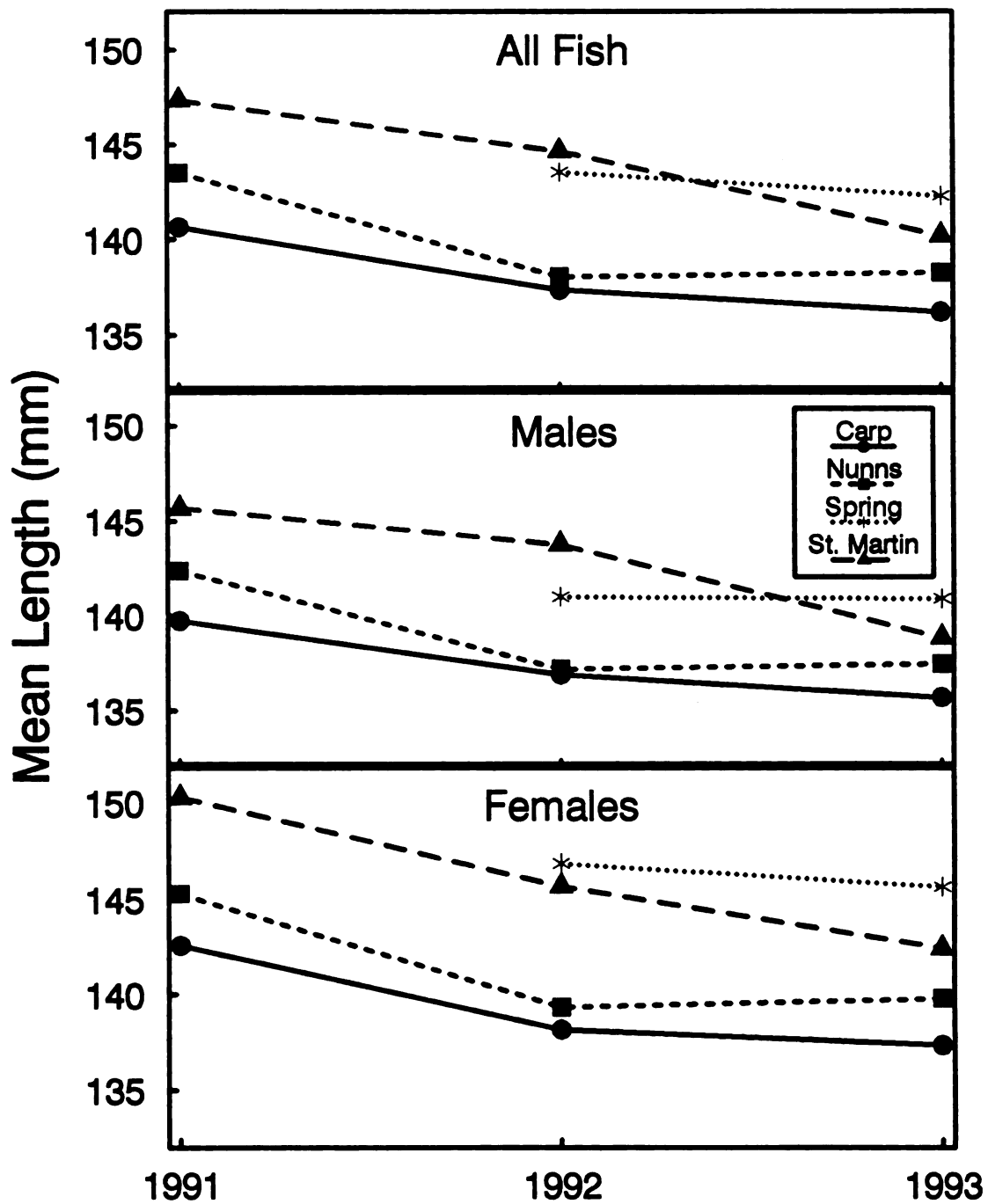


Figure 7. Mean length of spawning rainbow smelt collected from the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek (Mackinac County, Michigan) from 1991 to 1993.

Length-Age Keys

Chi-Square tests indicated no significant differences in the length-age relationships between tributaries within years ($P = 0.452$), but significant differences in length-age relationships between years ($P = 0.0217$). Based on these results, I pooled age length keys for all tributaries within years, but developed and used separate length-age keys for 1991 to 1993 (Appendices 1, 2, and 3, respectively). I found no significant differences in mean lengths at age for age classes 2 and 3 between years (Table 9). Significant differences between years were due to differences in the mean length at age for age classes 4 and 5 (Table 9).

Age Composition

Age composition of rainbow smelt sampled from all tributaries for 1991 to 1993 is shown in Figures 8 to 10, respectively. Spawning populations on all streams in all years were dominated by age 2 and 3 fish (<95% of fish sampled). Large overlaps in the length frequency distributions between these two age classes occurred in the 135 to 150 mm length increment (Figures 8 to 10). Age 2 fish were dominant in the 1991 and 1993 samples, while age 3 fish dominated in the 1992 samples (Table 10). Age 4 and older fish never accounted for more than 3% of the samples in any year.

Table 8. Results of Kolmogorov-Smirnov tests to detect differences in the length-frequency distributions of spawning rainbow smelt sampled from four St. Martin Bay tributaries from 1991 to 1993.

Year(s)	Tributary(s)	Sample Size		Kolmogorov - Smirnov Test Results		
		Year ₁	Year ₂	T ₁ < > T ₂ P-Value	T ₁ > T ₂ P-Value	T ₁ < T ₂ P-Value
1991	Carp, Nunns	1047	1594	0.0002	—	0.0001
1992	Carp, Nunns	1625	875	0.5397	—	—
1993	Carp, Nunns	1763	860	0.0006	—	0.0003
1991-1993	Carp, Nunns	4435	3329	0.0000	—	0.0000
1992	Carp, Spring	1625	970	0.0000	—	0.0000
1993	Carp, Spring	1763	481	0.0000	—	0.0000
1992-1993	Carp, Spring	4435	1451	0.0000	—	0.0000
1991	Carp, St. Martin	1047	909	0.0000	—	0.0000
1992	Carp, St. Martin	1625	748	0.0000	—	0.0000
1993	Carp, St. Martin	1763	831	0.0000	—	0.0000
1991-1993	Carp, St. Martin	4435	2488	0.0000	—	0.0000
1992	Nunns, Spring	875	970	0.0000	—	0.0000
1993	Nunns, Spring	860	481	0.0000	—	0.0000
1992-1993	Nunns, Spring	1735	1451	0.0000	—	0.0000
1991	Nunns, St. Martin	1594	909	0.0000	—	0.0000
1992	Nunns, St. Martin	875	748	0.0000	—	0.0000
1993	Nunns, St. Martin	860	831	0.3007	—	—
1991-1993	Nunns, St. Martin	3329	2488	0.0000	—	0.0000
1992	Spring, St. Martin	970	748	0.0470	—	0.0235
1993	Spring, St. Martin	481	831	0.0208	0.0104	—
1992-1993	Spring, St. Martin	1451	2488	0.1091	—	—

Table 9. Mean length (mm) of rainbow smelt sampled from Lake Huron in 1975-76 by Argyle (1982) and from 1991-1993 by the current study.

Date	I	II	III	Age IV	V	VI	VII
Spring 1975 ^a	-	128	149	168	180	191	193
Spring 1976 ^a	102	130	152	170	193	208	183
Spring 1991 ^b	-	130	149	175	199	-	-
Spring 1992 ^b	-	129	152	178	202	-	-
Spring 1993 ^b	-	132	150	168	181	-	-

^a Argyle (1982). Bottom trawl sampling at five sites in Lake Huron.

^b Current Study. Dip net sampling in four tributaries to St. Martin Bay, Lake Huron.

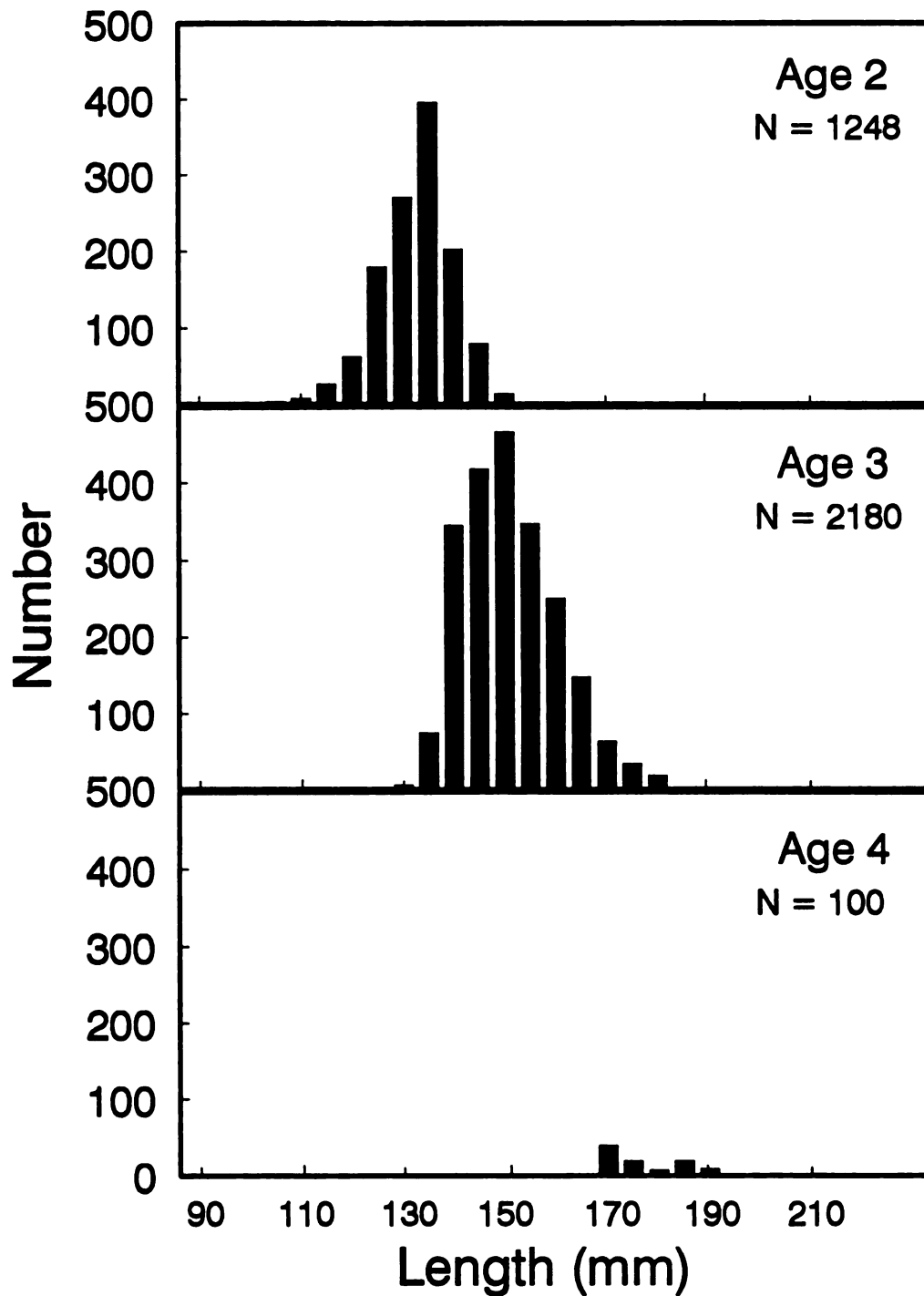


Figure 8. Length frequency distributions by age of spawning rainbow smelt sampled from the Carp River, Nunns Creek, and St. Martin Creek (Mackinac County, Michigan) in 1991.

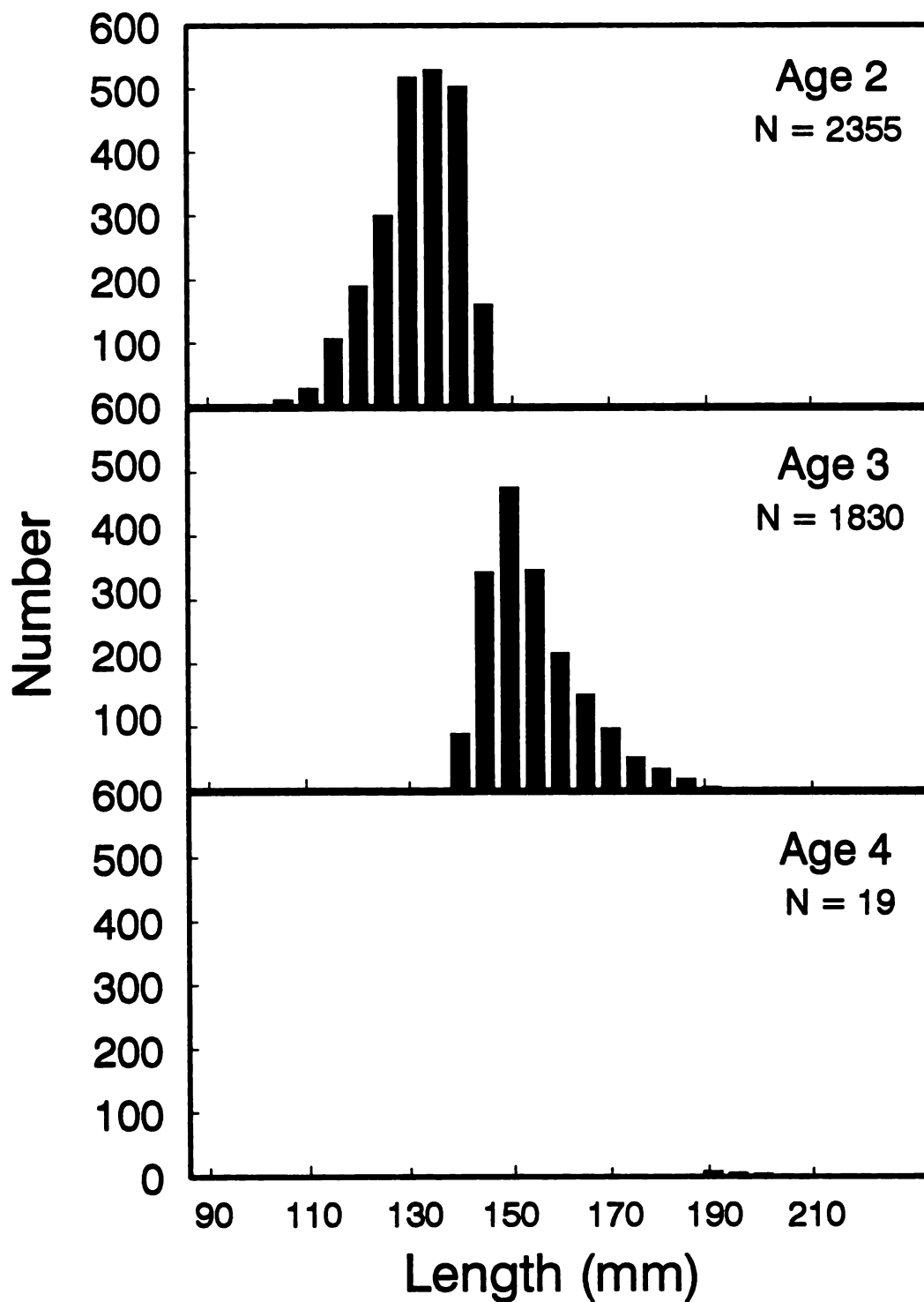


Figure 9. Length frequency distributions by age of spawning rainbow smelt sampled from the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek (Mackinac County, Michigan) in 1992.

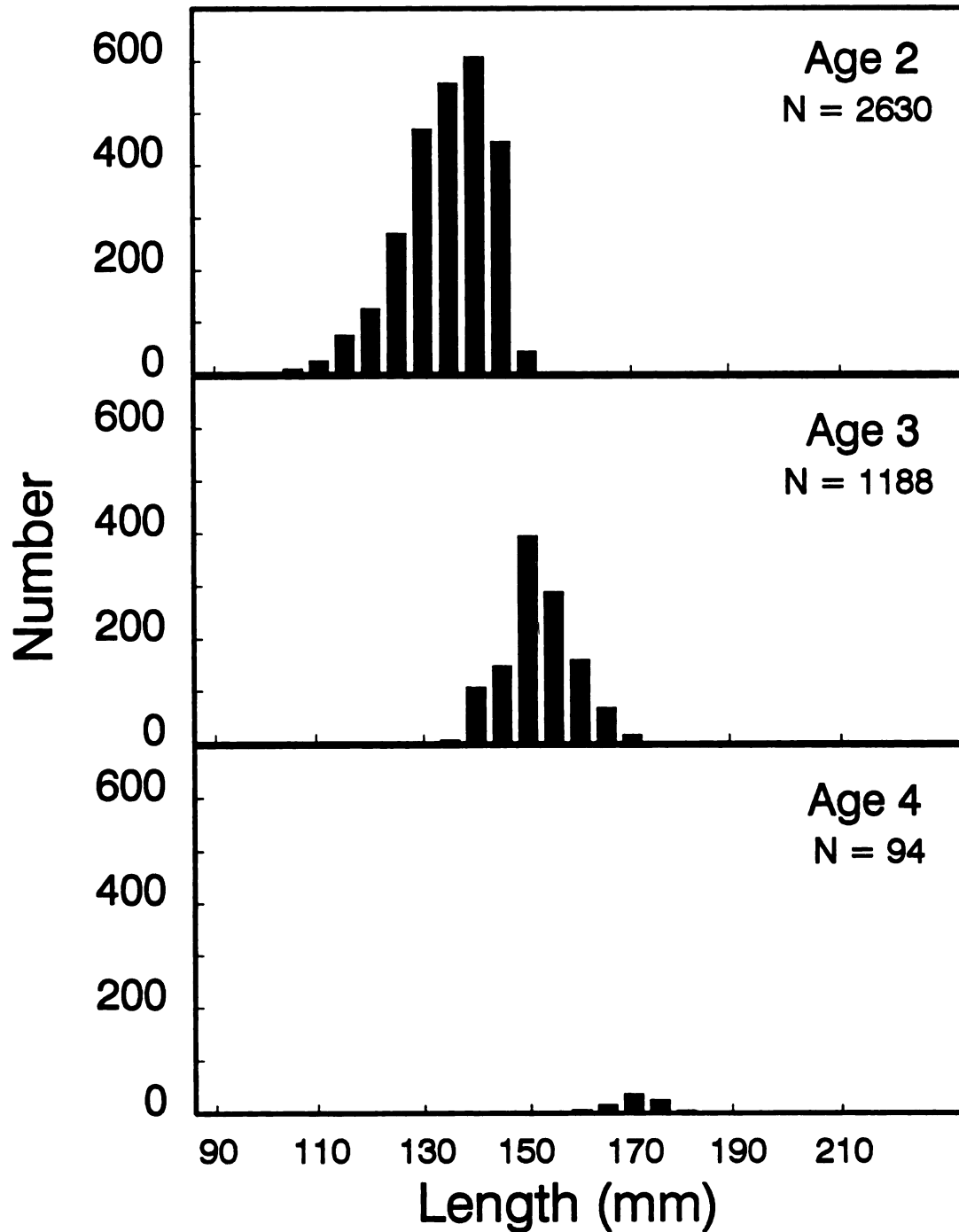


Figure 10. Length frequency distributions by age of spawning rainbow smelt sampled from the Carp River, Nunns Creek, Spring Creek and St. Martin Creek (Mackinac County, Michigan) in 1993.

Table 10. Percent age composition data for rainbow smelt sampled in Lake Huron during different time periods.

Years	I	II	III	Age IV	V	VI	VII
1948-1957 ^a	0.0	58.3	39.2	2.1	0.3	0.1	0.0
1958-1964 ^a	0.0	16.7	47.9	25.1	6.8	2.5	0.7
1975-1976 ^b	0.4	27.7	45.8	18.8	5.7	1.5	0.2
1991-1993 ^c	0.0	52.7	45.1	1.9	0.3	0.0	0.0

^a Frie and Spangler (1985). Dip net sampling in South Bay, Lake Huron.

^b Argyle (1982). Bottom trawl sampling at five sites in Lake Huron.

^c Current Study. Dip net sampling in four tributaries to St. Martin Bay, Lake Huron.

Table 11. Length-weight regressions by year and tributary for rainbow smelt sampled in four St. Martin Bay tributaries from 1991 to 1993.

Year	Tributary	Sex	Sample Size	Slope	Intercept	R ²
1991	All	Both	2069	3.10874	-5.49862	0.9304
1992	All	Both	2006	3.05284	-5.37280	0.9507
1993	All	Both	1992	3.02061	-5.30575	0.9289
1991-1993	Carp River	Both	1631	3.09561	-5.46108	0.9432
1991-1993	Nunns Creek	Both	1892	3.06223	-5.40057	0.9277
1991-1993	Spring Creek	Both	982	3.03463	-5.33732	0.9460
1991-1993	St. Martin	Both	1562	3.05458	-5.37806	0.9428

Length-Weight Regressions

Length-weight relationships for individual tributaries by year are shown in Appendix 4, while summary relationships by year (pooled tributaries) and tributary (pooled years) are shown in Table 11. Females had higher slope values for 8 of 11 tributary-year combinations, indicating a general trend of greater weight at size for female fish. Slopes of the length-weight regression equations declined annually between 1991 and 1993 (Table 11), and were significantly different between years (ANCOVA, $P = 0.0149$).

Sex Ratios

Sex ratios of rainbow smelt sampled during spawning were always skewed toward male fish, but the relative level of skewness was not consistent between years. Sex ratios were most highly skewed toward males in 1993 (range 67 to 71%) and least highly skewed in 1992 (55 to 66%) on all study tributaries (Table 12). The degree of skewness in sex ratios appears to be related to the size and age distributions of sampled fish. The relative percentage of male fish showed a steady decline with increasing size classes of spawners in the three years of this study (Figure 11). In smaller size classes (< 150 mm), males comprised greater than 60% of spawners, while in the largest size classes (> 170 mm), females were more abundant than males (Figure 11). These patterns appear to be related to the age composition of spawners. The relative abundance of male fish declined from greater than 60% for age 2 fish to less than 30% for age 5+ fish (Figure 12).

Table 12. Sex ratios (percent males) of spawning rainbow smelt sampled from the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek (Mackinac County, Michigan) from 1991 to 1993.

Tributaries	1991	1992	1993
Carp River	68.0	65.6	70.0
Nunns Creek	62.7	53.6	66.6
Spring Creek	---	57.6	71.1
St. Martin Creek	63.9	55.2	68.1
Total	64.6	59.3	69.2

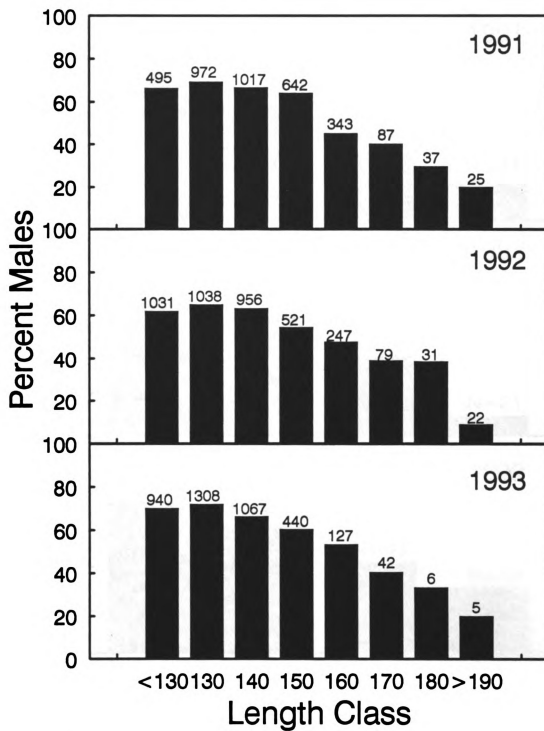


Figure 11. Sex ratio (percent males) by 10-mm size class for spawning rainbow smelt sampled in four St. Martin Bay tributaries from 1991 to 1993. Sample sizes are shown above each bar.

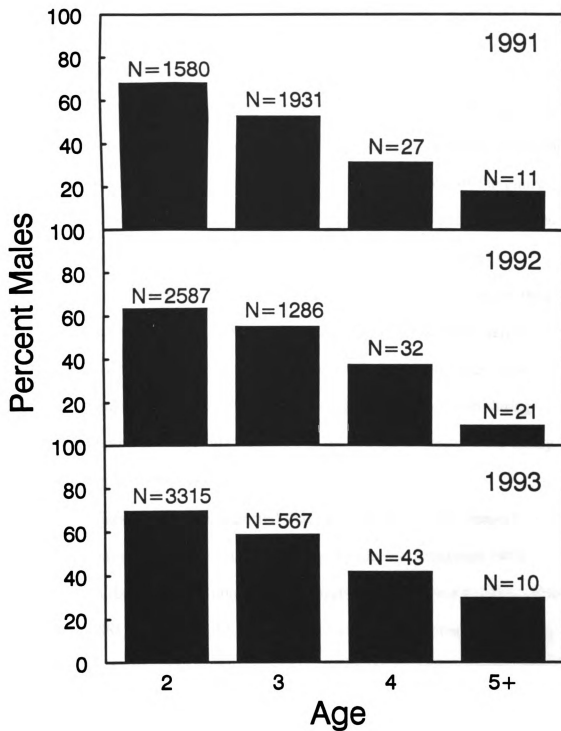


Figure 12. Sex ratio (percent males) by age of spawning rainbow smelt sampled from four St. Martin Bay tributaries from 1991 to 1993. Sample sizes are shown above each bar.

Discussion

Sex Ratio and Length Frequency Patterns

During the spawning season, sex ratios of samples collected during spawning runs were male dominated except at peak spawner abundance, when the percentage of female spawners approached 50%. Over the course of the entire spawning season, the percentage of males sampled ranged from 59.3% in 1992 to 69.2% in 1993. Male dominance in spawning samples can be attributed to differential spawning behavior of male and female rainbow smelt. Females tend to ascend a river and complete spawning in a single night, while males return repeatedly to spawning streams throughout the spawning season (Bailey 1964, Scott and Crossman 1985). Most investigators sampling rainbow smelt during spawning runs report sex ratios that are skewed toward males (Hale 1960, Bailey 1964, and Jilek et al. 1979, Gebhardt 1993).

Several investigators have reported that adult rainbow smelt sampled during non-spawning periods were dominated by female fish (Beckman 1942; Gordon 1957; Burbidge 1969; Robinson 1973; Argyle 1982; Gebhardt 1993). Frie and Spangler (1985) found that the proportion of males in spawning run samples were consistently higher than in gill net surveys made later in the summer. These patterns are probably attributable to two factors: 1. males are more vulnerable to capture during spawning because they ascend tributaries on multiple nights to spawn, while females normally spawn on a single night, and 2. males may experience higher mortality associated with spawning activities (McKenzie 1964,

Burbidge 1969, Murawski and Cole 1978, Nsembukya-Katuramu et al. 1981, Schaefer et al. 1982). Frie and Spangler (1985) found that the percentage of males in spawning run samples increased from 60% to 78% after cessation of recreational exploitation in South Bay, Lake Huron. Schaefer et al. (1982) found that post spawning die-offs of rainbow smelt in Lake Superior contained a significantly higher proportion of male fish than would be expected from measured spawning ratios. Schaefer (1979) found that total annual mortality of males was higher than females for rainbow smelt in Lake Superior.

Sex ratio and length frequency differences in this study indicate that female rainbow smelt may experience a lower total annual mortality rate when compared with males. If spawning related mortality due to natural predators or the recreational fishery is significant, males will experience higher mortality rates during this period. Differences in vulnerability between sexes to dip-net fishing were evident in my data set where the ratio of males to females was 1.79:1 over the entire study period. Declines in the proportion of male fish in larger size and age classes provides further evidence for differential mortality between sexes. Observed larger mean lengths of female rainbow smelt were not caused by differences in growth rates between sexes as mean lengths between male and female rainbow smelt within age classes were not significantly different from one another. Significant differences in mean lengths between sexes were due to the presence of a greater percentage of older female fish when compared to the age composition of male fish.

Tributary differences in length frequency distributions and mean lengths may be related to recreational fishery intensity. The most heavily exploited tributaries (Carp River and Nunns Creek) had the smallest mean lengths and length frequency distributions observed. These tributaries also have higher levels of recreational fishery effort. Differences in mean size were due to differences in age composition rather than differential growth rates between sexes or tributaries. If tributary-related differences are due to changes in age composition resulting from differing mortality rates, these differences may indicate that spawning populations at the Carp River, Nunns Creek, and Spring/St. Martin Creeks may represent distinct spawning stocks. Genetic analysis would be needed to provide support for this hypothesis.

Length-Weight Relationships

The slope of length-weight relationships reported in this study were within the range of coefficients reported for rainbow smelt during the same time period, and in the Great Lakes during other time periods. Length-weight relationships were more variable for female rainbow smelt because of the presence of gravid, partially spawned, and completely spawned females collected in samples.

The slope of length-weight relationship declined annually from 1991 to 1993; however, the decline was not consistent with changes in sampled age composition or sex ratio. The negative trend in length-weight slopes may indicate a decline in the average condition of spawning rainbow smelt.

Age Composition

Age 2 fish were dominant in the 1991 and 1993 samples, while age 3 fish dominated in the 1992 samples. It appears that a relatively strong year class (1989) dominated the 1991 samples as age 2 fish and the 1992 samples at age 3. A relatively strong 1991 year class appears to dominate the age composition as age 2 fish in 1993. Age composition data indicated broad overlaps in the length distribution at age of rainbow smelt sampled in this study. Bailey (1964) reported large ranges in length at age with broad overlaps in the length distributions of ages 2 to 6. Such differences may be caused by variation in individual growth rates or the production of multiple cohorts within a year resulting in significantly different first year growth.

Mean lengths at age did not vary between years for younger fish (ages 2 and 3), but there were significant differences in the mean lengths of older fish (ages 4 and 5) between years. These differences may reflect growth differences because older fish utilize different food resources (*Mysis*, *Pontaporea*, and fish) than younger fish (primarily zooplankton) (Gordon 1961, Foltz and Norden 1979).

Mean lengths at age appear to have remained fairly constant during the last two decades when compared to mean lengths at age from Argyle (1982). However, there have been significant shifts in the age composition from the late 1940's to the 1991 to 1993 time period. Frie and Spangler (1985) reported age composition data for dip net sampled rainbow smelt from South Bay, Lake Huron during a period of intense recreational fishing (1948 to 1957) and period when recreational fishing was absent (1958 to 1964). During the period of intense

Table 13. Length-weight regression coefficients reported for populations of rainbow smelt in the upper Great Lakes.

Location	Years	Months	Sex	N	Slope	Interce pt
Carp River, Nunns Creek St. Martin Bay Lake Huron	1991-1993	April	Both	6067	3.06	-5.39
			Males	3825	3.04	-5.35
			Females	2242	3.06	-5.38
Days River Green Bay Lake Michigan	1990-1992	April	Males	85	2.97	-5.16
			Females	80	2.93	-5.09
Squaw Creek Green Bay Lake Michigan	1990-1992	April	Males	73	3.08	-5.38
			Females	72	3.08	-5.34
Point Beach Lake Michigan	1990-1992	April	Males	72	3.05	-5.33
			Females	80	3.00	-5.22
Red Arrow Park Green Bay Lake Michigan	1990-1992	April	Males	88	3.00	-5.27
			Females	75	2.94	-5.13
Turtle Creek Green Bay Lake Michigan	1990-1992	April	Males	74	3.26	-5.85
			Females	89	3.30	-5.91
Whitefish Bay Creek Lake Michigan	1990-1992	April	Males	68	2.82	-4.85
			Females	83	3.31	-5.91
Two Rivers, Wisconsin Lake Michigan	1971-1972	March, May	Both	Not Given	3.28	-5.88
Zion, Illinois Lake Michigan	1971-1972	March, May	Both	Not Given	3.27	-5.81

recreational fishing (1948 to 1957, total annual mortality = 86 to 90%), age compositions of spawning fish were dominated by age 2 and 3 fish (97.5%).

During a period without recreational fishing (1958 to 1964, total annual mortality = 66 to 67%), age compositions of spawning fish contained a greater proportion of older fish. Argyle (1982) reported that younger fish (< age 4) represented 73.9% of the adult population in 1975 to 1976 at five sites in Lake Huron. In the current study, these younger age classes represented 97.0%, 99.3%, 97.1% of the adult population in 1991 to 1993, closely resembling the age composition reported by Frie and Spangler (1985) for heavily exploited populations in South Bay.

These shifts in the age composition toward a younger age composition reflect higher total annual mortality rates during the 1991 to 1993 time period. The current (1991 to 1993) population is vulnerable to significant declines or collapse if the population were to experience 2 to 3 years of recruitment failure.

Conclusions

Age composition of tributary spawning rainbow smelt in St. Martin Bay is largely comprised of younger fish (ages 2 and 3). Although variable year class strength was responsible for alteration of the age composition of spawning rainbow smelt, age 2 and 3 fish comprised greater than 95% of spawners during this study. Age composition of spawning fish is much younger than was reported for Lake Huron populations in the 1970's and closely resembles the age composition reported for heavily exploited South Bay populations in the late 1940's and 1950's (Frie and Spangler 1985).

Young age distributions, low sex ratios of male fish, and declining length-weight regression slopes are indications of stressed populations. Poor recruitment of rainbow smelt since 1987 has resulted in a decline in the relative abundance of rainbow smelt in Lake Huron. In addition, high adult mortality rates associated with salmonine predation, recreational fishery extractions, and other unidentified sources have resulted in a young age composition typical of a less stable population. The recreational fishery in St. Martin Bay appears to have a localized impact on heavily exploited tributary spawning populations, but its effect on the overall population in northern Lake Huron is probably negligible. If current levels of low recruitment continue to occur, populations of rainbow smelt can be expected to decline further. It is important to recognize that rainbow smelt populations are resilient, and that populations in South Bay, Lake Huron survived annual mortality rates of 90% during the 1940's and 1950's without collapse (Frie and Spangler 1985). Current estimates of annual mortality rates for rainbow smelt populations in Lake Huron are approximately 80% (Ralph Stedman, National Biological Survey - Great Lakes Science Center, Personal Communication). Species and population specific life history characteristics including variable spawning locations, early maturation, and high fecundity all contribute to the resiliency of rainbow smelt populations.

**CHAPTER 2: SEASONAL PATTERNS IN EGG DEPOSITION AND
LARVAL OUTMIGRATION OF RAINBOW SMELT FROM
FOUR TRIBUTARIES TO ST. MARTIN BAY, LAKE
HURON**

ABSTRACT

To investigate seasonal and interannual patterns in the timing and magnitude of egg deposition, egg survival, and larval outmigration, I sampled spawner abundance, egg deposition, and outmigration of rainbow smelt from four St. Martin Bay tributaries. Indices of spawner abundance indicated that spawning generally occurred two to five days earlier in the Carp River and Nunns Creek than on Spring and St. Martin Creeks. Water temperature at peak spawning was consistent within tributaries, but varied between 3.5 and 7.0 C between tributaries. Spawning in all tributaries was delayed by prolonged cold water temperatures (< 2 C) in 1992. Nightly egg deposition was strongly correlated with spawner abundance, except during the early portions of spawning runs when males comprised greater than 80% of the spawning fish. Egg densities on streams were negatively affected by recreational fishery activity with high levels of fishery effort resulting in significant nightly declines in egg density.

Larval outmigration occurred five to nine days earlier on the Carp River and Nunns Creek than on Spring and St. Martin Creeks due to earlier spawning times and warmer water temperatures during egg incubation. Diel patterns were consistent between tributaries with greater than 90% of larval outmigration occurring between 2100 and 0600 hours. Nightly peak larval outmigration

occurred between 0000 and 0100 hours. Of the four study tributaries, the Carp River dominated larval production, producing 72.8%, 74.8%, and 96.4% of the total larval output from 1991 to 1993, respectively. The four tributary streams produced a total of 46 million larvae in 1991, 13 million larvae in 1992, and 32 million larvae in 1993, with annual differences due to variable levels of egg deposition and survival between years. The magnitude of differences in tributary larval production measured during this study was sufficient to cause significant interannual variation in recruitment from tributary spawning areas.

INTRODUCTION

Rainbow smelt populations in Lake Huron have demonstrated variable levels of year class formation that appear to fluctuate independently of stock size (Argyle 1994). An important first step in the identification of causes for variable year class formation is to quantify production of eggs and larvae in principal spawning areas. In the upper Great Lakes, rainbow smelt spawning occurs during mid to late April and early May in tributary streams and nearshore lake areas (Scott and Crossman 1985). Anadromous spawning occurs primarily at night in the lower portions of rivers and streams, with spawning fish usually returning to lake areas prior to dawn (Bailey 1964). Eggs are released in clusters and become adhesive, attaching to substrate or vegetation after fertilization (McKenzie 1964). Downstream displacement or drift of rainbow smelt eggs may occur as a consequence of (1) spawning activity, (2) loss of adhesiveness of the egg

membrane, (3) increased stream velocity, (4) attachment of eggs to floating vegetation or (5) dislodgement of eggs by animal or human activities (Johnston and Cheverie 1988).

Cold water temperatures or stormy weather during the normal spawning period may increase the incidence of shoal or shoreline spawning by rainbow smelt (Scott and Crossman 1985). Shore spawning by rainbow smelt has been documented in Crystal Lake, Michigan (Lievens 1954) and Branch Lake, Maine (Rupp 1965), and the occurrence of shore spawning in Lakes Michigan and Huron are believed to be significant (Personal Communication, R. Stedman, NBS-Great Lakes Science Center, Ann Arbor, MI).

Egg incubation times are inversely related to water temperature, ranging from 5 (at 16 C) to 30 (at 3 C) days (Hoover 1936; McKenzie 1964; Cooper 1978). Immediately after hatching, larvae have large yolk sacs and limited swimming ability (Cooper 1978). Larvae are transported downstream by tributary currents to receiving waters where they grow and develop into juveniles (Johnston and Cheverie 1988). Outmigration of rainbow smelt follows a diel pattern with peak drift rates occurring at night (Ouellet and Dodson 1985; Johnston and Cheverie 1988; Winnell and Jude 1991).

To further understand factors affecting year class formation of rainbow smelt, information is needed concerning seasonal and interannual patterns of spawning, egg deposition, and larval outmigration from tributaries. Quantification of egg deposition and larval production and estimation of survival rates from egg deposition to larval outmigration from tributary streams represent important step

needed to identify factors controlling the early survival of rainbow smelt. The goal of this study was to identify and quantify factors important in determining larval production of rainbow smelt in tributaries to northern Lake Huron. My specific objectives were to:

1. Estimate the timing and magnitude of spawner abundance and egg deposition in St. Martin Bay tributaries.
2. Evaluate the impact of the recreational dip net fishery on egg deposition.
3. Measure the timing and relative contribution of larval rainbow smelt outmigration from St. Martin Bay tributaries.
4. Estimate survival rates between egg deposition and larval outmigration.

METHODS

Spawner Abundance

The abundance of spawning rainbow smelt in tributary streams was indexed by measuring catch per unit effort (CPUE) of fish captured using a wire mesh dip net (45 cm diameter, 40 cm depth, 1 cm mesh). Sampling was conducted to measure CPUE at fixed sites on each tributary twice nightly, once between 2200 and 0100 and again between 0100 and 0400. Preliminary sampling in 1990 and 1991 indicated that spawning fish were rarely present in streams prior to 2130 or after 0400. During each sampling period, I recorded the number of spawning fish captured during a timed sampling period ranging from 5 and 60 minutes. Sampling was normally conducted until 100 individuals had been collected, or until the sampling period had elapsed. Sampling was conducted for at least 5

minutes at times when spawner densities were high (CPUE > 5000 fish/hour) to provide an accurate estimate of CPUE.

Egg Deposition Sampling

Egg deposition was sampled on three of the study tributaries, Nunns Creek, Spring Creek, and St. Martin Creek (Figure 2). The Carp River was not sampled due to unwadable depths and drastically fluctuating discharge during spawning. During this study, spawning generally occurred between April 15 and May 2. Egg deposition was monitored on Nunns Creek in 1991, and sampling was expanded to include Spring and St. Martin Creeks in 1992 and 1993. Commencement and termination of egg deposition sampling was determined by examination of artificially placed substrate for egg deposition and detection of spawning female rainbow smelt through dip net sampling. Total annual sampling effort ranged from 9 to 14 days depending on the duration of spawning (Table 14). Upstream fish movement on Spring and St. Martin Creeks was restricted to within 150 m of the mouth by road culverts. In 1991, fish spawning in Nunns Creek had unrestricted access upstream, although most fish remained within 150 m of the stream mouth. Between 1991 and 1992, a lowhead barrier dam was installed on Nunns Creek restricting fish movement to within 150 m of the stream mouth. In all years, recreational fishing activity on Nunns Creek was limited to 59 m

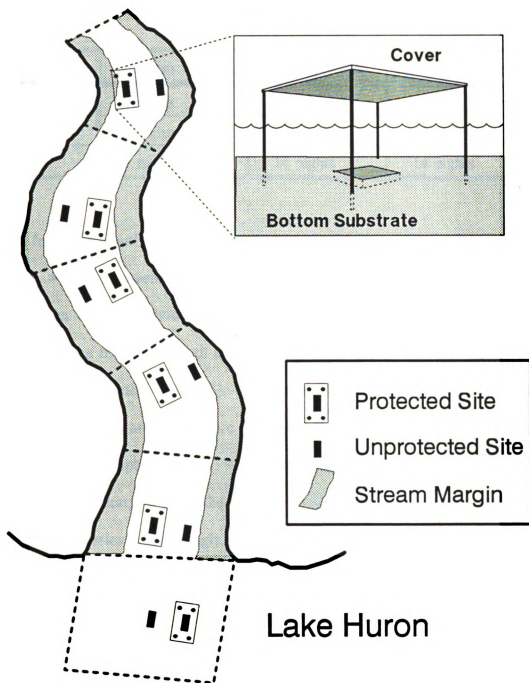


Figure 13. Sampling design used to measure the impact of dip-net activity on egg deposition. A plywood cover supported by four metal rods was used to protect one sampling site in each strata from dip net activity and wading by recreational fishers.

Table 14. Total egg deposition sampling effort on Nunns, Spring, and St. Martin Creeks, 1991 to 1993.

Year	Nunns Creek	Spring Creek	St. Martin Creek
1991	9 nights	---	---
1992	11 nights	10 nights	10 nights
1993	14 nights	14 nights	14 nights

upstream from the mouth by private property, providing a spawning refuge area (82 m long, 495 m²) between the property line and the barrier dam. On Spring and St. Martins Creeks, I divided the spawning area into six equidistant strata, five upstream from the tributary mouth and a sixth located immediately downstream from the tributary mouth (Figure 13). On Nunns Creek, three sites were located upstream of the mouth and three were located in the stream plume in St. Martin Bay. Observations of spawning in 1990 indicated that rainbow smelt tended not to spawn in stream margins given the water velocities (0.1 to 1.1 m/sec) available in our study tributaries. Accordingly, fixed sampling sites were randomly located within the middle 60% of the thalweg of the tributary within each strata.

Sampling sites remained fixed during the study, except that two sites were relocated in 1992 because of changes in tributary morphology (shifting sandbars) at the mouth of Nunns Creek. At each site, two paired sample locations were identified that had similar depth, velocity, distance from tributary mouth, and substrate characteristics. One sample location at each site was randomly chosen

and protected with a 30 X 30 cm plywood cover (Figure 13), which protected the area beneath from wading and dip-net activity.

I used 19.2 X 9.2 cm concrete bricks covered with burlap to estimate egg deposition at each site. At each sampling site, this artificial substrate was placed flush with the tributary bottom (Figure 13). Artificial substrates were placed at each sampling site before each sampling night. On retrieval, the burlap covers were removed and eggs were counted in the laboratory under 3x magnification. Eggs were identified using criteria developed by Cooper (1978).

On each sampling night, egg density estimates at the six protected and six unprotected sites were pooled to produce density estimates at protected and unprotected sites. The Wilcoxon Signed-Rank Test was used to compare paired samples on each sampling night. To evaluate the effect of protective shelters on egg deposition, I made 13 measurements of egg deposition on nights when there was no recreational fishing effort. I was also able to obtain 4 additional nights of observation by placing additional sampling sites above the private property line on Nunns Creek where they were not vulnerable to the fishery.

To quantify the effect of recreational fishing activity on egg density, I evaluated the relationship between fishing effort on nights when the mean egg deposition was greater than 2,831 eggs/m² (equal to a mean of 50 eggs/brick) and fishing effort. I determined that egg densities less than 2,831 eggs/m² were too low to allow accurate measurement of fishery effects because of highly variable spatial distribution of eggs at low spawner abundance. Generally, levels of recreational fishing effort were low (less than 5 people/100 m²) on nights when

egg densities were less than 2,831 eggs/m² (n = 24 nights), because of low densities of spawning rainbow smelt.

Diel Sampling of Larval Outmigration

I conducted diel sampling surveys of larval rainbow smelt to determine daily patterns in outmigration from tributary streams. Drift samples were collected every three hours (0000, 0300, ... , 1800, 2100) over a 24 hour period to estimate diel patterns in larval outmigration. On the Carp River, a total of six 24 hour samples were collected from 1991 to 1993 (Table 15). On the Nunns, Spring, and St. Martin Creeks, four 24 hour samples were collected.

Diel patterns were interpreted by estimating the proportion of the total 24 hour drift (collected in all eight samples) that was collected during each of the eight time periods. Because seasonal trends of increasing or decreasing larval drift were incorporated into the raw data, I tested for significant relationships in the two 0000 samples preceding and following the 24 hour sample date. I found a significant trend in the seasonal patterns for 14 of the 18 diel sampling dates. When significant patterns were found, the diel drift data were detrended by correcting for the slope of the regression equation between the four sample dates (see Figure 14). Because greater than 90% of the larval outmigration occurred between 2100 and 0600, I also sampled hourly between 2100 and 0600 for one night each on the Carp River and Spring Creek in 1992, and one night on Nunns Creek in 1993.

Table 15. Dates when diel patterns in the outmigration of larval rainbow smelt were measured on the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek, 1991 to 1993.

Tributary	Total Days Sampled	1991 Sample Dates	1992 Sample Dates	1993 Sample Dates
Carp River	6	May 18 May 20	May 14 May 15	May 15 May 16
Nunns Creek	4	May 20 May 22	-- --	May 15 May 16
Spring Creek	4	-- --	May 29 May 30	May 26 May 27
St. Martin Creek	4	-- --	May 29 May 30	May 26 May 27

Variance for diel patterns were estimated as the standard error of the diel patterns between sampling dates. Results of diel sampling were used to estimate the daily outmigration and obtain seasonal estimates of larval production for each tributary.

Nightly Sampling of Outmigrating Larval Rainbow Smelt

Larval rainbow smelt production for four St. Martin Bay tributaries was estimated through drift net surveys. I sampled one large river (Carp River), a medium size creek (Nunns Creek), and two smaller creeks (Spring and St. Martin Creeks) nightly between May 6 to June 12, 1991 to 1993 (Table 1). On the Carp River, a 0.5-m diameter, 2.5-m long, 363- μ mesh conical net was used for sampling in 1991, while a 1.0-m diameter, 3.0-m long, 363- μ mesh conical net was

used in 1992 to 1993. All nets on the Carp River were fished at mid-depth in the water column. On Nunns Creek, sampling was conducted using a 0.5-m diameter, 2.5-m long, 363- μ mesh conical net that generally fished from the surface to bottom. On the smaller creeks, 610 mm by 305 mm square drift nets with 363- μ mesh were deployed across the entire water column to sample outmigrating larvae.

Conical nets were fitted with a General Oceanics flow meter with a low speed rotor to estimate the volume of water filtered during sampling. Shallow water depths at the sampling sites on smaller tributaries prevented the use of flowmeters to estimate volume filtered. On these tributaries, I used a Marsh-McBirney digital flowmeter to develop regression relationships between sampling site velocity and stream staff gauge (discharge) measurements. Volume filtered was then estimated based on the sampling time and staff gauge reading taken just before and after each sampling period.

On Nunns, Spring and St. Martin Creeks, drift net sampling was conducted at the mouth of each tributary. On the Carp River, drift net sampling was conducted at the first point that had consistent unidirectional downstream flow that was unimpeded by lake seiche activity (approximately 200 m upstream from the mouth). The majority of spawning activity on the Carp River occurs in two riffle areas, approximately 800 and 1200 m upstream from the mouth.

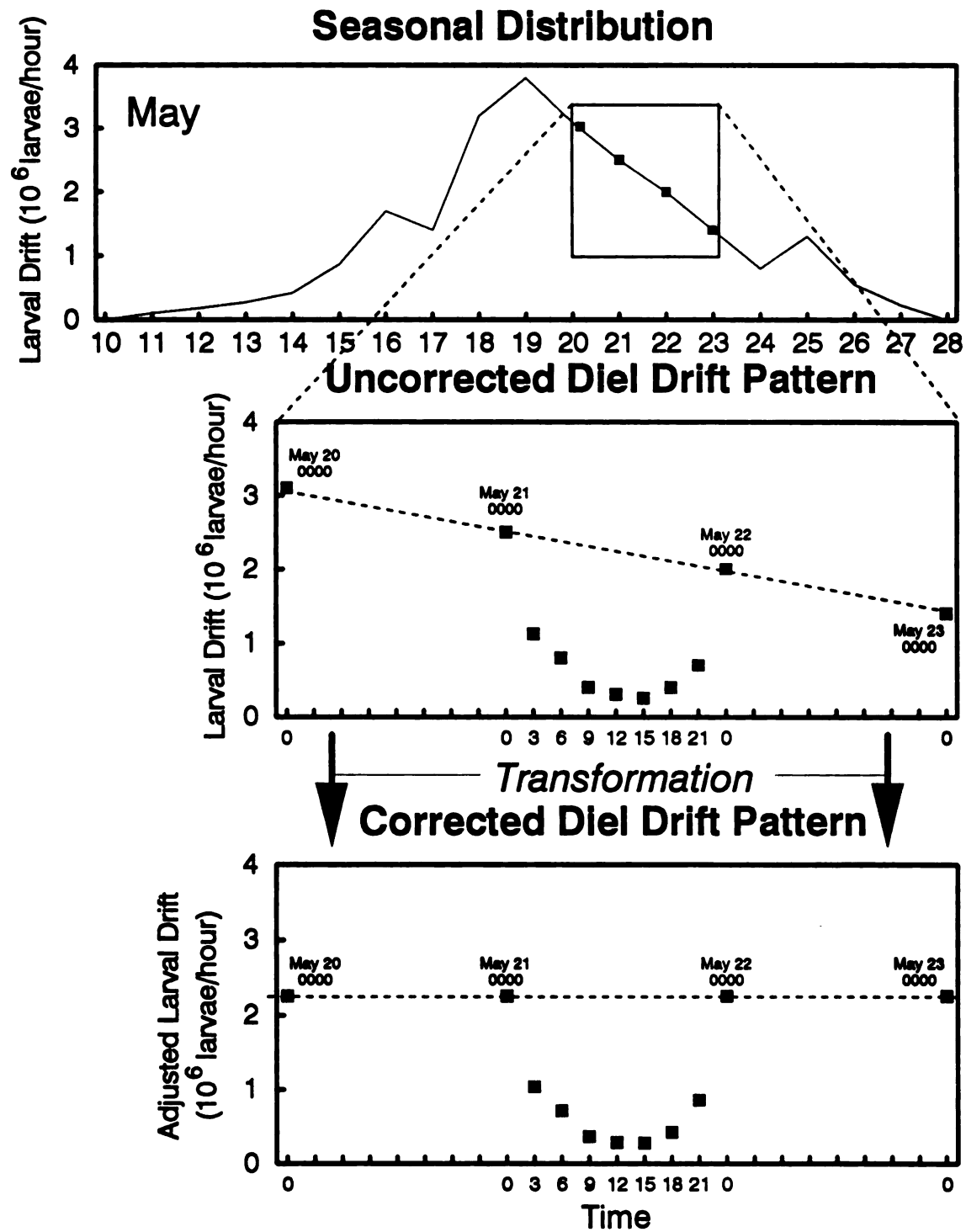


Figure 14. Diagram showing the process for correcting diel outmigration data to eliminate seasonal trends. When significant positive or negative slopes in peak nightly outmigration were detected, data were detrended to eliminate seasonal effects.

Diel sampling in 1991 and previously published studies (Clifford 1972, Gale and Mohr 1978, Winnell and Jude 1991) indicated that larval outmigration peaked at night, so all sampling was conducted between 22:00 and 02:00 hours. At each site, three replicate samples were collected by deploying nets at three fixed sites to estimate the mean outmigration rate and associated variance. Because larval drift rates varied by several orders of magnitude during the period of larval outmigration, I adjusted sampling time on each night between 2 to 10 minutes depending upon the prevailing larval drift rates. Sampling time was adjusted to maintain larval catch rates that would allow for accurate estimate of outmigration rates without sampling excessive numbers of larvae (capture rates ranged as high as 1500 larvae/minute). I adjusted sampling times to maintain larval capture rates at a minimum of 50 larvae per net set. I used a maximum sampling time of 10 minutes at each site to allow for sampling on four tributaries nightly during the peak period of diel outmigration. When larval outmigration rates were low, capture rates fell below 50 larvae per 10 minute net sets. All captured material was preserved in a 5% formalin solution. In the laboratory, larval rainbow smelt were separated from other collected material, counted, and preserved in 95% ethyl alcohol.

Seasonal Estimates of Tributary Mortality

Estimates of instantaneous and seasonal mortality from egg deposition to larval outmigration were calculated based on estimates of total seasonal egg deposition and seasonal larval outmigration. I estimated total egg deposition by multiplying total seasonal egg deposition (estimated at protected sites only) by the

area of available spawning habitat in each tributary. Estimates of total larval outmigration were calculated from nightly peak outmigration estimates and diel patterns in larval outmigration. Instantaneous mortality estimates were estimated by methods outlined in Ricker (1975) as follows:

$$z = \frac{\ln N_t - \ln N_0}{t}$$

where

- z = instantaneous mortality rate;
- N_t = total seasonal larval outmigration;
- N_0 = total seasonal egg deposition; and
- t = time in days between peak spawning and peak outmigration.

Environmental Conditions

Tributary temperatures were measured by deploying Ryan recording thermographs on tributary streams from April through early June of each year. I did not deploy a thermograph on Spring Creek in 1991 and the thermograph on Spring Creek failed in 1993. Temperature patterns for Spring Creek in 1993 were estimated by developing a multiple regression relationship for 1992 when temperatures were measured on all tributaries. Temperature patterns between these tributaries follow similar patterns and the multiple regression relationships used to estimate temperatures were robust (R^2 s > 0.97).

Discharge estimates were obtained by establishing staff gauges and developing discharge-staff gauge reading relationships for each tributary. Fixed staff gauges were established on each tributary at a point upstream from the influence of lake seiches. On each sampling night, staff gauge readings were taken prior to and just after sampling has been completed. Stream discharge was measured across a range of staff gauge readings to a discharge curve relationship related to fixed staff gauges on each stream. Staff gauge readings were used to estimate discharge during each sampling period.

RESULTS

Timing and Magnitude of Spawning

Spawning activity of rainbow smelt was concentrated between April 12th and May 4th on tributaries to St. Martin Bay, Lake Huron. Egg deposition was generally closely correlated with spawner CPUE on all tributaries. On all tributaries spawning occurred later and was temporally compressed in 1992. Although there were consistent trends in the water temperature at peak spawning within tributaries, peak spawning across tributaries occurred over a range of temperatures from 3 to 7 C.

From 1991 to 1993, spawning rainbow smelt were generally present in the Carp River between April 14th and May 2nd (Figure 15). In 1991, concentrations of spawning fish were present from April 14th to April 26th. In 1992, cold water temperatures resulted in delayed and temporally compressed spawning runs

compared to 1991 (Figure 16). In 1993, concentrations of spawning fish were present from April 18th to April 28th, with the highest CPUE of adults occurring from April 18th to April 20th. In 1991 and 1992, peak spawner abundance occurred when water temperatures were 5 to 7 C, while in 1993 peak spawner abundance when water temperatures were only 3.5 C.

In Nunns Creek, the timing and duration of spawning activity closely resembled patterns observed for the Carp River. In 1991, extensive spawning occurred over a two week period from April 16th to April 30th, although the majority of egg deposition occurred from April 21st to April 26th (Figure 17). In 1992, cold water temperatures (< 3 C) resulted in delayed and temporally compressed spawning in Nunns Creek (Figure 18). Egg deposition was closely correlated with spawner CPUE with peak spawning activity occurring on April 26th (Figure 17). In 1993, spawner abundance and egg deposition were bimodally distributed with peak activity occurring on April 20th and April 27th (Figure 17). In all three years, peak spawner abundance and egg deposition were associated with water temperatures of 5 C (Figure 18).

On Spring Creek, water temperature, spawner abundance, and egg deposition data were not collected in 1991. Egg deposition was closely correlated with spawner CPUE in 1992 and 1993 (Figure 19). Peak spawning activity in 1992 and 1993 were associated with water temperatures of 4 C (Figure 20). In 1992, spawning activity ranged from April 23rd to May 4th with peak spawner abundance and egg deposition occurring on April 26th (Figure 19). In 1993,

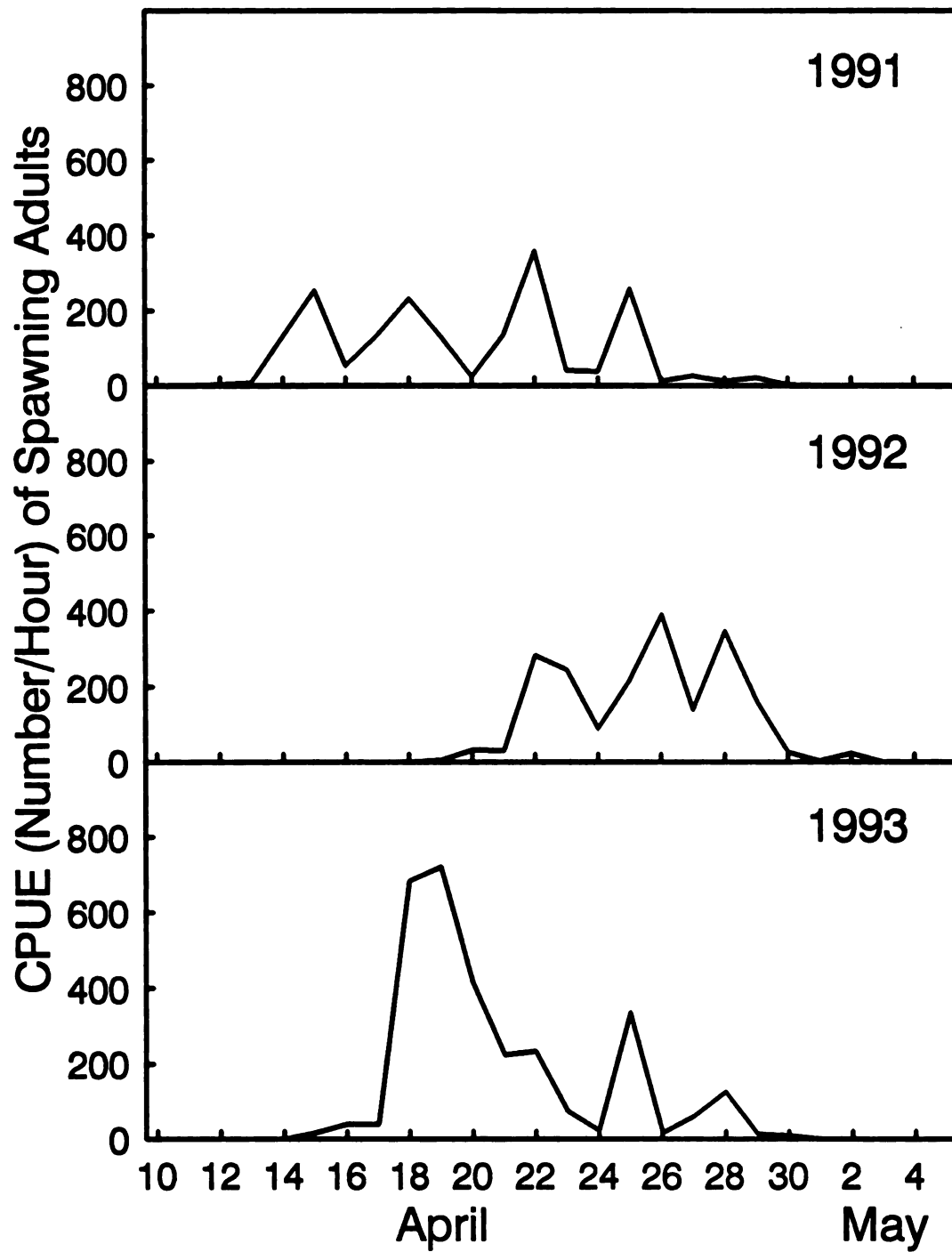


Figure 15. Spawner abundance of rainbow smelt spawning in the Carp River, Mackinaw County, Michigan from 1991 to 1993.

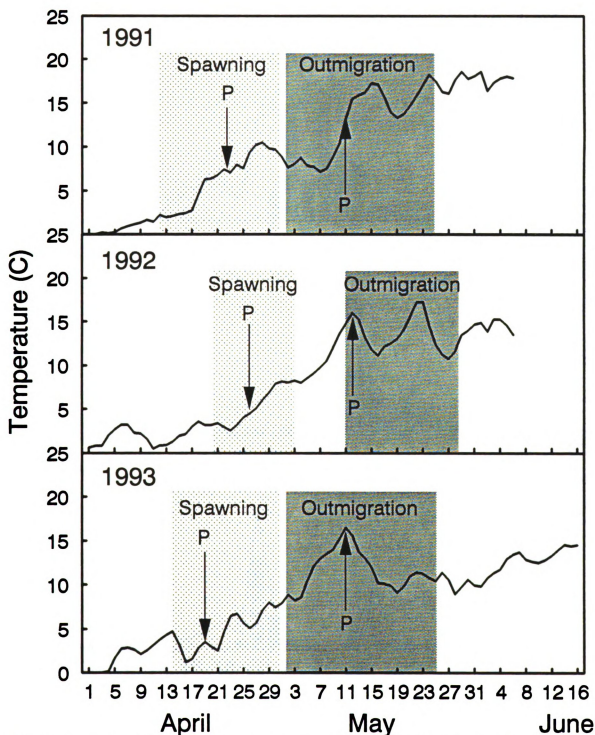


Figure 16. Water temperatures during spawning and larval outmigration from the Carp River from 1991 to 1993. Shaded areas indicate periods of spawning activity and larval outmigration (arrows indicate peaks).

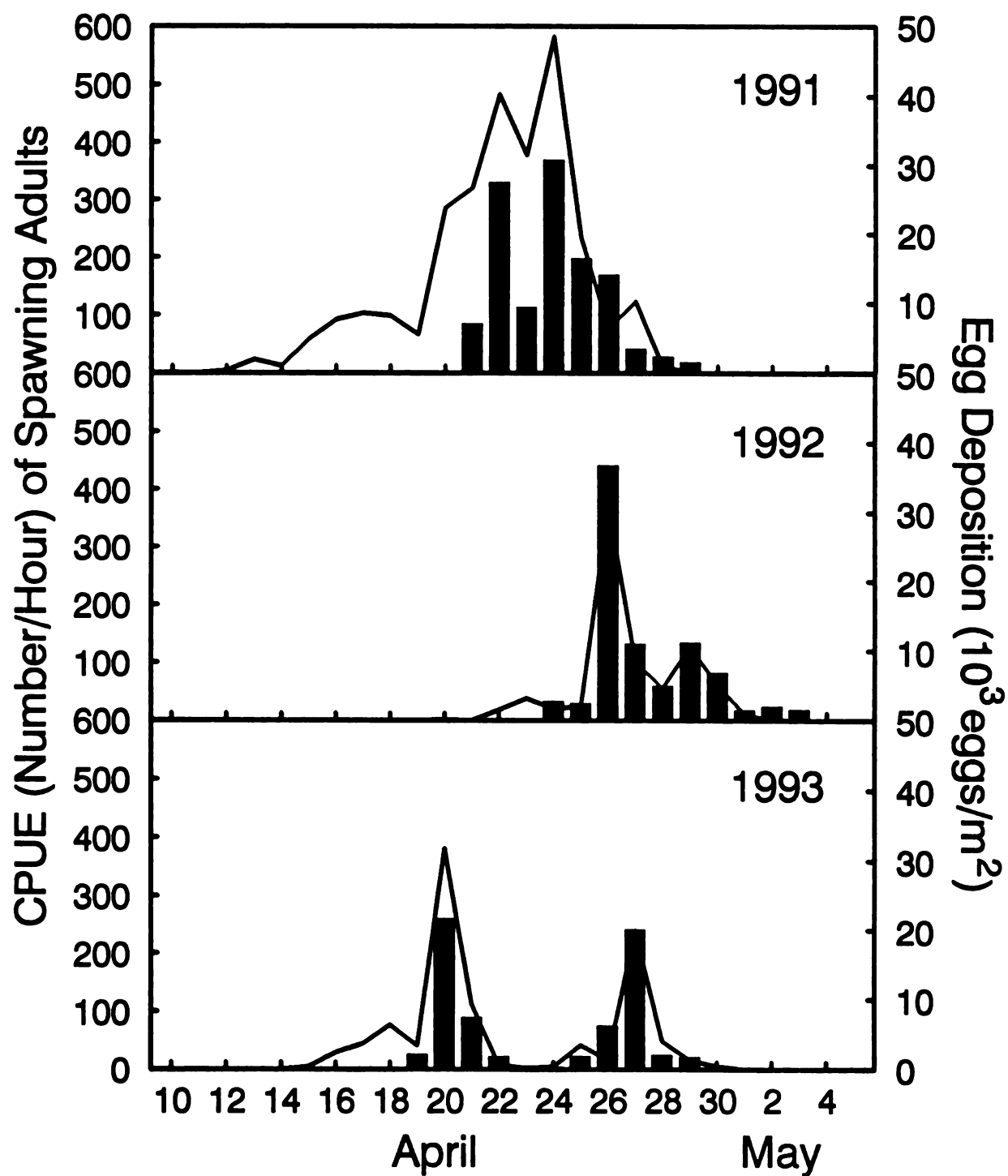


Figure 17. Spawner abundance (solid line) and mean egg deposition (bars) of rainbow smelt spawning in Nunns Creek, Mackinac County, Michigan from 1991 to 1993.

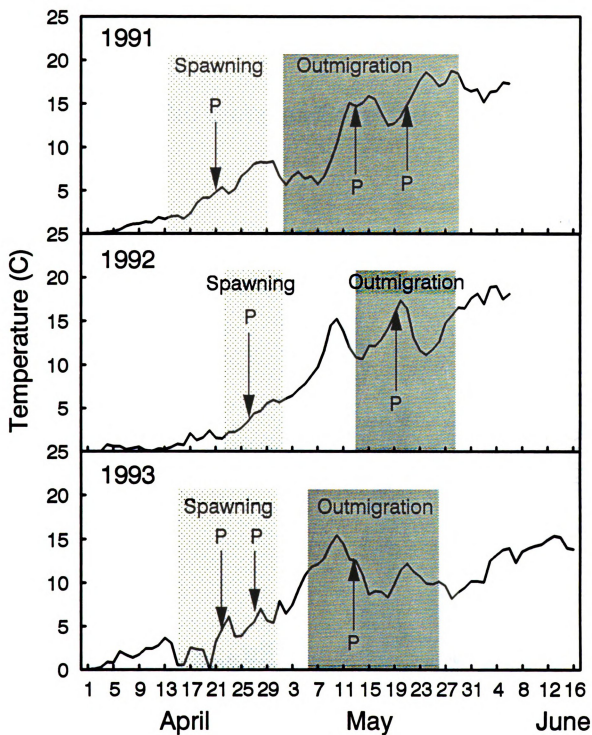


Figure 18. Water temperature during spawning and larval outmigration from Nunns Creek from 1991 to 1993. Shaded areas indicate periods of spawning activity and larval outmigration (arrows indicate peaks).

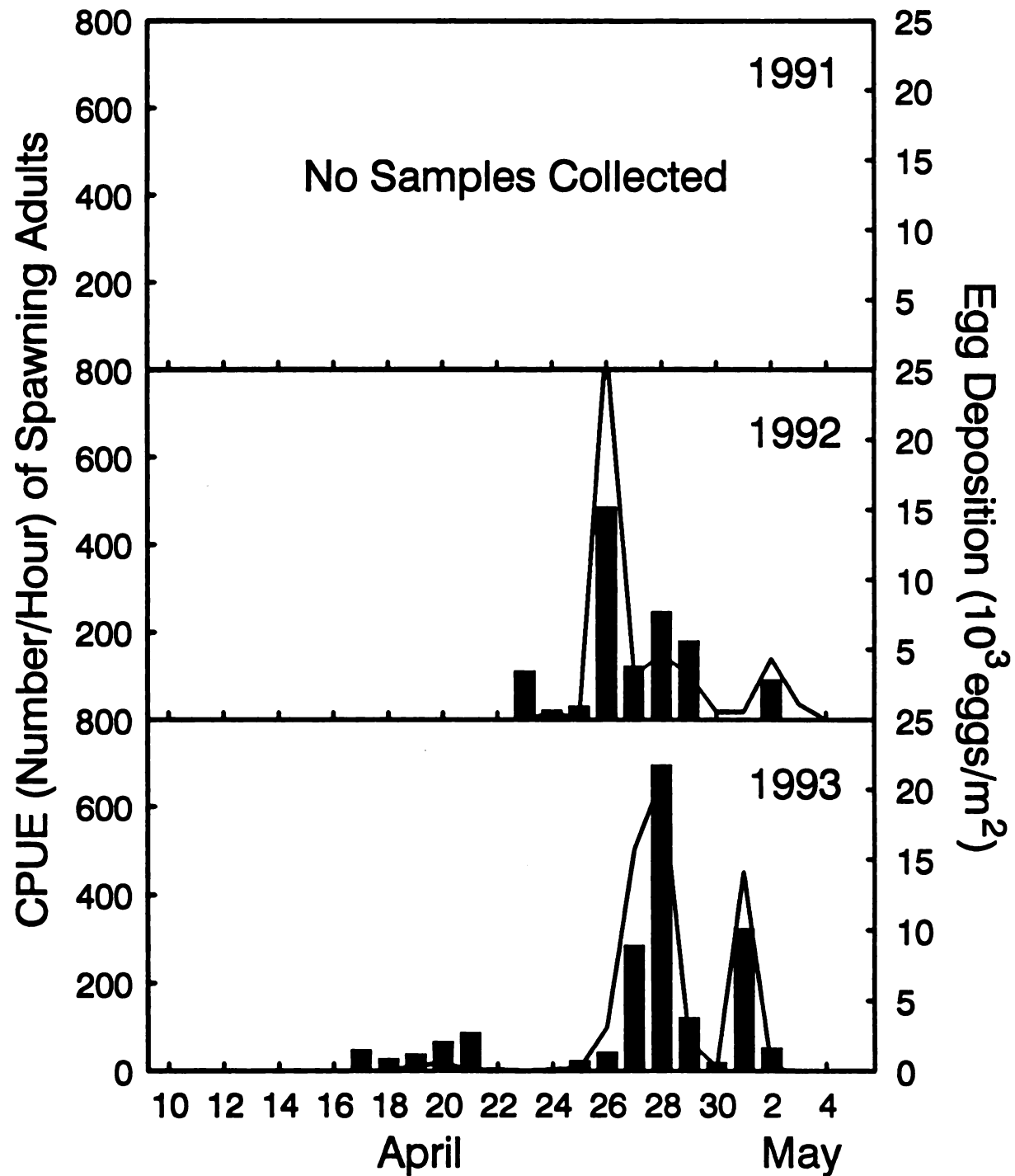


Figure 19. Spawner abundance (solid line) and mean egg deposition (bars) of rainbow smelt spawning in Spring Creek, Mackinac County, Michigan from 1992 to 1993.

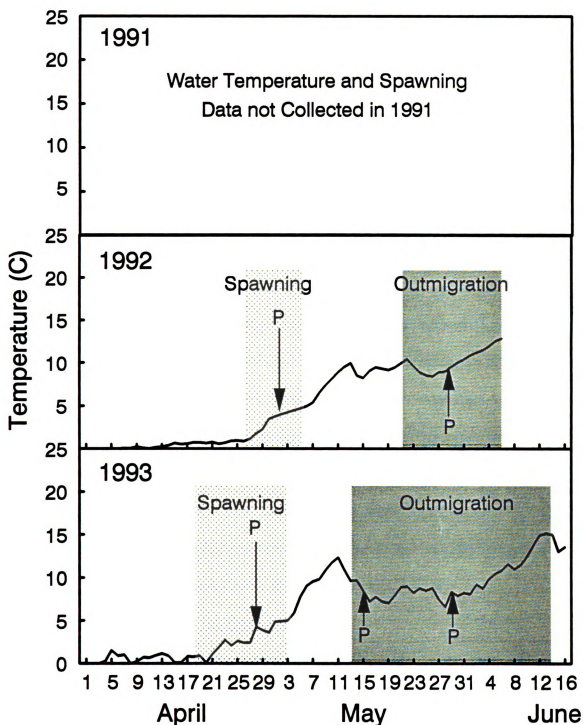


Figure 20. Water temperature during spawning and larval outmigration in Spring Creek from 1992 to 1993. Shaded areas indicate periods of spawning activity and larval outmigration (arrows indicate peaks).

water temperatures in Spring Creek rose above 3 C approximately 7 days earlier than in 1992, resulting in an earlier and prolonged spawning period (Figure 20). In 1993, spawning activity ranged from April 17th to May 2nd with peak spawning and egg deposition occurring on April 28th and 31st (Figure 19). Spawning generally occurred 3 to 7 days later on Spring Creek than on the Carp River and Nunns Creek due to slower warmer of tributary water temperatures (Figures 16, 18, & 20).

The timing and duration of spawner abundance and egg deposition on St. Martin Creek closely resembled the pattern on Spring Creek due to similar water temperatures (Figure 21). In all three years, peak levels of spawner activity were associated with water temperatures of 5 to 6 C. Spawning activity in 1991 ranged from April 16th to April 27 with peak spawner abundance occurring on April 21st (Figure 22). In 1992, spawning was delayed by cold water temperatures and ranged from April 22 to May 3rd (Figures 21 & 22). In 1993, spawning activity was bimodally distributed with peak spawner abundance occurring on April 19th and April 28th (Figure 22). This pattern was similar to the bimodal distribution of spawning observed in Nunns Creek in 1993 (Figures 17 & 22).

Recreational Fishery Effects on Egg Deposition

I found that protected sites had significantly higher egg densities (Wilcoxon Signed Rank Test, Normal T Approximation 4.564, $P < 0.0001$) than unprotected sites, suggesting that recreational fishery activity caused a decline in the density of eggs nightly. To evaluate the effect that the protective shelters may have had in either increasing or reducing egg deposition, I compared egg densities between

protected and unprotected sites on nights when there was no recreational fishing effort. Comparison of these paired observations demonstrated no significant differences between protected and unprotected sites (Wilcoxon Signed Rank Test, Normal T Approximation $T = 0.349$, $P = 0.7268$) on nights when recreational fishing activity was absent.

I found a negative relationship between recreational fishing effort and percent change in egg deposition between protected and unprotected sites (adjusted $r^2 = 0.633$, $P < 0.0001$, Figure 23). Levels of recreational fishing effort below 5 people/100-m² had little effect on egg densities, while levels of effort ranging from 12 to 17 people/100-m² resulted in 30 to 70% reductions in egg density.

Seasonal Egg Deposition Estimates

Because recreational fishery activity resulted in significant declines in egg density, I used egg deposition estimates from protected sites to estimate total seasonal egg deposition. Nightly egg deposition estimates were summed over the course of the spawning season to produce a seasonal egg deposition estimate. On Nunns Creek, total egg deposition was highest in 1991 and declined annually between 1991 and 1993 (Table 16). Total egg deposition on Spring Creek was slightly less than the 3-year average on Nunns Creek in 1992, but declined substantially in 1993 (Table 16). Total egg deposition on St. Martin Creek was approximately equal to egg deposition on Spring Creek in 1992, but also declined between 1992 and 1993 (Table 16).

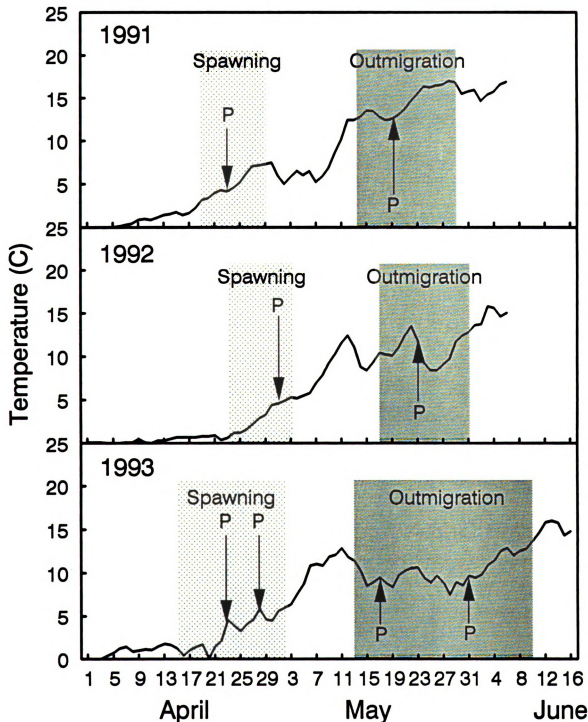


Figure 21. Water temperature during spawning and larval outmigration in St. Martin Creek from 1991 to 1993. Shaded areas indicate periods of spawning activity and larval outmigration (arrows indicate peaks).

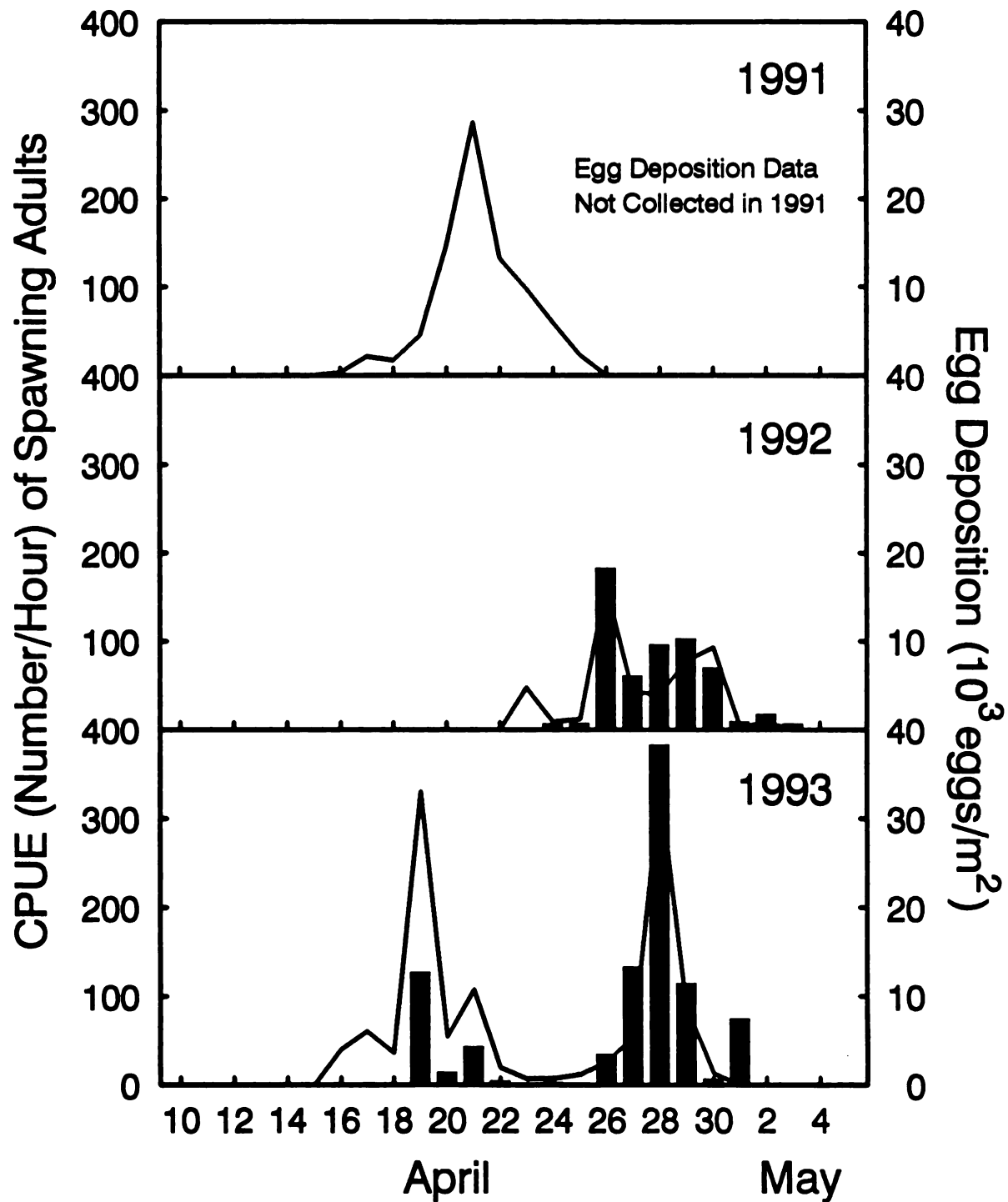


Figure 22. Spawner abundance (solid line) and mean egg deposition (bars) of rainbow smelt spawning in St. Martin Creek, Mackinac County, Michigan from 1991 to 1993.

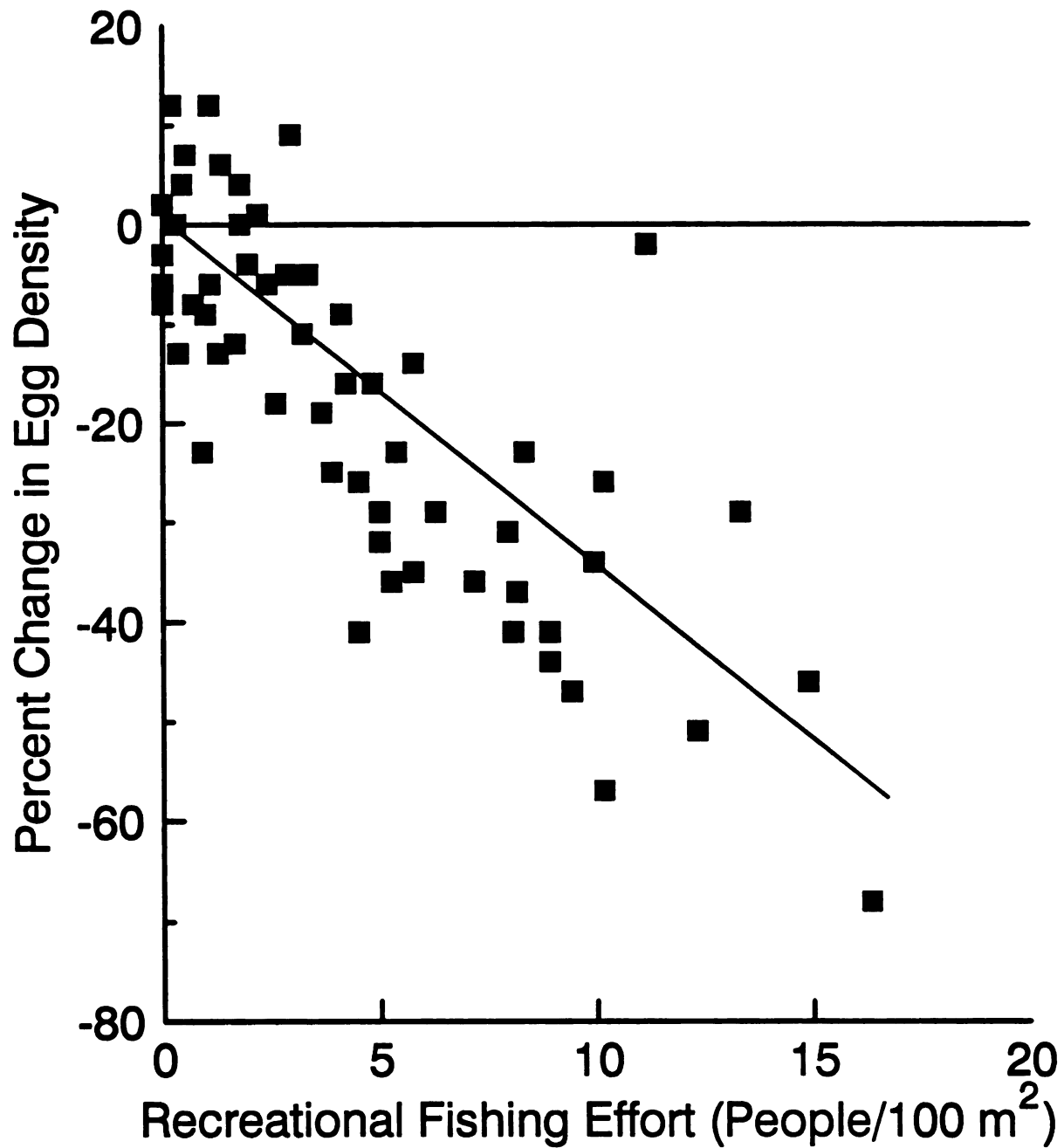


Figure 23. Relationship between recreational fishing effort and percent change in egg density at paired sampling sites in Nunns, Spring, and St. Martin Creeks sampled in April 1991 to 1993.

Table 16. Total egg deposition (millions) by rainbow smelt spawning in three tributaries to St. Martin Bay, Lake Huron from 1991 to 1993.

Tributary	Total Egg Deposition ($\times 10^6$)		
	1991	1992	1993
Nunns Creek	113.4	84.4	70.9
Spring Creek	-----	69.4	19.0
St. Martin Creek	-----	60.3	8.4

Diel Patterns in Larval Drift

All rainbow smelt larvae sampled during drift net surveys were at the prolarval stage (yolk sacs present). Diel sampling of larval outmigration demonstrated that the peak and vast majority of larval outmigration occurred at night (Figure 24). Diel patterns were remarkably similar between sampling dates as evidenced by small standard errors (Figure 24), indicating that diel patterns were stable between tributaries on a seasonal basis. Diel patterns between tributaries were consistent and not significantly different from one another (Chi Square₂₁ = 2.153, $P > 0.30$). The Carp River, Nunns Creek, and Spring Creek were each sampled hourly on one night between 2100 and 0600 to produce a finer resolution of the outmigration pattern during nightly peak events. Results of this sampling indicate that the nightly distribution of larval outmigration was approximately normally distributed with peak outmigration occurring between 2300 and 0100 (Figure 25).

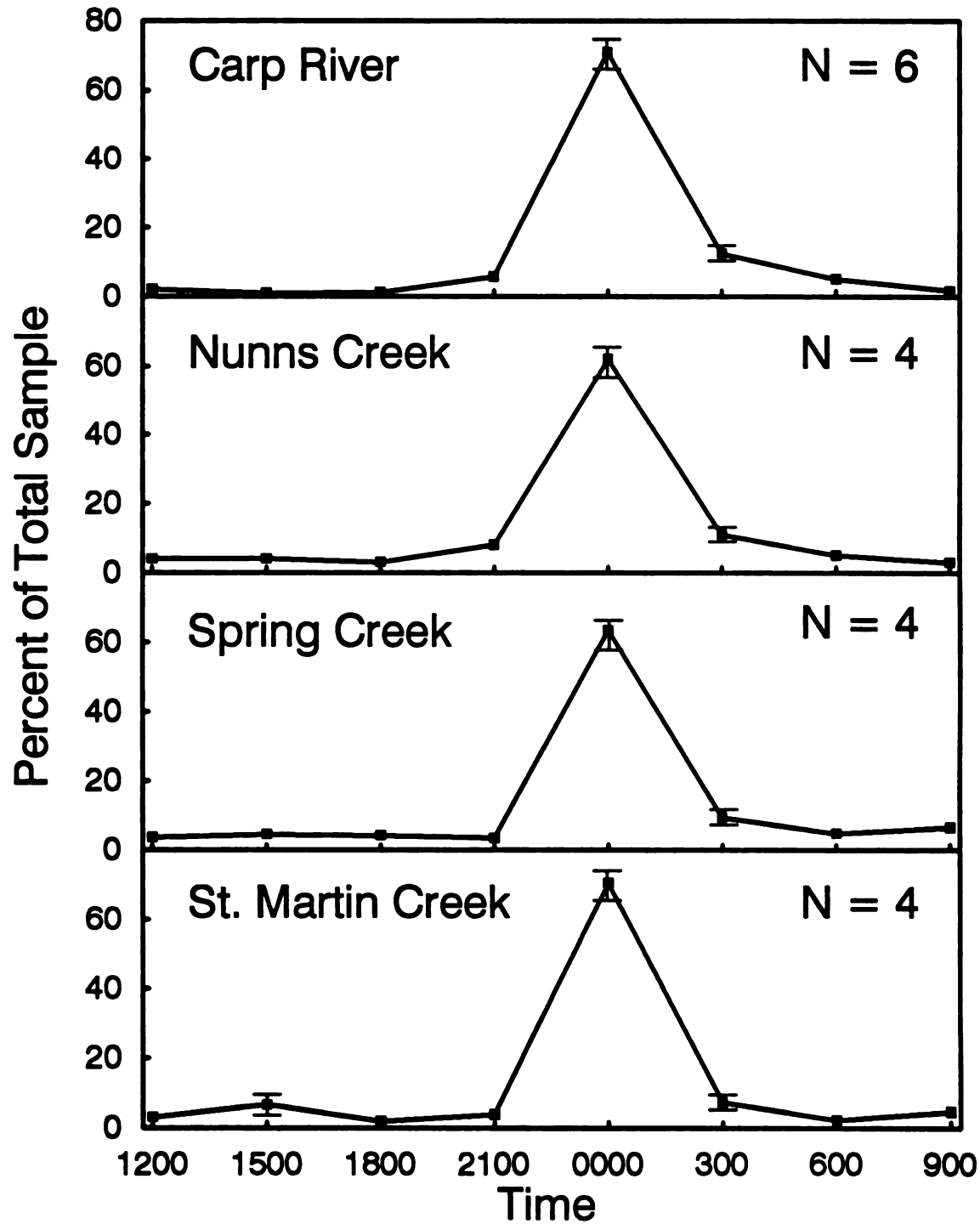


Figure 24. Diel larval outmigration patterns occurring in the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek. Values are expressed as a percentage of the total larvae captured during the 24-hour period.

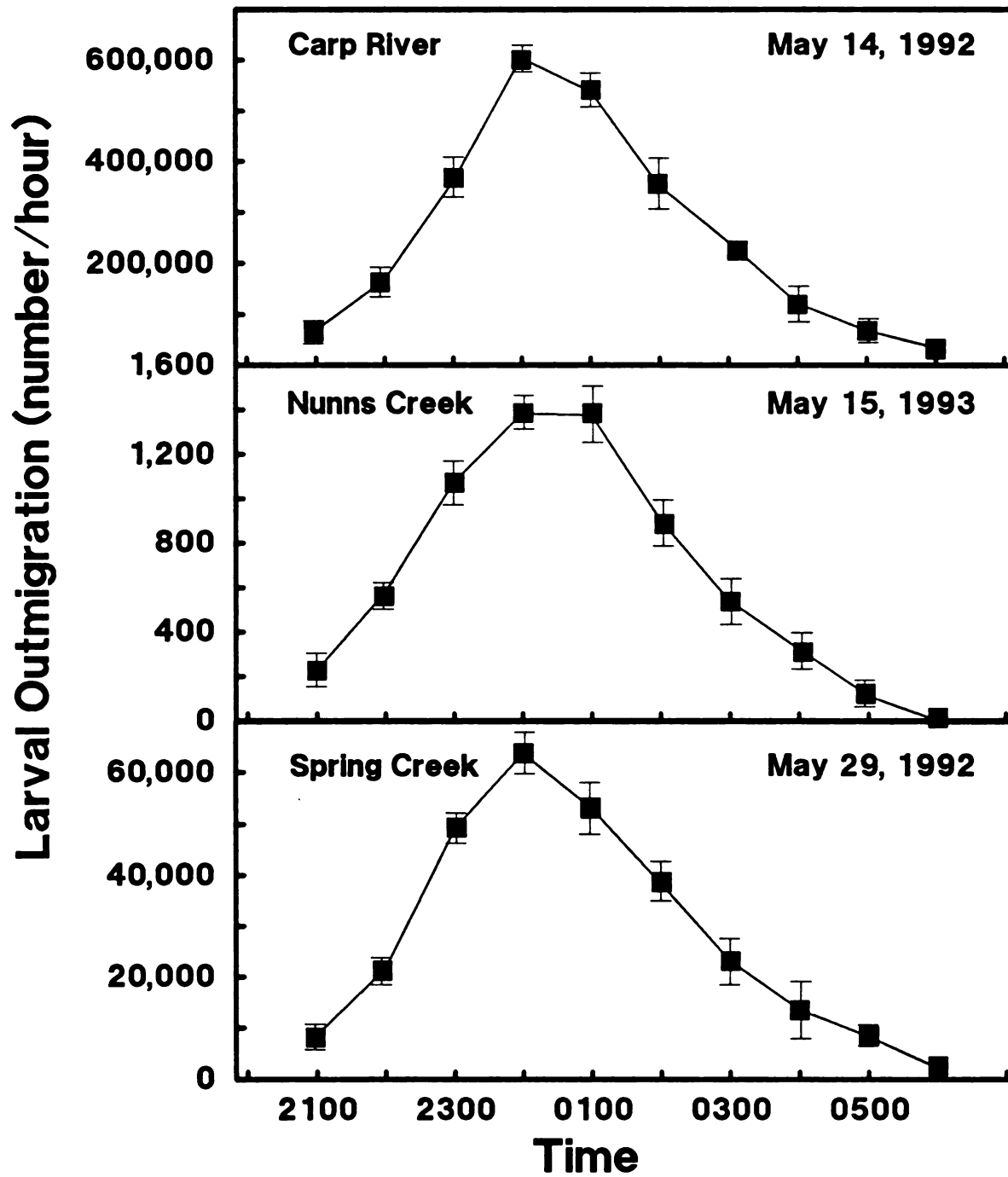


Figure 25. Nightly pattern of larval outmigration (number/hour) occurring on the Carp River, Nunns Creek and Spring Creek between 2100 and 0600.

Seasonal and Interannual Patterns in Larval Drift

The Carp River dominated larval production on the four study tributaries, producing 72.8%, 74.8%, and 96.4% of the total larval output from these tributaries in 1991 to 1993, respectively (Table 17). High larval output from the Carp River is associated with the large area of available spawning habitat and large spawning populations in the river system. In 1991, larval outmigration occurred from May 2nd to May 25th, with peak hourly outmigration of approximately 1.2 million larvae/hour on May 10th (Figure 26). Larval outmigration in 1992 occurred between May 11th and May 28th, with the peak hourly larval outmigration of approximately 860,000 larvae/hour on May 13th. In 1993, larval outmigration occurred between May 2nd and May 25th, with the peak hourly larval outmigration of approximately 900,000 larvae/hour on May 11th. In 1992 and 1993, peak larvae outmigration coincided with a peak in tributary water temperature. Total larval production in the Carp River was highest in 1991 (33.85 million larvae) and lowest in 1992 (9.88 million larvae, Table 17). Discharge on all tributaries declined throughout the larval outmigration periods, and there was no consistent relationship between discharge levels and outmigration on any tributary.

Nunns Creek was a minor contributor to the total larval production of these tributaries, producing 0.7%, 1.6%, and 1.7% of the total larval production in 1991 to 1993, respectively (Table 17). The start, peak, and end of larval outmigration on Nunns Creek occurred several days after the corresponding events on the Carp River (Figures 26 & 27). In 1991, larval outmigration

occurred between May 4th and May 28th, with two peaks in hourly outmigration on May 13th (13,700 larvae/hour) and May 21st (11,780 larvae/hour, Figure 27). Larval outmigration in 1992 occurred between May 13th and May 26th, with the peak hourly migration of 22,000 larvae/hour on May 18th. In 1993, larval outmigration occurred between May 6th and May 26th with the peak hourly migration of 53,000 larvae/hour on May 13th (Figure 27). Total larval production in Nunns Creek was highest in 1993 (550,000 larvae) and lowest in 1992 (210,000 larvae, Table 17).

Spring Creek produced the latest larval outmigration of the four study tributaries in all three years of the study due to colder water temperatures that delayed spawning and increased egg incubation time (Figure 28). Spring Creek had relatively high levels of larval production in 1991, producing almost 10 million larvae and representing 21.4% of the total larval production of the four study tributaries (Table 16). In 1991, larval outmigration occurred between May 14th and June 1st with the peak hourly outmigration of 773,000 larvae/hour occurring on May 24th (Figure 28). Larval outmigration in 1992 occurred between May 21st and June 6th with the peak hourly migration of 83,000 larvae/hour on May 28th (Figure 28). In 1993, larval outmigration occurred between May 20th and June 15th with the peak larval outmigration of 23,560 larvae/hour on May 26th (Figure 28). Total larval output from Spring Creek was highest in 1991 (9.97 million larvae) and lowest in 1993 (390,000 larvae, Table 16).

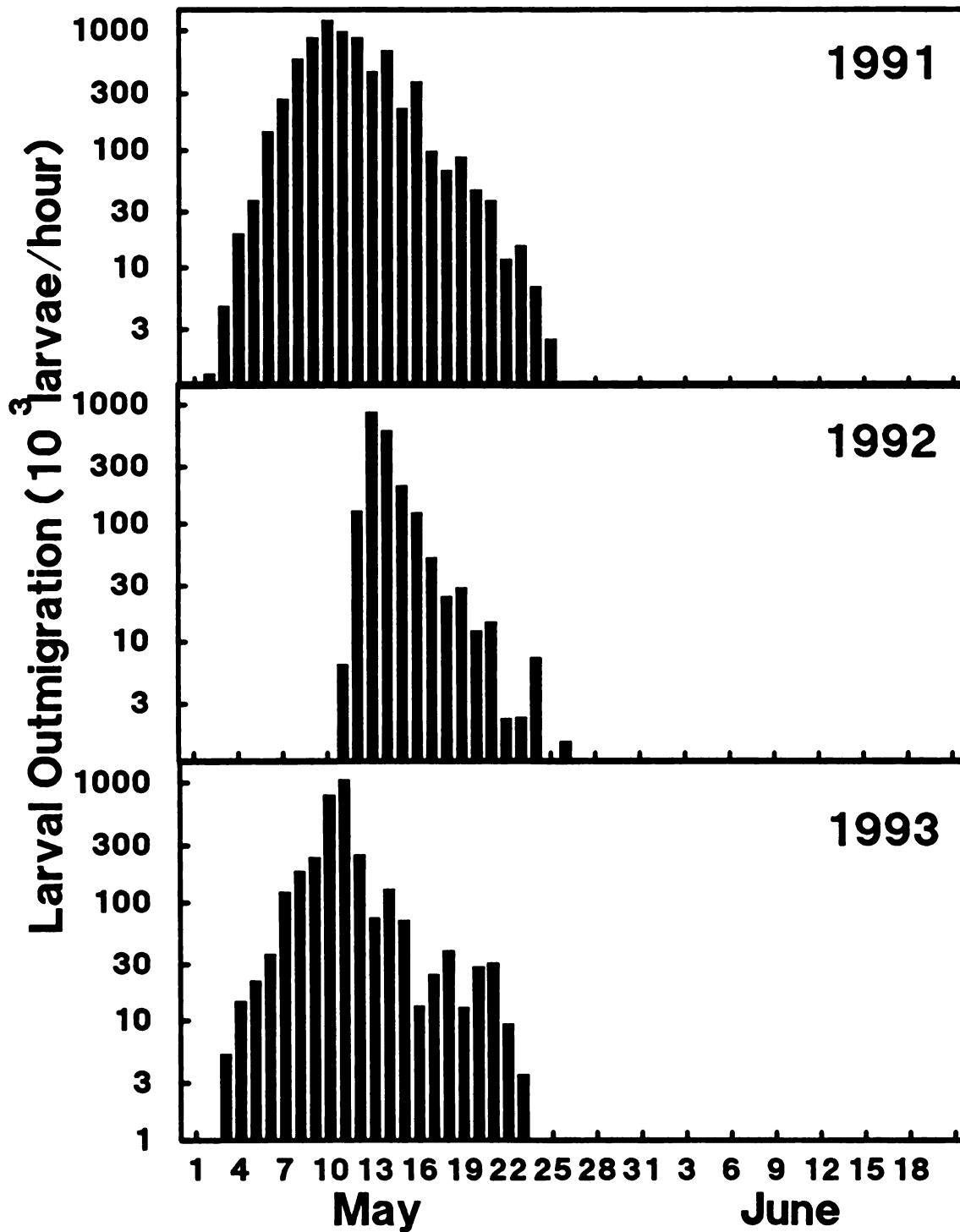


Figure 26. Peak nightly outmigration (number/hour) of larval rainbow smelt sampled between 2200 and 0200 on the Carp River, Mackinac County, Michigan from 1991 to 1993.

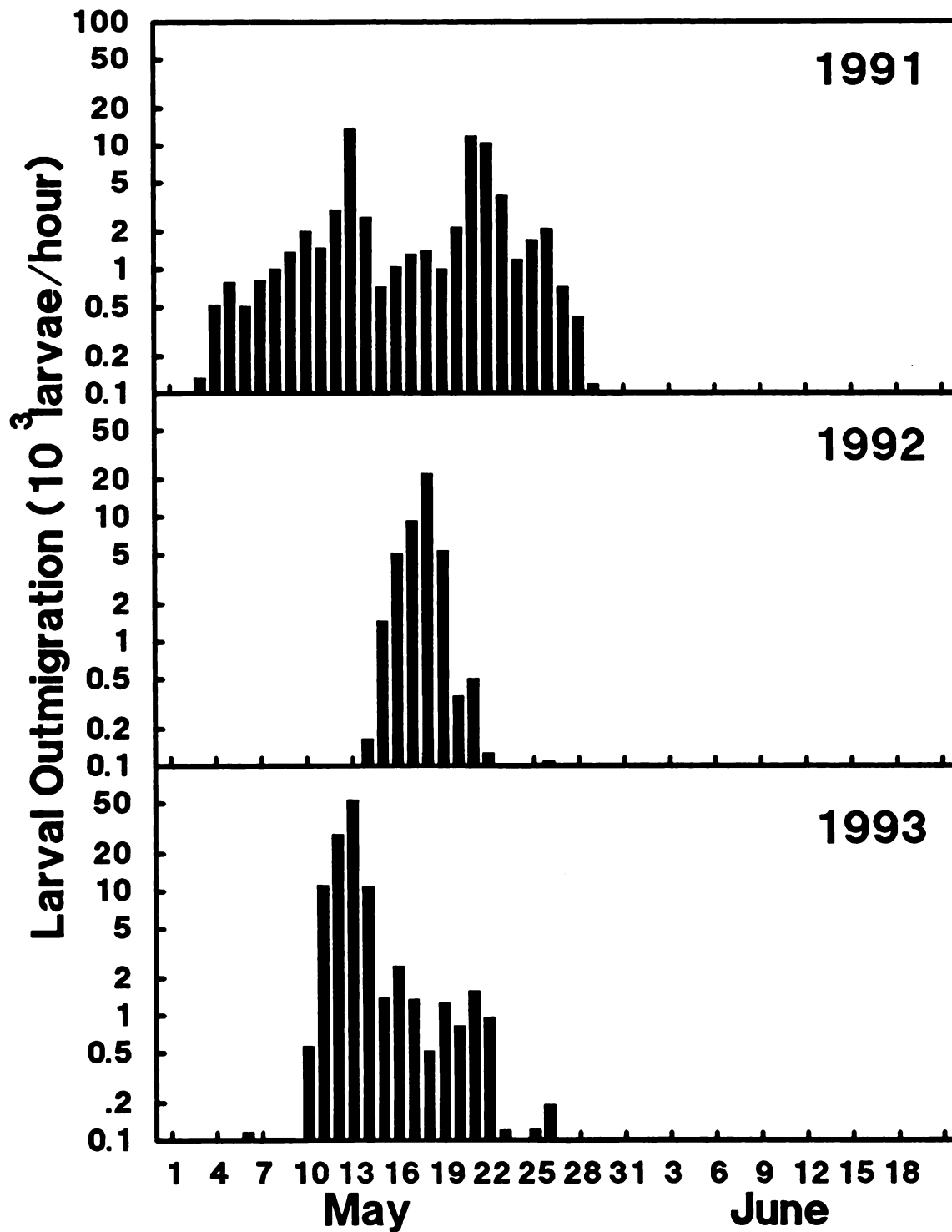


Figure 27. Peak nightly outmigration of larval rainbow smelt (number/hour) sampled between 2200 and 0200 on Nunns Creek, Mackinac County, Michigan from 1991 to 1993.

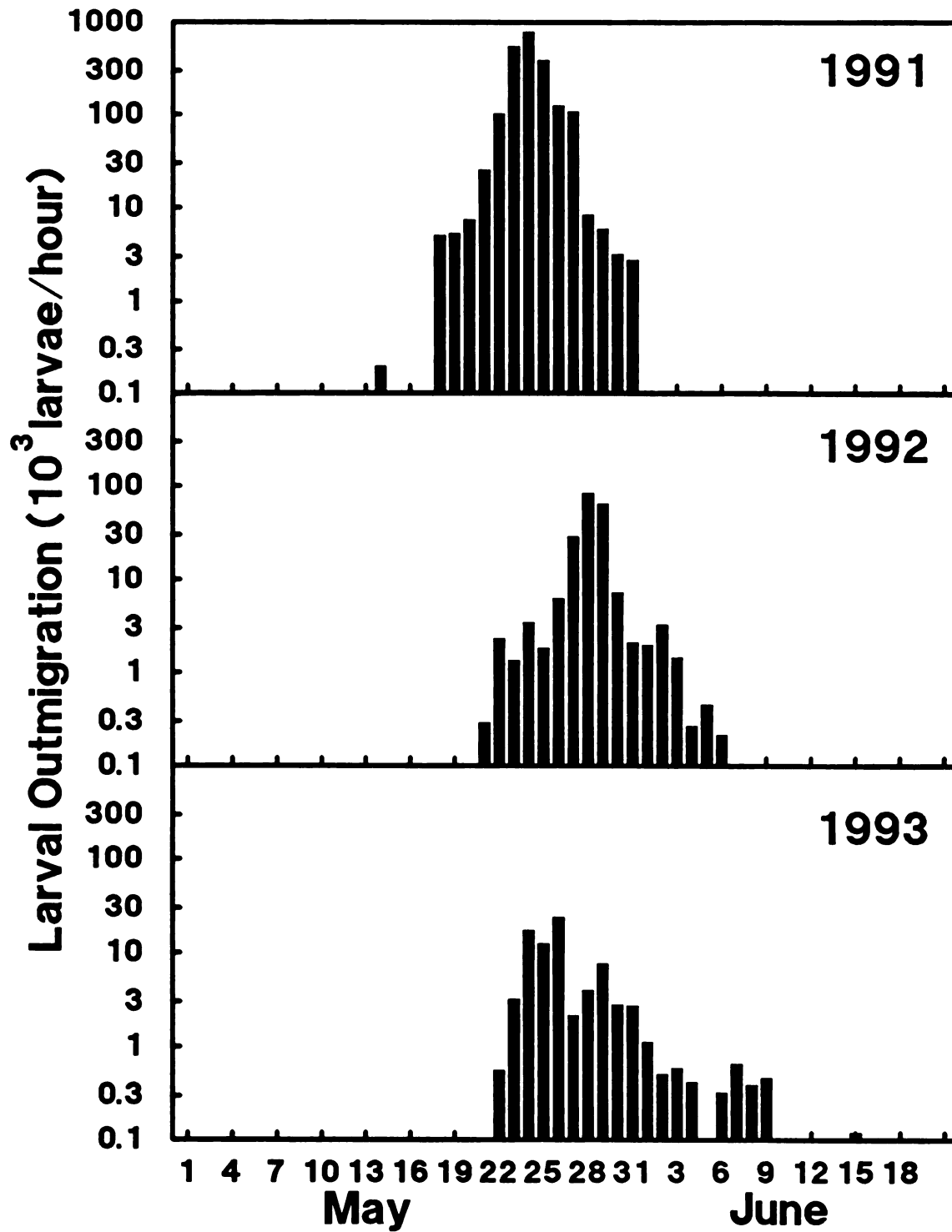


Figure 28. Peak nightly outmigration of larval rainbow smelt (number/hour) sampled between 2200 and 0200 on Spring Creek, Mackinac County, Michigan from 1992 to 1993.

Table 17. Total outmigration (millions) of larval rainbow smelt from four tributaries to St. Martin Bay, Lake Huron from 1991 to 1993.

Tributary	1991	1992	1993
Carp River	33.85	9.88	30.58
Nunns Creek	0.32	0.21	0.55
Spring Creek	9.97	0.99	0.39
St. Martins Creek	2.35	2.13	0.20
Total	46.49	13.21	31.72

St. Martin Creek was a minor contributor to total larval production in 1991 and 1993, but produced 16.1% of the total larval production of the four study tributaries in 1992 because of relatively low larval production from other tributaries. In 1991, larval outmigration occurred from May 13th to May 29th with the peak hourly outmigration of 66,000 larvae/hour on May 15th (Figure 29). Larval outmigration in 1992 occurred from May 17th to May 31st with a peak hourly outmigration of 225,000 larvae/hour on May 22nd (Figure 29). In 1993, larval outmigration occurred from May 12th to June 10th with no discernable peak in hourly outmigration (Figure 29). Total larval output from St. Martin Creek was highest in 1991 (2.35 million larvae) and lowest in 1993 (200,000 larvae, Table 16).

Total larval production from the four study tributaries was highest in 1991 and lowest in 1992. Earliest larval outmigration began on approximately May 3rd in 1991 and 1993, but cold water temperatures delayed the initiation of larval

outmigration until May 11th in 1992 (Figure 30). In all three years, larval outmigration from tributaries had subsided by approximately June 5th (Figure 30).

Tributary Mortality

Tributary mortality rates were estimated for the period from egg deposition to larval outmigration for tributaries and years when egg deposition estimates were available. Instantaneous mortality was highest in Nunns Creek (Table 18), while mortality rates were similar between Spring and St. Martin Creeks (Table 18). Patterns between 1992 and 1993 were consistent among tributaries, with higher survival occurring in 1993. Because instantaneous mortality rates were also higher in 1992, low survival in 1992 was not strictly a function of increased incubation time (Table 18).

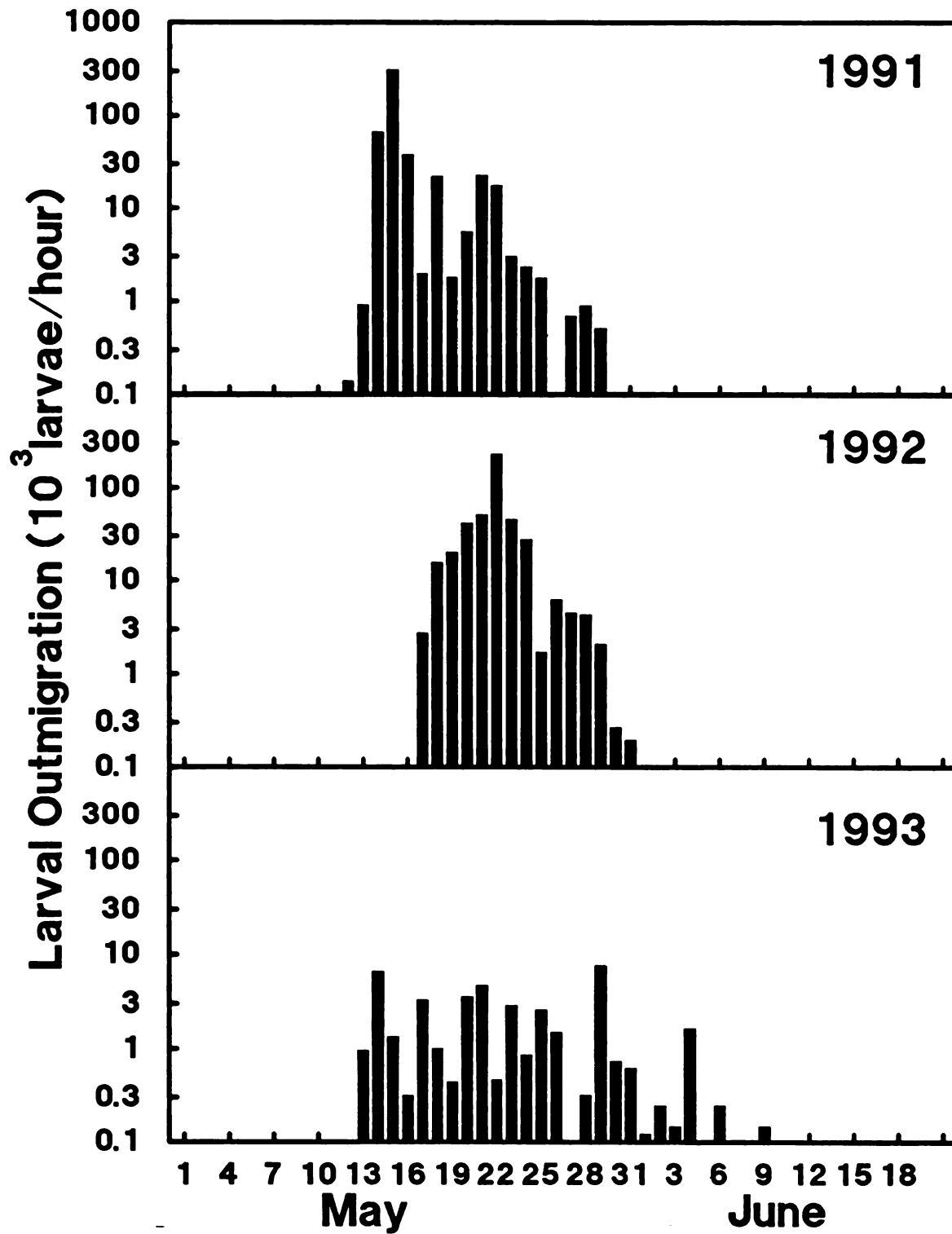


Figure 29. Peak nightly outmigration of larval rainbow smelt (number/hour) sampled between 2200 and 0200 on St. Martin Creek, Mackinac County, Michigan from 1991 to 1993.

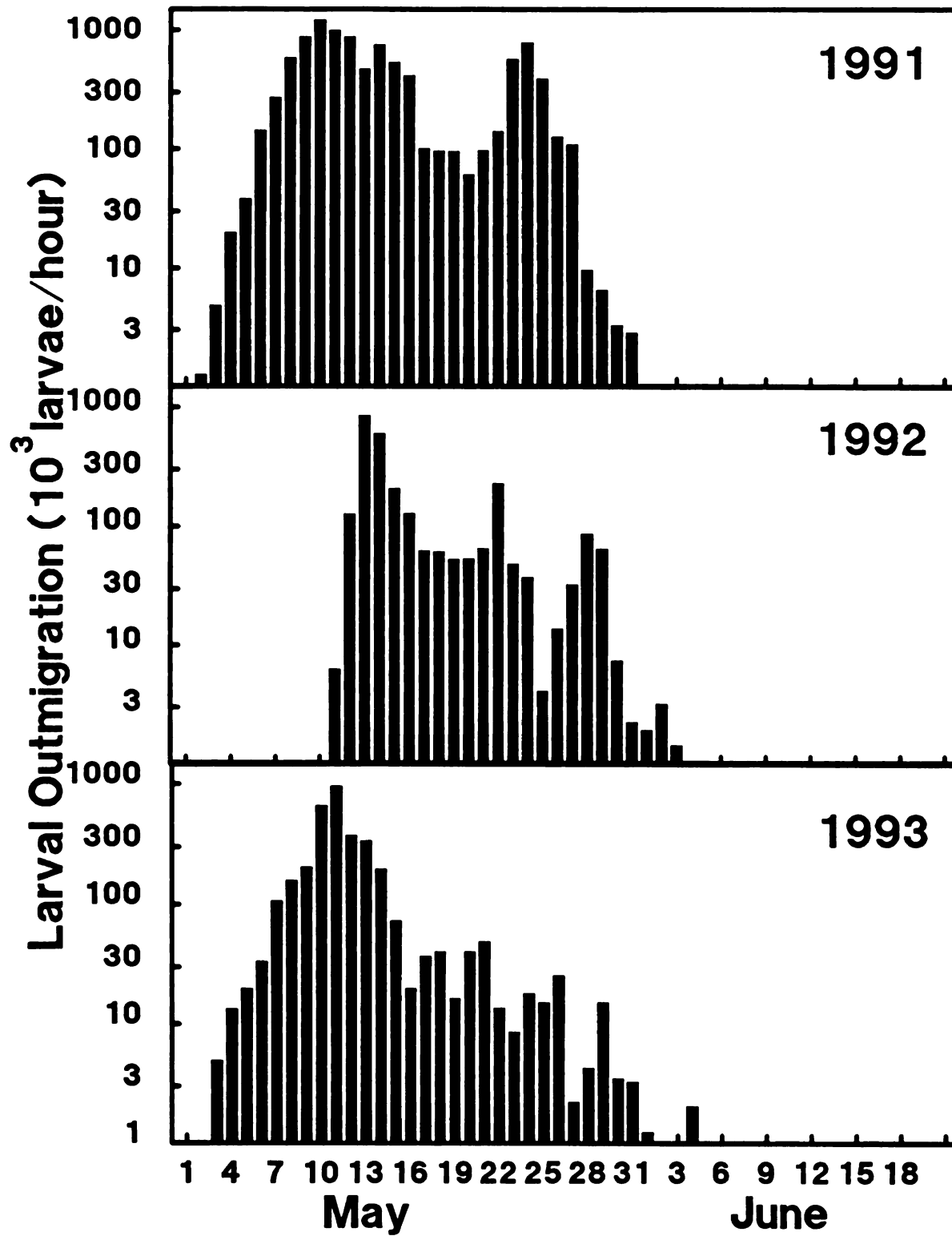


Figure 30. Total peak larval outmigration (number/hour) sampled between 2200 and 0200 on the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek from 1991 to 1993.

Table 18. Instantaneous mortality (Z) and seasonal survival rates (%) of rainbow smelt from egg deposition to larval outmigration on three tributaries to St. Martin Bay, Lake Huron from 1991 to 1993.

Instantaneous Mortality Rates (Z)

Tributary	1991	1992	1993
Nunns Creek	0.232	0.260	0.194
Spring Creek	-----	0.163	0.139
St. Martin Creek	-----	0.159	0.138

Seasonal Survival Rates (%)

Tributary	1991	1992	1993
Nunns Creek	0.300	0.249	0.776
Spring Creek	-----	1.426	2.053
St. Martin Creek	-----	1.875	2.371

DISCUSSION

Effect of Temperature on the Timing of Spawning

Normally, spawning activity commenced in the four tributary streams once snowmelt associated runoff subsided and tributary water temperatures reached 3 to 5 C. In some years, initial spawning activity was curtailed by a late snowfall (e.g. April 19 to 20, 1993), which quickly melted resulting in depressed tributary water temperatures. In this study, peak spawning occurred at temperatures of 3

to 7 C, and varied between tributaries. In mid-April, adults (primarily males) were often present in tributaries when water temperature were less than 1 C. Peak spawning in the all four tributaries occurred at colder water temperatures (3 to 7 C) than has been previously reported (8.9 C) by Scott and Crossman (1985).

Egg Deposition and Survival

Egg deposition was highly correlated with spawner abundance, except during the earliest portion of spawning runs when spawning populations were dominated (>80%) by males. Egg to outmigrating larvae survival rates were approximately an order of magnitude lower on Nunns Creek than on Spring or St. Martin Creeks. There are three factors that might adversely affect survival rates of eggs and larvae on Nunns Creek. First, water temperatures on this tributary were generally warmer than on the other two tributaries. Warmer water temperatures during incubation may lead to increased growth of saprochytic fungi which has been previously documented as a source of mortality for rainbow smelt eggs (Rothschild 1961). I did observe fungal growth in areas with dense egg densities on Nunns Creek. Second, Nunns Creek hosts a dense spawning run of white (*Catostomus commersoni*) and longnose (*C. catostomus*) suckers, which generally occurred during egg incubation of rainbow smelt. Spawning activity by suckers may increase mortality by dislodging eggs and by declines in dissolved oxygen due to dense concentrations of eggs. During periods of intense spawning by suckers, I observed increased numbers of drifting rainbow smelt eggs during drift net surveys. Adult suckers may also feed directly on rainbow smelt eggs, although this would be difficult to document due to the rapid digestion rates of

fish eggs. Third, recreational fishing effort is significantly higher on Nunns Creek than on Spring or St. Martin Creeks. Because recreational fishing activity was shown to significantly reduce egg densities in these study streams, higher levels of activity on Nunns Creek probably contribute to higher mortality rates between egg deposition and larval outmigration.

Egg survival rates reported in this study were within the range of survival rates reported by other investigators. Rupp (1965) reported egg survival rates ranging from 0 to 2% (average 1.06%) for shoreline spawning rainbow smelt in Branch Lake, Maine. Rothschild (1961) reported egg survival of 24% to the prehatching stage, and 0.55% to the prolarval stage for rainbow smelt spawning in Dean Brook, Maine.

At high egg densities, egg survival is negatively related to egg density because the close proximity of eggs results in limited dissolved oxygen and facilitated spread of fungal growth. McKenzie (1947) found a negative relationship between egg density and hatching success in an enclosed stream area. He reported hatching success ranging from 0.05% at an egg density of 581,000 eggs/m² to 3.7% at egg densities of 5,200 eggs/m². Rothschild (1961) reports that maximum prolarval production occurred at egg densities of approximately 126,000 eggs/m². Average seasonal egg deposition densities in the current study were generally less than 126,000 eggs/m², indicating that study tributaries may not be receiving optimal levels of egg deposition reported to produce maximum larval outmigration (Rothschild 1961).

Recreational Fishery Effects on Egg Deposition

Differences in egg densities between protected and unprotected sites may have resulted from localized fish removal prior to spawning, egg dislodgement, or egg destruction at unprotected sites. Dislodged eggs were likely transported downstream to lake areas where they were vulnerable to wind and wave action (Rupp 1965). Although I cannot identify the ultimate fate of dislodged eggs, I noted that wave action often deposited wind rows of eggs on shore following major spawning events. In addition, Johnston and Cheverie (1988) found that 41% of drifting rainbow smelt eggs in West River, Prince Edward Island were dead. Wading activity associated with the recreational fishery also may have been an important source of direct and indirect mortality of deposited eggs. Previous research found that angler wading had a significant effect on survival of egg and fry survival of rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*O. clarki*; Roberts and White 1992). In addition, Rupp (1965) reported destruction of rainbow smelt eggs along the Branch Lake (Maine) shoreline associated with wading and boat launching.

While results of this study measured localized effects of fish removal and egg dislodgement/destruction, the experimental design does not address whether the fishery deters schools of spawning fish from entering tributaries. Further, I did not measure cumulative effects of multiple nights of recreational fishing activity at sites over the course of the spawning season. In 1991, I attempted to measure cumulative reduction in egg density by placing egg sampling substrate during the entire spawning season on Nunns Creek. The majority of these bricks

were either transported downstream by repeated "capture and discarding" by dip nets, or buried under 50 cm of substrate due primarily to dislodged gravel and sand from recreational fishing activity. If any of these factors is important, our results will underestimate the total impact that the fishery has on egg deposition and survival in tributary habitats.

Our results indicate that disturbance of egg deposition by the recreational fishery can be significant in areas where effort is high (> 10 people/100 m²). Rainbow smelt have been introduced into a number of inland lakes to provide forage for a variety of gamefish species. In systems where spawning habitat is limited, recreational fishery disturbance may impair recruitment of rainbow smelt. In such cases, management actions such as regulations to limit fishing effort or provide spawning refuges may be necessary to enhance recruitment of rainbow smelt.

Diel Outmigration Patterns

Diel patterns observed in this study were similar to those observed by Johnston and Cheverie (1988) for rainbow smelt in the West River, Prince Edward Island, Canada. In both studies, the majority of larval outmigration occurred at night, with peak larval outmigration occurring between 0000 and 0200. Sampling of yolk sac rainbow smelt larvae in the St. Lawrence estuary indicated that larval drift also peaked at night (Ouellet and Dodson 1985). They found that although light conditions influenced the vertical distribution of yolk sac larvae, the influence of current speed appeared to be more important in determining riverine drift patterns.

There are two possible explanations for the appearance of high densities of larvae at night. First, hatching may occur throughout the 24 hour period and upward movement by larvae at night results in increased drift of larvae. This explanation is unlikely because of the relatively poor swimming abilities of prolarval rainbow smelt in relation to prevailing stream velocities. A more plausible suggestion is that peak hatching of eggs occurs at night resulting in higher drift rates. Nocturnal hatch may represent an adaptive mechanism to allow for displacement into river estuaries at a time when visually feeding predators are limited by light conditions (Johnston and Cheverie 1988).

During the current study, I was unable to detect a nightly "bigeminous" (two peaks occurring after sunset and before sunrise) drift pattern described by other investigators studying larval fish outmigration (Clifford 1972; Reisen 1972; Armstrong and Brown 1983; Iguchi and Mizuno 1990). In this study, larval outmigration was typically normally distributed with peak outmigration occurring between 2300 and 0100. Johnston and Cheverie (1988) were also unable to detect bigeminous drift patterns for larval rainbow smelt outmigrating from tributaries to the St. Lawrence River.

Seasonal Larval Outmigration Patterns

The relative seasonal timing in larval outmigration between streams followed a constant pattern in all three years with outmigration occurring on the Carp River, then Nunns Creek, followed by St. Martin Creek and Spring Creek. Seasonal timing of outmigration in these tributaries is controlled by water temperature, which affects the timing of spawning and the incubation time of

eggs. In 1992, spawning activity and larval outmigration were both temporally compressed into relatively short time periods on all tributaries. The compressed spawning period was caused by delayed warming of tributary waters before spawning. The compressed outmigration periods resulted from both the compressed spawning period and rapid warming during the late stages of incubation and hatching. Rapid warming associated with low discharge levels during this period resulted in rapid development and hatching of rainbow smelt eggs. In all three years, larval outmigration had essentially ceased by the end of the first week in June.

CONCLUSIONS

Spawner abundance and egg deposition levels varied between tributaries and between years. Egg deposition was higher when suitable water temperatures were present in tributaries during spawning. Recreational fishery activity significantly reduced nightly egg densities in tributaries when effort exceeded 5 people/m². Timing of egg deposition and larval outmigration was related to tributary water temperatures. Cold water temperatures during spawning and early egg deposition, coupled with warm water temperatures during late incubation and hatching, resulted in a compressed period of larval outmigration on all tributaries in 1992. Of the four study tributaries, the Carp River dominated larval production, producing 72.8%, 74.8%, and 96.4% of the total larval output. The four tributary streams produced a total of 46 million larvae in 1991, 13.21 million

larvae in 1992, and 31.72 million larvae in 1993. Variation in tributary larval production was caused by interannual differences in spawner abundance, egg deposition, and egg survival during incubation. Interannual variation in egg deposition, egg survival and larval outmigration were sufficient to independently cause a three-fold variation in recruitment levels of rainbow smelt in St. Martin Bay.

**CHAPTER 3: LARVAL GROWTH, SURVIVAL, AND JUVENILE
RECRUITMENT OF RAINBOW SMELT IN ST. MARTIN
BAY, LAKE HURON**

ABSTRACT

Larval and juvenile stages of rainbow smelt were sampled in St. Martin Bay, Lake Huron from 1991 to 1993 to estimate relative abundance and growth and survival rates. To determine distributional patterns of larval rainbow smelt, I sampled larval populations using surface and vertically stratified larval trawl surveys. I used a vertically stratified larval sampling design to evaluate temporal and spatial patterns in the distribution of rainbow smelt larvae across time of day, season, depth contour, and depth strata in St. Martin Bay, Lake Huron from 1991 to 1993. Day samples contained significantly lower densities and significantly smaller larval size distributions once larvae reached a length of 10-mm (early to mid-July). I found significant trends in larval density and larval size distribution with increasing depth strata once mean larval size exceeded 10-mm in July. During late July and August, I found larger larval size distributions with increasing depth along the 2.5-m, 5.0-m, and 10.0-m depth contours.

Estimates of larval abundance, growth and survival were used to determine the relative contribution of early hatching cohorts (larvae hatching during tributary outmigration) and late hatching cohorts (lake spawned larvae hatching after tributary outmigration had ceased). In 1991, high tributary larval production (46.0 million larvae) and high degree of spatial overlap between larvae and zooplankton prey resources resulted in relatively high growth rates ($G = 0.0314$

d^{-1}) and relatively low mortality ($z = 0.098 d^{-1}$) of early hatching larvae. Otolith derived hatch date distributions indicate that early hatching, tributary-produced larvae comprised 88% of juvenile recruits in 1991. Juvenile recruitment in 1991 (CPUE = 25.0), as indexed by a standardized bottom trawl survey, was the highest recorded during the three year period of this study. In 1992, low tributary production of larvae (13.2 million larvae), low densities of zooplankton prey resources, and poor spatial overlap between larval populations and prey resources resulted in relatively low growth rates ($G = 0.0182 d^{-1}$) and relatively high mortality rates ($z = 0.184 d^{-1}$) of the early larval cohort (hatching prior to June 5). Juvenile recruitment was poor (CPUE = 2.9), indicating that recruitment of late spawning larvae made a relatively small contribution to recruitment. In 1993, intermediate levels of tributary larval production (31.7 million larvae) and a high degree of spatial overlap with moderate densities of zooplankton prey resources resulted in intermediate growth ($G = 0.0209 d^{-1}$) and mortality ($z = 0.137 d^{-1}$) of early hatching larvae. Late hatching larvae also encountered intermediate densities of prey resources, resulting in moderate growth ($G = 0.0284 d^{-1}$) and intermediate mortality ($z = 0.126 d^{-1}$) of this cohort. Juvenile recruitment in 1993 was moderate (CPUE = 10.9), indicating a moderate year class of rainbow smelt was produced. Although the relative contribution of late hatching larvae to juvenile recruitment ranged between 12 and 65 percent, interannual variation in year class strength of rainbow smelt in St. Martin Bay resulted primarily from variable contributions of tributary spawned larvae between years.

INTRODUCTION

Historical records reflect unstable levels of rainbow smelt abundance in the upper Great Lakes over the past sixty years with periods of marked increases followed by precipitous declines (Baldwin et al. 1979). Variability in the stock abundance of many fish species is often related to interannual variability in recruitment (Fritz et al. 1990). Standardized bottom trawl surveys by the National Biological Survey (NBS)-Great Lakes Science Center indicate variable levels of year class strength in Lake Huron since 1973 (Figure 1). Fluctuations in the abundance of rainbow smelt have been attributed to variable recruitment caused by cannibalism (Regier et al. 1969), disease (Van Oosten 1947), parasitism (Nepszy et al. 1978), and climatic factors during spawning including wave action and water temperatures (Rothschild 1961; Rupp 1965). An annual cycle of alternating year class dominance of rainbow smelt in Lake Erie between 1963 and 1974 has been attributed to cannibalism by yearling on age 0+ rainbow smelt (Henderson and Nepszy 1989).

In the upper Great Lakes, rainbow smelt spawn in tributary streams and lake environments (Scott and Crossman 1985). Although the relative contribution of tributary vs. lake spawning to overall recruitment has not been estimated, spawning by rainbow smelt in lake habitats has been shown to be significant in other inland lakes (Rupp 1965, Legault and Delisle 1968, Plosila 1984). Because the timing of spawning and hatching of larval rainbow smelt differs between these

two habitats (Tin and Jude 1983), the relative contribution of each larval source may contribute to variability in year class formation of rainbow smelt. Although distribution patterns of larval rainbow smelt have been previously described for Lake Michigan (Jude et al. 1980, Tin and Jude 1983), Lake Huron (Emery 1973, O’Gorman 1983, 1984), Lake Erie (Ferguson 1965), and Lake Ontario (Dunstall 1984), there are no published estimates of larval growth or survival rates of rainbow smelt in the upper Great Lakes. Overall patterns of larval distribution, growth and survival of rainbow smelt in the Laurentian Great Lakes are difficult to interpret due to differences in time (day vs. night), date, depth contours and depth strata sampled by previous investigators. Year class strength of rainbow smelt appears to be determined by early fall, once juvenile fish become demersal at a size of 30 to 40 mm (Henderson and Nepszy 1989). Variability in year class strength of rainbow smelt translates directly into variability in the adult standing stock because greater than 90% of adult spawning stocks in Lake Huron are currently comprised of only two age classes (Chapter 1).

The importance of rainbow smelt as a key forage species, predator, and competitor of other Great Lakes fishes underscores the importance of identifying and understanding the variability in the abundance of adult rainbow smelt in the Great Lakes. To understand the underlying causes for the variability in recruitment of rainbow smelt, the factors influencing their year class strength need to be identified. The overall goal of this study was to investigate factors

influencing growth and survival of larval rainbow smelt in St. Martin Bay, Lake

Huron. My specific objectives were to:

1. Describe spatial and temporal patterns in the distribution of larval rainbow smelt.
2. Measure the abundance, growth, and survival of larval rainbow smelt during the pelagic larval stage.
3. Describe the relative distribution of important zooplankton prey resources in relation to the spatial distribution of larval rainbow smelt.
4. Index the year class strength of age 0+ juvenile rainbow smelt through bottom trawl surveys.
5. To estimate the relative contribution of early (hatching during tributary outmigration) vs. late (hatching after tributary outmigration had subsided) larval cohorts to overall recruitment.

METHODS

Spatial and Vertical Distribution Patterns

I conducted depth-stratified oblique trawling surveys on a monthly basis from May to August, 1991 to 1993 to determine spatial and vertical distribution patterns of larval rainbow smelt in the nearshore regions of St. Martin Bay, Lake Huron (Figure 31). I used a weighted net frame modified from a design by Nester (1987) to sample larval fish at depth. This frame eliminated obstructions at the front of the net (bridle and towing) cable that create a pressure wave resulting in avoidance of the net by larval fish. Net frames were fitted with 0.5-m, 2.5-m long, 500- μ mesh nets, which have previously been demonstrated to be

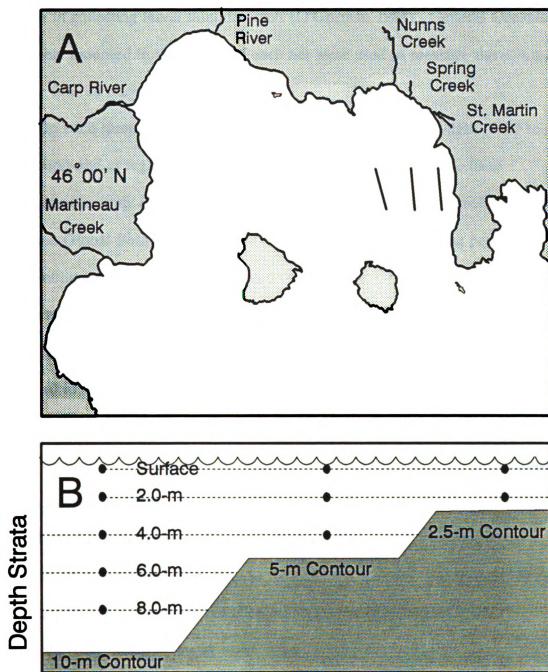


Figure 31. Map showing locations of fixed sampling sites for vertical larval trawling (Panel A), and stratified sampling design across depth contours and strata (Panel B).

effective in collecting larval rainbow smelt (O’Gorman 1984). General Oceanics flowmeters mounted in the mouth of each net were used to measure the volume of water filtered during each sample.

On each sampling date, samples were collected during daylight (1200 to 2000 hours) and at night (2200 to 0300 hours). Sampling sites were fixed throughout the study (Figure 31) and sites were located using Loran-C (1991 and 1992) and Global Positioning System (1993). During each sampling period, 10 minute oblique tows at an average speed of $1.17 (\pm 0.05)$ m/sec were made at constant depths over the 2.5-m, 5.0-m, and 10.0-m contours. Replicated tows were collected at each of ten contour-depth combinations, with depths ranging from the surface (0 to 0.5-m depth) to within 1-m of the bottom at 2.0-m depth intervals (Figure 31). Two nets were deployed during each tow and depths were staggered so that replicate tows at a given depth strata were never collected simultaneously.

Surface Larval Trawling

I conducted surface trawl surveys to determine spatial distributions of larvae on alternate weeks from May to August, 1991 to 1993. Because previous investigations and preliminary sampling indicated that larvae were most vulnerable to surface trawling at night, all sampling was conducted between 2200 and 0300. Twelve fixed transects were established along the 2.5-m, 5.0-m, and 10.0-m contours at each of four sites in St. Martin’s Bay (Figure 32). Each site was located using Loran-C coordinates (1991 and 1992) and a Global Positioning System (1993). At each site, paired 0.5-m diameter, 2.5-m long, 363μ mesh

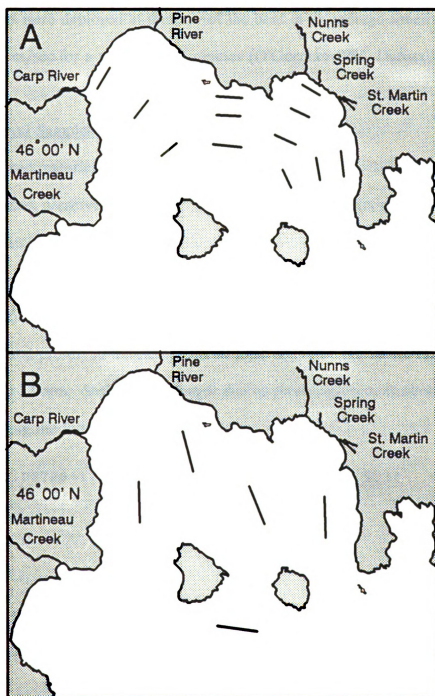


Figure 32.

Map showing locations of fixed sampling sites for surface larval trawling (Panel A) and bottom trawling (Panel B).

conical push nets were deployed at the bow of the boat at an average speed of 1.04 ($\pm$ 0.0056) m/sec for a period of 10 minutes (O’Gorman 1984, Dunstall 1984).

Handling of Larval Samples

All captured material was preserved in 95% ethanol (Butler 1992). Larval fish were separated, preserved in fresh 95% ethanol within 24 hours of capture, and identified using a larval fish key by Auer (1982). Rainbow smelt were measured to the nearest 0.1-mm using a computerized digitizing system (Brown and Taylor 1992). Shrinkage due to preservation in alcohol was determined by obtaining fresh and preserved measurements of total length of 263 larvae ranging in size from 5 to 32 mm. Shrinkage in length due to preservation in alcohol was corrected for using the following equation:

$$CL = 0.08726 + 1.06373 \text{ PL} \quad (r^2 = 0.936, \quad n = 263)$$

where

CL = corrected length (mm) and

PL = preserved length (mm).

Data Analysis of Larval Trawling Data

Numbers of larvae caught during each trawl were adjusted to number of larvae per 1,000 m of water filtered. I used a $\log_e(x+1)$ transformation for all ANOVA tests (O’Gorman 1984), because variance of both larval density and

mean length increased with higher values and larval densities had a non-parametric distribution.

I tested for diel differences in larval density and mean larval length for paired day/night samples using the Wilcoxon Signed Rank test (Siegle 1956, Snedecor and Cochran 1980). I compared samples collected for each of ten contour-depth strata combinations when there was adequate data (minimum 10 larval rainbow smelt in each paired sample) to test at least 3 of the 10 sampled contour-depth strata combinations for a given sampling date. There were adequate sample sizes of larval length data to test diel differences in mean larval length for 9 of 11 sampling dates.

I used only the night samples to test for differences in larval density and size across depth contours and depth strata between dates and years because of inadequate sample sizes from day samples. I tested for differences in larval density and mean length between depth strata, date and year using a Split-Plot ANOVA design (Table 19, Maceina et al. 1993). Separate ANOVA analyses were performed for each depth contour because the number of depth strata sampled over each depth contour differed (2 depth strata over the 2.5-m contour, 3 depth strata over the 5.0-m contour, and 5 depth strata over the 10.0-m contour). I also used a Split-Plot ANOVA design (Table 19) to test for differences in larval density and mean length between depth contours, dates, and years. When significant differences were detected for depth strata or sampling

Table 19. Split-plot ANOVA designs used to test for differences in density and mean length of larval rainbow smelt across contours. (Depth Strata = S; Depth Contours = C; Sampling Date = D; Year = Y)

Model A: Used to test for differences in density and mean length between depth strata.

<u>Description</u>	<u>Degrees of Freedom</u>
Main Plot A	
Depth Strata	(S - 1)
Date	(D - 1)
Depth Strata * Date	(S - 1)(D - 1)
Subplot B	
Date	(D - 1)
Date * Year	(Y - 1)(D - 1)
Error	S(D - 1)(Y - 1)
Corrected Total	(SDY - 1)

Model B. Used to test for differences in density and mean length across depth contours.

<u>Description</u>	<u>Degrees of Freedom</u>
Main Plot A	
Depth Contour	(C - 1)
Date	(D - 1)
Depth Contour * Date	(C - 1)(D - 1)
Subplot B	
Date	(D - 1)
Date * Year	(D - 1)(Y - 1)
Error	C(D - 1)(Y - 1)
Corrected Total	(CDY - 1)

date, I used Tukey's multiple comparison of means methods to test for differences in individual values (Snedecor and Cochran 1980, Steel and Torrie 1980).

Analysis of Larval Growth and Mortality Rates

Growth rates of larval rainbow smelt from late May through mid-July were estimated using a length-based method (Hackney and Webb 1978, Zigler and Jennings 1993). I calculated an abundance-weighted mean date of capture for each 1-mm length group. Growth rates were calculated separately for an early hatching cohort (larvae hatching during tributary outmigration) and a late hatching cohort (larvae hatching after tributary outmigration had ceased). Growth rates for early and late hatching cohorts were then estimated by:

$$L = a e^{Gt}$$

where

L = lower limit of each length interval (mm);

a = the length axis intercept (mm);

G = coefficient of instantaneous growth (day^{-1}); and

t = time in days.

Length groups with mean larval densities less than 10 larvae per 1000 m^3 were not used to estimate growth or mortality. There was generally adequate data to estimate larval growth and mortality rates for larval size classes from 5 to 20 mm.

I used a cohort-specific catch curve method to obtain within-season estimates of larval rainbow smelt mortality (Campana and Jones 1992). Size related changes in catchability (vulnerability to sampling gear) made it difficult to determine instantaneous mortality rates using methods by Crecco et al. (1983) and Essig and Cole (1986). To utilize cohort-specific catch curve methods, I needed to estimate the difference in catchability coefficients (q) between early and late spawned larvae.

I used an analysis technique by Hoenig et al. (1990) to compare the relative survival of two groups of larvae spawned in the same season. This analysis technique remains robust when catchability (q) is unequal between groups and when larval patchiness is problematic (Hoenig et al. 1990). I used the ratio of catches of early to late spawned larvae sampled at times $t_1 \dots t_n$ (where n is the total number of samples) to calculate ratios of late to early spawned larvae (R_t). I regressed the log of R_t against t . The slope of this regression line represents an estimate of the difference in instantaneous mortality rates between the cohorts of fish (C).

Once I had estimated a catchability correction factor, I was able to estimate time period-specific instantaneous mortality rates with CPUE data based on previous methods by Crecco et al. (1983) and Essig and Cole (1986) using the following equation:

$$Z = C \frac{-\ln\left(\frac{N_t}{N_0}\right)}{t}$$

where

- Z = instantaneous mortality rate (day^{-1});
- C = estimate of catchability correction factor;
- N_t = larval density (number/1000 m^3) at the end of the time period;
- N_0 = larval density (number/1000 m^3) at the beginning of the time period;
- t = days during the time period.

I used only the descending limb of the catch curve to estimate larval mortality rates because late May larval trawl samples were collected prior to peak larval abundance.

Larval Diet

I used larvae collected during surface larval trawling surveys in 1991 to determine zooplankton prey species utilized by larval rainbow smelt in St. Martin Bay. I analyzed stomachs containing ingested prey items from 168 larval rainbow smelt ranging in size from 6 to 30 mm collected from May to early August. Larvae used for gut analysis were collected in supplemental samples during both surface and depth-stratified larval trawling surveys. To prevent egestion of gut contents, all larvae were anesthetized with tricaine methanesulfonate, and

preserved in 10% buffered formalin. I measured total length (nearest 0.1-mm) of each larvae, and contents of the entire digestive tract were removed (McCullough and Stanley 1981). Identifiable gut contents were identified to the lowest possible taxa using keys by Balcer et al. (1984) and Torke (1974), counted, and measured for total length.

Zooplankton prey availability was obtained from zooplankton samples collected in conjunction with corresponding surface and depth-stratified larval trawl samples. For each larval rainbow smelt, I calculated selectivity using the Strauss electivity index (Stauss 1979, 1982) as follows:

$$L = r_i - p_i$$

where L represents the difference between the relative abundance of prey item *i* in fish gut (r_i) and the relative abundance of that prey item in the field (p_i).

Values of each zooplankton taxon range between -1 and +1; -1 indicating complete rejection and +1 indicating complete positive selection of a prey taxon.

Zooplankton Sampling

Zooplankton samples were collected in conjunction with surface larval trawling surveys to assess the relative abundance of principal prey taxa required by rainbow smelt. Paired zooplankton samples were collected with each surface larval tow. Samples were collected using a 0.5-m diameter, 2.5-m long, 64- μ mesh net. At each site replicate samples were collected from the top 1.0-m of water to correspond with the depth strata sampled during surface larval trawling.

Collected material was preserved in 5% buffered formalin.

Zooplankton were examined using a projecting microscope and identified using taxonomic keys by Balcer et al. (1984) and Torke (1974). All cladocerans were identified to species, while copepods were identified as Cyclopoida, Calanoida, copepodites, or nauplii. Rotifers were identified to genus. Cladocera and copepods were measured for total length using a computerized digitizing system (Brown and Taylor 1992). Zooplankton samples were subsampled using either a sample splitter or a Henson-Stemple pipette to obtain subsamples containing a minimum of 100 measurable cladocerans and copepods. Rotifers were counted, but not measured. I used lake water strained (0.126 m^3) and the subsample volume to estimate overall densities of zooplankton ($\#/l$) at specific sites in the bay. I used the results from larval diet studies to produce estimates of prey abundance of taxa and sizes of zooplankton selected by rainbow smelt.

I used site specific estimates of larval density and zooplankton prey density to describe the spatial overlap between the distribution of larval rainbow smelt and prey resources. To describe the relative abundance and spatial overlap, I produced maps of relative densities for sampling dates from late May through July, 1991 to 1993

Bottom Trawl Sampling

The abundance of juvenile (age 0+) and yearling rainbow smelt was indexed through a standardized bottom trawl survey. Bottom trawl surveys were conducted on a monthly basis from June to October 1991, and from May to September 1992 to 1993 at each of five index stations in St. Martin Bay (Figure

32). At each index station, two replicate trawl samples were collected during each sampling period. Trawl index stations were located using Loran C coordinates in 1991 to 1992 and a Global Positioning System in 1993. Trawl routes were made along standardized compass headings across depth contours. Because preliminary sampling indicated that yearling and adult rainbow smelt vertically migrated at night and were not susceptible to bottom trawling after dark, all bottom trawl sampling was conducted during daylight hours.

Bottom trawls were made using a 4.9-meter, 2-seam slingshot balloon trawl (33 mm body mesh, 5 mm codend mesh) that was fished for 10-minutes (bottom time) at an average speed of 2.7-knots. For each tow, I recorded the starting and ending location coordinates, depth, engine RPM range, and speed for each trawl sample. All captured rainbow smelt were measured, weighed, and preserved in 95% ethanol to preserve sagittal otoliths for subsequent age analysis. Age 0+ and age 1+ rainbow smelt were easily distinguished on the basis of length. Age 0+ CPUE data in August and September were used to index year class strength of rainbow smelt.

Otolith Aging and Validation

Otoliths were removed from juvenile rainbow smelt captured in August and September bottom trawl samples for determination of daily age and assessment of hatch date distributions (Secor et al. 1991, Epperly et al. 1991). Sagittae were removed from juveniles, cleaned with 5% sodium hypochlorite and dried for storage. I embedded sagittae in electron microscopy embedding resin (Embed-

812) to prevent cracking of the otolith during sectioning and polishing (Secor et al. 1992). Embedded otoliths were sectioned using a frontal sectioning plane with a low speed radial-arm saw (300-400 rpm) using parallel diamond wafer blades (0.015 mm) to produce thin sections (< 0.5 mm). These sections were then mounted on microscope slides with thermoplastic resin (CrystalBond). Each section was progressively polished with 220, 400, and 600-grit wet/dry sandpaper to produce a thin section ($< 50 \mu$) at the otolith core (Secor et al 1992). Final polishing was completed using aluminum polishing powder (Buehler Micropolish II 0.3 μ alumina) and a metallurgical polishing cloth.

Polished otolith sections were examined under a light microscope and the number of growth increments from the point of initial increment formation to the edge of the otolith were counted. Each otolith sample was read three times by a single reader and mean increment counts were used for subsequent analysis.

Scanning Electron Microscopy (SEM) Work

To identify the point at hatching and search for subdaily increments in rainbow smelt otoliths, I prepared sagittae for inspection using SEM (Secor et al. 1992). All SEM work was completed at the Belle W. Baruch Institute for Marine Biology and Coastal Research at the University of South Carolina. To prepare otoliths for SEM examination, I mounted and polished each otolith to expose the core region. I etched each otolith using a 5% solution of tri-sodium ethylenediaminetetraacetate (EDTA) for a period of 30 seconds to 2 minutes to

enhance daily increments. Samples were then mounted on an SEM stub and sputter coated with gold (100 Angstroms) and examined under SEM at 15 kV.

Validation of the Formation of Daily Increments

Validation was defined by Wilson et al. (1983) as "the confirmation of the temporal meaning of an increment". There are two areas of otolith related assumptions that needed to be validated in this study:

1. Time of initial increment formation (i.e. the age of larvae when regular increment formation begins and how well ring structure relates to incubation and hatching).
2. Deposition rate (i.e. how increment structure can be used as a chronological record of daily scale).

To validate the formation of initial increment formation, I took two independent approaches. First, I visually examined the core of several otoliths using SEM to determine the nature of initial increment formation. At the core, there was several subtle increments located inside of an obvious and consistent increment. From my analysis, it appeared that rainbow smelt form otoliths in the egg stage (prior to hatching), and that there was a sharp, consistent increment corresponded to hatching.

To confirm this hypothesis, I designed an experiment to determine the point in the otolith structure that corresponds to hatching. In 1993, I incubated and hatched rainbow smelt larvae in the laboratory. Incubation water was changed daily to remove previously hatched larvae and to ensure that larvae had hatched on the date sampled. On May 18th, otoliths of newly hatched larvae (age

0 days) were marked with Alizarin Complexone by immersing larvae into a 200 mg/l solution for a period of 6 hours (Tsukamoto et al. 1989). Marking with Alizarin Complexone results in a clear area of red fluorescence appearing on the otolith corresponding with the time of marking (Geffen 1992). Larvae were maintained under laboratory conditions; harvested after 3 to 10 days posthatch; sacrificed; and dissected to remove sagittae for examination. I examined larval otoliths from this study and was able to confirm that formation of the first clear increment corresponded with hatch date, and that increments formed inside of this increment were formed during the egg stage.

To validate the formation of daily increments, I examined otoliths from 112 known age larvae held under laboratory conditions and in field enclosures. Newly hatched larval rainbow smelt were collected adjacent to the lowhead dam on Nunns Creek in 1993 using drift nets. Because this was the upstream barrier for spawning migrations in this system, all larvae were assumed to be newly hatched. Bony structures in all captured larvae were marked with Alizarin Complexone (200 mg/l exposure for 6 hours) to provide a reference point for subsequent aging. Approximately 200 larvae captured on a single night (May 13, 1993) were held under laboratory conditions for a maximum period of 10 days. Larvae collected on May 13 and 17, 1993 were marked with Alizarin Complexone (200 mg/l exposure for 12 hours) and added to enclosures in St. Martin Bay to grow under field conditions.

Larvae raised under laboratory conditions were harvested, sacrificed, and preserved in ethanol on a daily basis between 3 and 10 day posthatch. Approximately 50 larvae (true ages 14 to 18 days) and 36 larvae (true ages 55 to 68 days) were harvested from enclosures, sacrificed, and preserved in ethanol for subsequent analysis. I removed and prepared otoliths using methodology that was previously described. I was able to prepare and read 60 otoliths from laboratory raised samples (known ages 3 to 10 days), 27 enclosure raised samples (known ages 14 to 18 days), and 25 enclosure raised samples (known ages 55 to 68 days). Neither length nor age of otoliths were known to the reader during analysis. All samples were counted three times by a single reader and estimated age was considered to be the mean increment counts for each sample.

I found a significant linear relationship ($r^2 = 0.951$, $P < 0.001$) between the mean number of sagittal increments and the known chronological age (Figure 33), indicating the age estimates from increment counts represented a valid estimate of true age. The slope of this relationship was greater than the expected 1.0, indicating that increment counts increasingly underestimated true age at older ages. This underestimation may occur because readers fail to identify and correctly interpret increments or because larvae do not produce otolith increments on a daily basis. Because increment counts appear to consistently underestimate true age, I used the regression equation between estimated age and true age to correct age estimates for older larvae. Maximum error in the analysis of sagittal

increments from 112 known age larvae was ± 4 days, and 95% confidence intervals around increment counts were generally ± 3.5 days.

Hatch Date Analysis

I used estimated daily ages of juvenile rainbow smelt to backcalculate hatch date distributions of successfully recruited juveniles. Individual larvae hatching earlier experience a greater cumulative mortality through the date of collection than larvae hatching later in the season (Campana and Jones 1992). Therefore, early season larvae are under represented in the backcalculated hatch date distribution relative to late hatching larvae. This effect is observed irrespective of the mortality rate, length of hatching period, and interval collection (Campana and Jones 1992).

Two factors generally control the magnitude of bias observed due to differential hatch date: (1) the relative mortality rate at the life stage when fish are collected, and (2) the duration of the spawning period from which larvae are recruited (Campana and Jones 1992). For larval populations of rainbow smelt in this study, juveniles used for hatch date estimation were relatively old and had a relatively low mortality rate compared to larval stages. This would effectively minimize the observed bias in hatch date distributions. However, the assumed hatching period of both tributary and lake spawned larvae was extensive (greater than 40 days) in my study. This effect would tend to enhance the relative bias of hatch date distributions calculated from otolith increments. Because of the extended hatching period of larvae, I used estimated instantaneous mortality rates

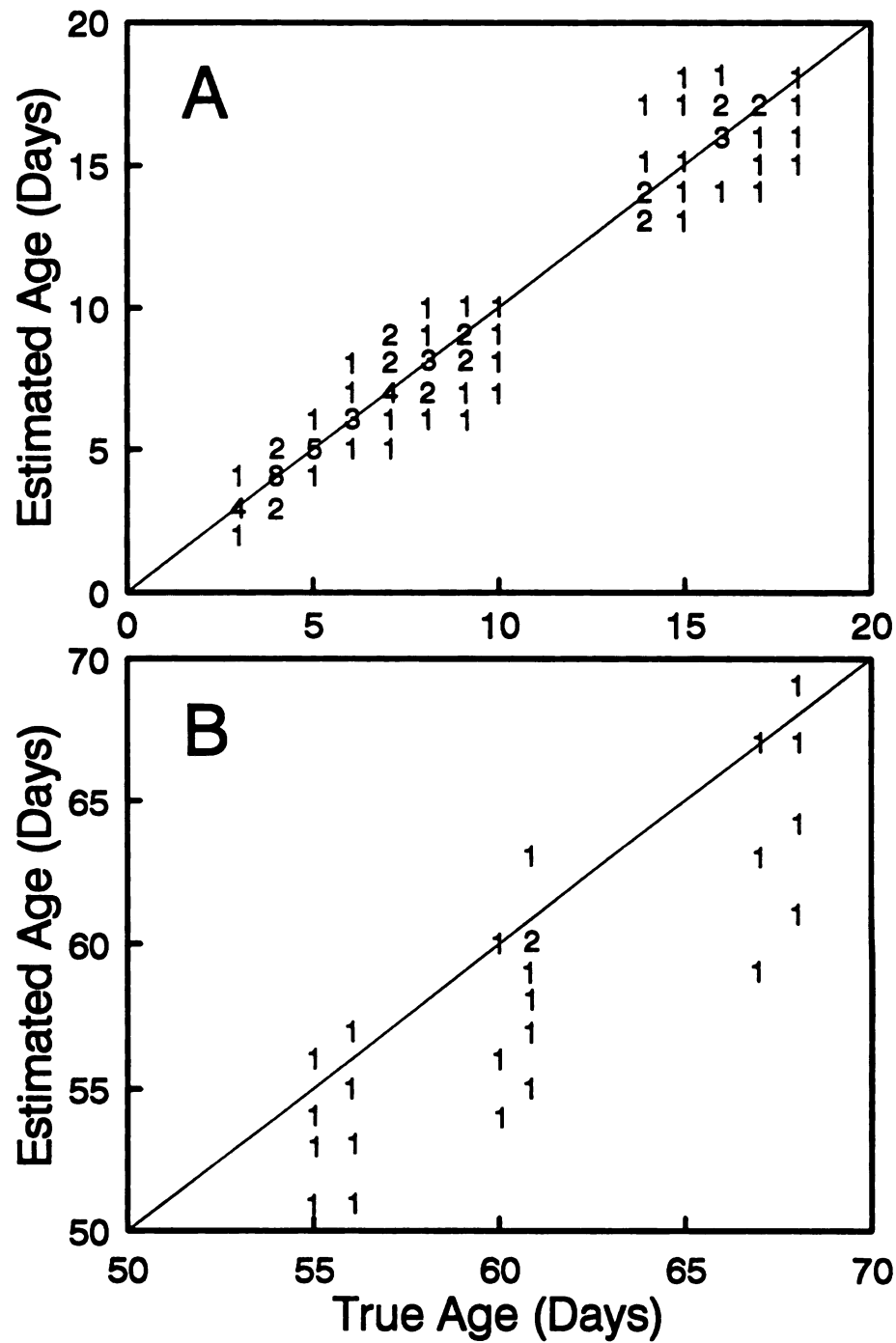


Figure 33. Results of validation of the formation of daily increments in larval rainbow smelt otoliths. Panel A shows results for larvae from age 3 to 20 days, while Panel B gives results for larvae from age 50 to 70 days.

estimates to correct hatch date distributions for differential mortality between early and late hatching larvae.

Hatch date backcalculations are subject to error because variation in increment counts increase with increasing age. Using the validation data collected in this study, a 95% confidence interval for estimated ages of older larvae (55 to 68 days) was approximately ± 3.5 days, after correcting for the slope between increment count and known age. Therefore, I used 7 day moving averages to achieve a better representation of backcalculated hatch date distributions.

RESULTS

Diel Differences in Larval Density and Size

I found significant differences in the densities of larval rainbow smelt collected during day and night (Table 20). Larval densities estimated from night samples were significantly higher ($P < 0.05$) in all years and for eight of the eleven sample dates (Table 20). There were no diel differences in density estimates for late May and early June (4 June, 1992 and 30 May, 1993) samples collected just after peak hatching. Day/night differences in density on 28 July, 1992 were marginally significant ($P = 0.06$).

I found significant diel differences in the mean lengths of larval rainbow smelt collected in paired day/night samples (Table 21). Mean lengths of larvae collected from night samples were significantly longer ($P < 0.05$) in all years and

for seven of nine sample dates (Table 21). I collected insufficient numbers of larvae during day samples to compare mean lengths for diel sampling on 21 August, 1991 and 24 August, 1992. The two sampling dates when I found no significant differences in larval length both occurred in late May to early June, immediately after peak hatch when mean larval lengths were 6 to 7-mm and no larvae exceeded 10 mm.

Density Patterns Between Contours

Split-plot ANOVAs revealed significant differences in larval density between depth contours ($P = 0.0519$), date ($P = 0.0917$) and year ($P < 0.0001$). Significant differences in larval densities along depth contours were due to high larval densities along the 5.0-m contour on July and August sampling dates (Figure 34). Tukey's comparisons indicated that larval densities along the 5.0-m contour were significantly ($P = 0.023$) higher than densities along the 2.5 and 10.0-m contours. Significant differences in density between dates were generally due to declining larval densities through the season (Figure 34). Highly significant year effects were associated with later sampling dates in 1991 resulting in lower densities of larval fish and differences between years due to variable year class strength (Figure 34). Tukey's comparisons indicated that larval densities were significantly ($\alpha = 0.05$) higher in 1993, but that there was no significant difference between larval densities in 1991 and 1992. The date*year interaction term was also significant ($P = 0.0045$) in our analysis indicating that density-date patterns were not consistent between years. This significant interaction term is indicative

Table 20. Results of Wilcoxon Signed Rank tests to compare larval densities collected in paired day and night samples. N = number of paired samples (depth contour-depth strata combinations) compared.

Year	Date	N	Highest Density	Normal T Approximation	P
1991	July 24	10	Night	2.242	0.0249
1991	August 8	10	Night	2.344	0.0191
1991	August 24	10	Night	2.223	0.0213
1991	All	30	Night	3.661	0.0003
1992	June 4	8	Night	0.510	0.6103
1992	June 30	10	Night	2.170	0.0300
1992	July 28	10	Night	1.815	0.0639
1992	August 24	10	Night	2.446	0.0144
1992	All	38	Night	2.538	0.0112
1993	May 30	10	Day	1.937	0.0528
1993	June 30	10	Night	2.752	0.0059
1993	July 27	10	Night	2.039	0.0415
1993	August 11	10	Night	2.650	0.0080
1993	All	40	Night	2.372	0.0177

of shifts from nearly uniform distributions across contours in May and June samples to concentrations of larval density along the 5.0-m contour by late July in 1992 and 1993 (Figure 34).

Table 21. Results of Wilcoxon Signed Rank tests to compare mean lengths of larvae collected in paired day and night samples. N = number of paired samples compared.

Year	Date	N	Highest Density	Normal T Approximation	P
1991	July 24	3	Night	2.336	0.0275
1991	August 8	4	Night	2.183	0.0304
1991	August 21	2	Insufficient Sample	-----	-----
1991	All	9	Night	1.659	0.0472
1992	June 4	6	Day	1.048	0.2945
1992	June 30	5	Night	1.888	0.0591
1992	July 28	8	Night	2.450	0.0143
1992	August 24	3	Insufficient Sample	-----	-----
1992	All	22	Night	3.117	0.0018
1993	May 30	9	Night	1.422	0.1551
1993	June 30	7	Night	2.282	0.0225
1993	July 27	9	Night	2.606	0.0092
1993	August 11	7	Night	2.775	0.0069
1993	All	32	Night	4.348	0.0001

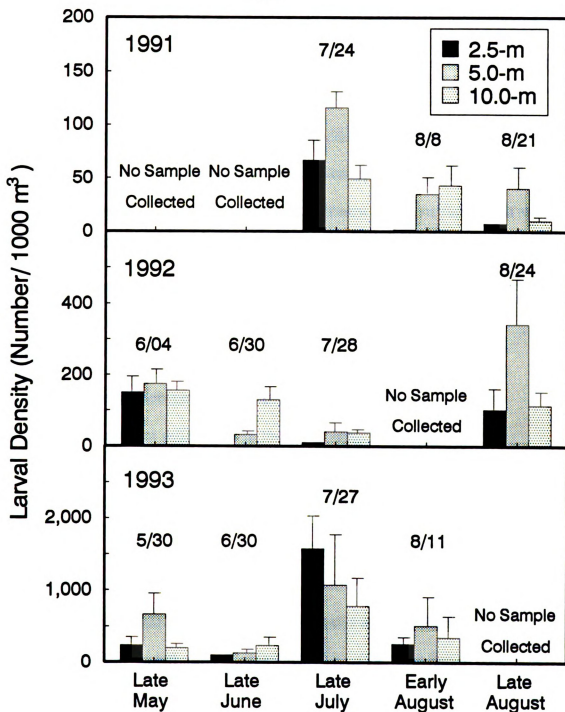


Figure 34. Densities of larval rainbow smelt sampled along the 2.5-m, 5.0-m, and 10.0-m contours of St. Martin Bay, Lake Huron from 1991 to 1993. Error bars represent $\pm$ one standard error of the mean.

Density Patterns Between Depth Strata

I found significant density differences between depth strata for the 2.5-m ($P = 0.0154$), but not the 5.0-m ($P = 0.5686$) and 10.0-m contours ($P = 0.6563$).

Results of Tukeys comparisons of means for individual depth strata on the 2.5-m contour indicated that larval densities were significantly higher at the 2.0-m depth strata than at the surface. Larval densities were lowest at the surface depth strata for 15 of the 16 depth strata-date combinations in 1992 (Figure 35). Larval densities were generally lowest at the surface strata across all contours; however, these differences were not significant due to high levels of variance and inconsistent patterns between deeper depth strata.

Size-Related Patterns Between Depth Contours

I found significant differences in the mean length of larvae sampled between dates ($P = 0.0497$) and years ($P < 0.0001$), but not between contours ($P = 0.4592$). These results indicate that contour-specific distributional patterns were not related to larval size. Significant differences between dates were due to larval growth occurring through the sampling season. Significant differences between years was primarily due to high growth rates and late sampling times during 1991, and low growth rates during 1992. The date*year interaction term was not significant ($P = 0.7852$) indicating that time-related patterns between years were consistent.

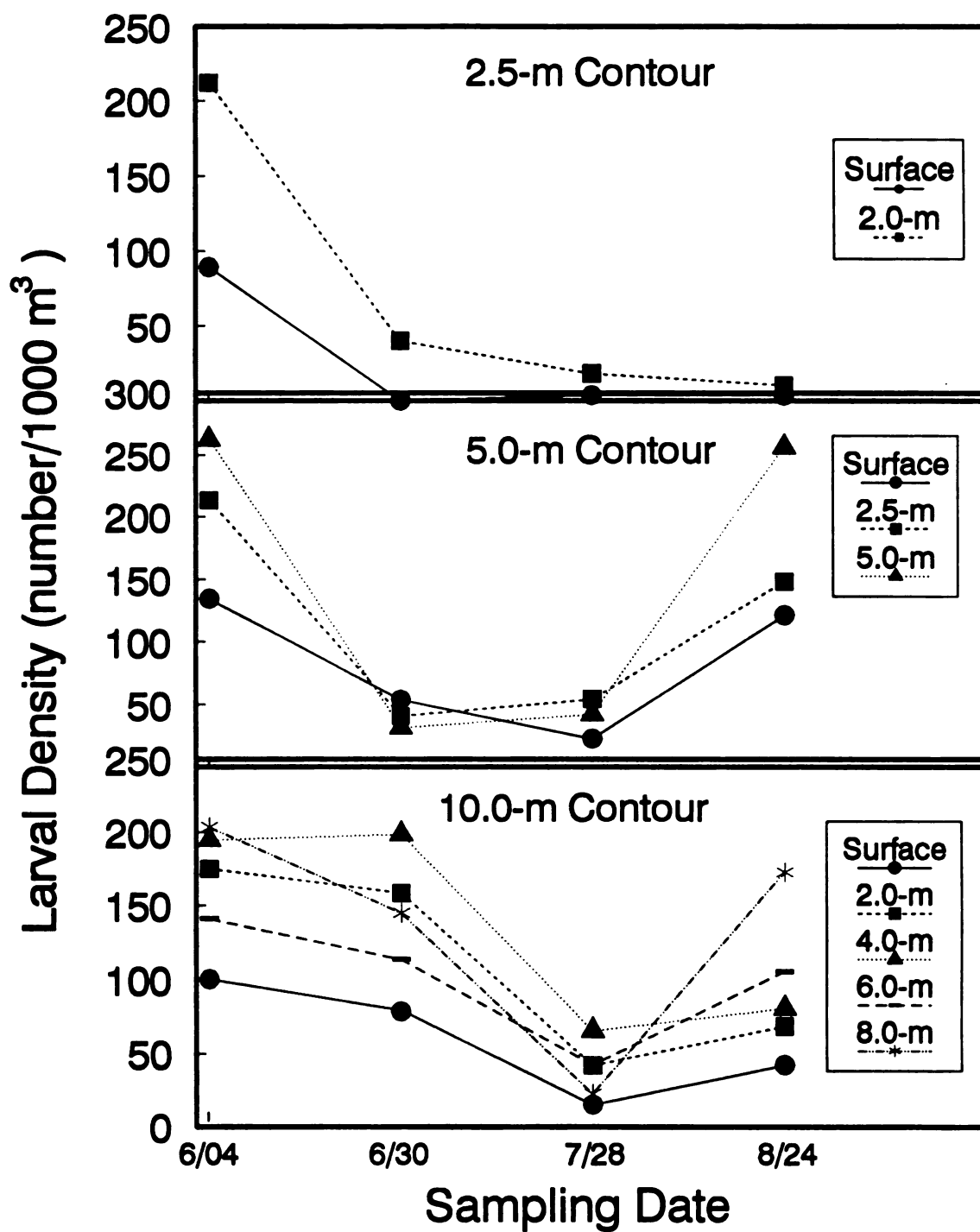


Figure 35. Densities of larval rainbow smelt sampled at depth strata along the 2.5-m, 5.0-m, and 10.0-m depth contours in St. Martin Bay, Lake Huron in 1992.

Size-Related Patterns between Depth Strata

I found significant differences in the mean length of larval rainbow smelt between depth strata for the 2.5-m ($P = 0.0488$), 5.0-m ($P = 0.0392$), and 10.0-m contours ($P = 0.0036$). Tukey's comparisons indicated a general pattern of increasing larval size with depth across all contours. For the 2.5-m contour, mean larval length was significantly higher for the 2.0-m depth strata than for the surface strata ($P < 0.05$). At the 5.0-m depth contour, mean larval length was significantly higher ($P < 0.05$) for the 4.0-m depth strata than the surface strata, although I detected no significant differences between the surface 0 and 2.0-m, and 2.0-m and 4.0-m depth strata combinations ($P > 0.05$). For the 10.0-m contour, mean larval lengths on the surface strata were significantly smaller ($P < 0.05$) than the 6.0-m and 8.0-m depth strata. I found no significant differences in mean lengths among the 2, 4, or 6-m depth strata over the 10-m contour.

Examination of length-frequency distributions for July and August samples indicates that larger larvae are distributed at increasing depths throughout the summer. To demonstrate size-related patterns observed later in the growing season (July and August), I present length frequency distributions across depth strata for the 2.5 and 5.0-m depth contours (Figure 36) and the 10.0-m contour (Figure 37). On all three contours, the mean length and overall size distribution shifted toward larger average lengths at deeper depth strata across all three depth contours. This pattern was not present on sampling dates earlier in the season

(May and June), and was not observed on sampling dates when small sample sizes of larvae were obtained.

Larval Diet

Larval rainbow smelt demonstrated ontogenetic shifts in their preference for zooplankton prey taxa as larval size increased. Immediately after hatching and yolk sac absorption, larval rainbow smelt less than 10-mm selected copepod nauplii, smaller cyclopoid copepods, and three species of rotifers, *Keratella*, *Polyarthra*, and *Trichocerca* (Table 22, Figure 38). Rotifer species and copepod nauplii declined in importance with increasing larval size between 10 and 16-mm. Cyclopoid copepods (primarily *Cyclops bicuspidatus thomasi*) increased in importance as larvae grew from 6 to 14-mm and gradually declined in importance as larvae grew from 14-mm to 22-mm (Table 22, Figure 38). Once larvae had reached 16-mm, calanoid copepods (primarily *Diaptomus sicilis*) gradually increased in diet importance. *Bosmina longirostris* became an important diet item once populations became abundant in July and August.

Spatial Distribution of Larvae and Zooplankton Prey

High output of larvae from tributaries in 1991 (Chapter 2) resulted in high initial densities of larval rainbow smelt in most areas of St. Martin Bay (Figure 39). High densities of larval rainbow smelt overlapped significantly with high densities of preferred prey species resulting in high survival and maintenance of high densities through the first 12 weeks post hatch (Figures 40 and 41). Length

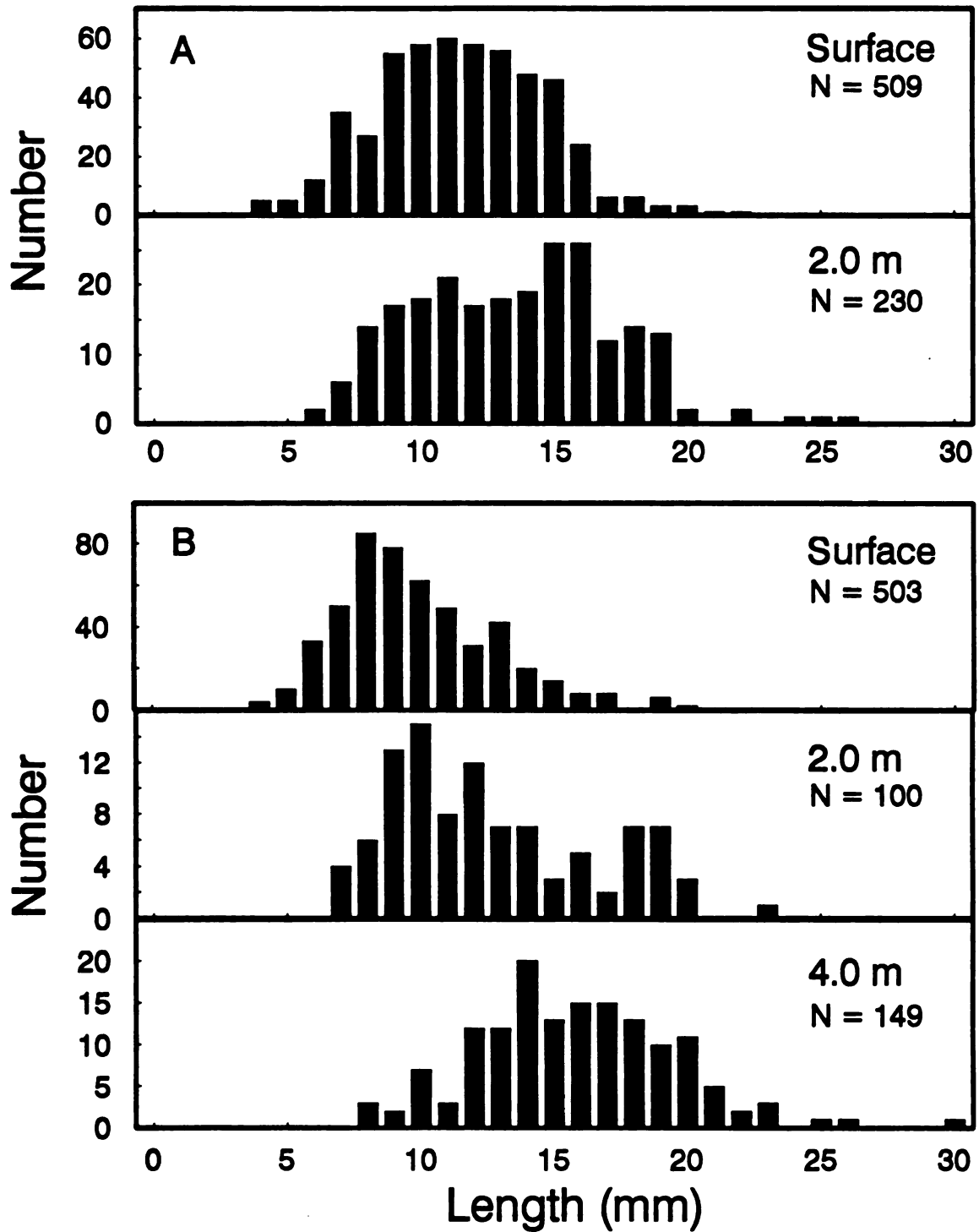


Figure 36. Length frequency distributions of larval smelt sampled at depth strata along the 2.5-m and 5.0-m depth contours in St. Martin Bay, Lake Huron on 27 July, 1993.

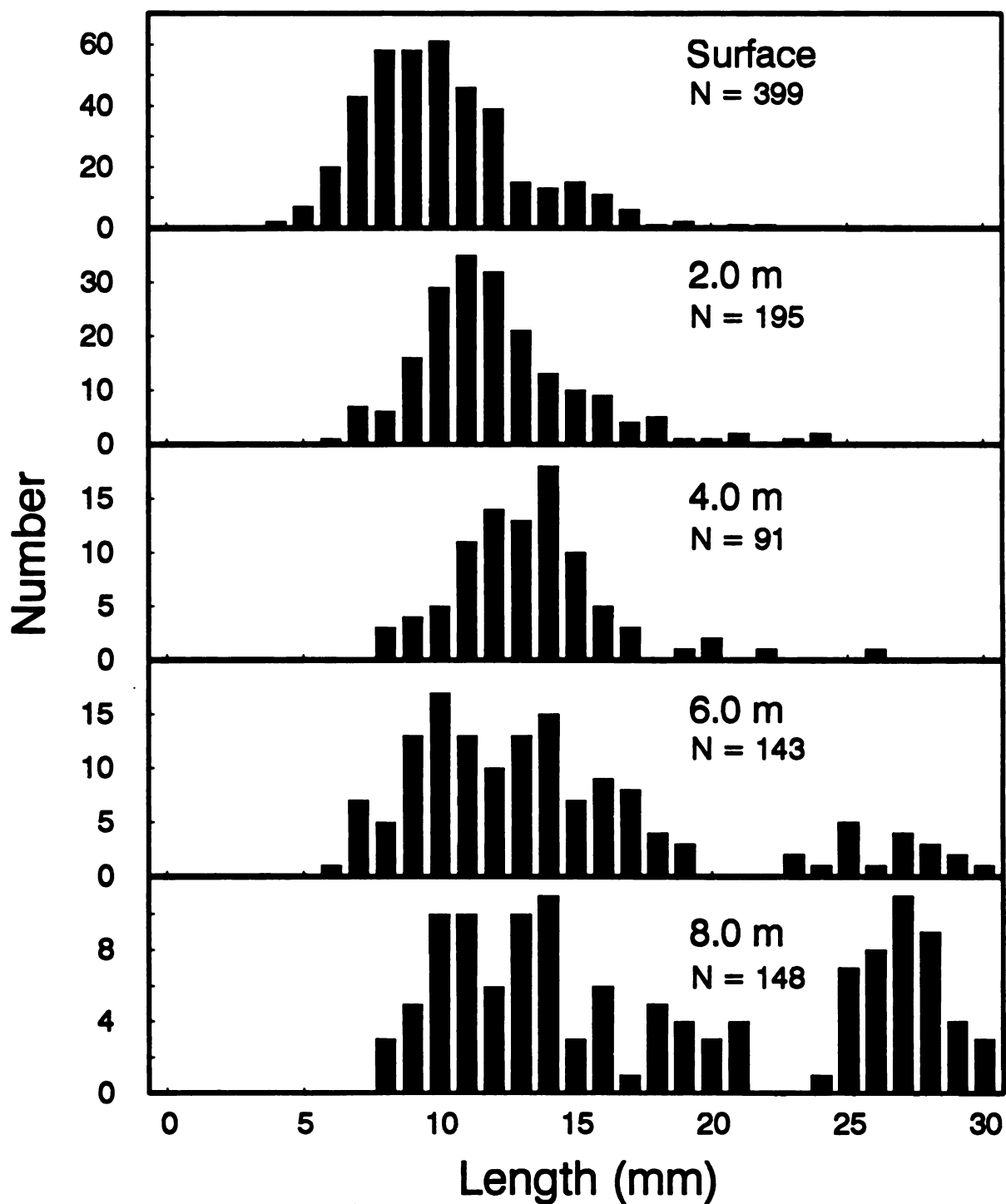


Figure 37. Length frequency distributions of larval rainbow smelt sampled at depth strata along the 10-m depth contour in St. Martin Bay, Lake Huron on 27 July, 1993.

Table 22. Mean number of prey items in the digestive tract of larval rainbow smelt and (in parentheses) percentages of larvae containing prey items.

Total Larval Length (mm)	Number Examined	Copepod nauplii	Cyclopoid Copepods	Calanoid Copepods	<i>Bosmina longirostris</i>	<i>Keratella</i>	<i>Polyarthra</i>	<i>Trichocerca</i>	Others
5.0 - 6.9	12	0.3 (33)	0.1 (8)			0.3 (25)	0.4 (58)		
7.0 - 8.9	15	0.9 (47)	0.4 (27)			0.6 (47)	0.3 (40)	0.2 (20)	0.2 (13)
9.0 - 10.9	9	1.1 (55)	1.8 (56)			0.8 (67)	0.4 (44)	0.7 (33)	0.1 (11)
11.0 - 12.9	13	2.2 (62)	1.4 (46)	0.2 (15)	0.1 (62)	0.4 (38)	1.3 (62)	0.3 (31)	0.8 (31)
13.0 - 14.9	11	0.4 (27)	3.7 (91)		0.3 (27)	0.1 (18)		0.1 (9)	0.3 (27)
15.0 - 16.9	8	0.1 (13)	2.3 (75)	1.3 (38)		0.1 (13)	0.2 (13)		0.5 (38)
17.0 - 18.9	12		1.9 (50)	2.1 (75)	0.9 (42)			0.1 (8)	0.6 (33)
19.0 - 20.9	12		0.7 (33)	3.4 (83)	1.6 (67)		0.1 (8)		1.1 (50)
21.0 - 22.9	17	0.2 (6)	0.2 (12)	2.9 (53)	2.3 (65)				0.4 (29)
23.0 - 24.9	12			4.1 (92)	3.4 (75)				
25.0 - 26.9	9			3.9 (78)	2.8 (67)				0.9 (44)
27.0 - 28.9	10			5.8 (90)	4.5 (80)				1.4 (60)
29.0 - 30.9	12			7.9 (83)	5.3 (83)				1.9 (58)

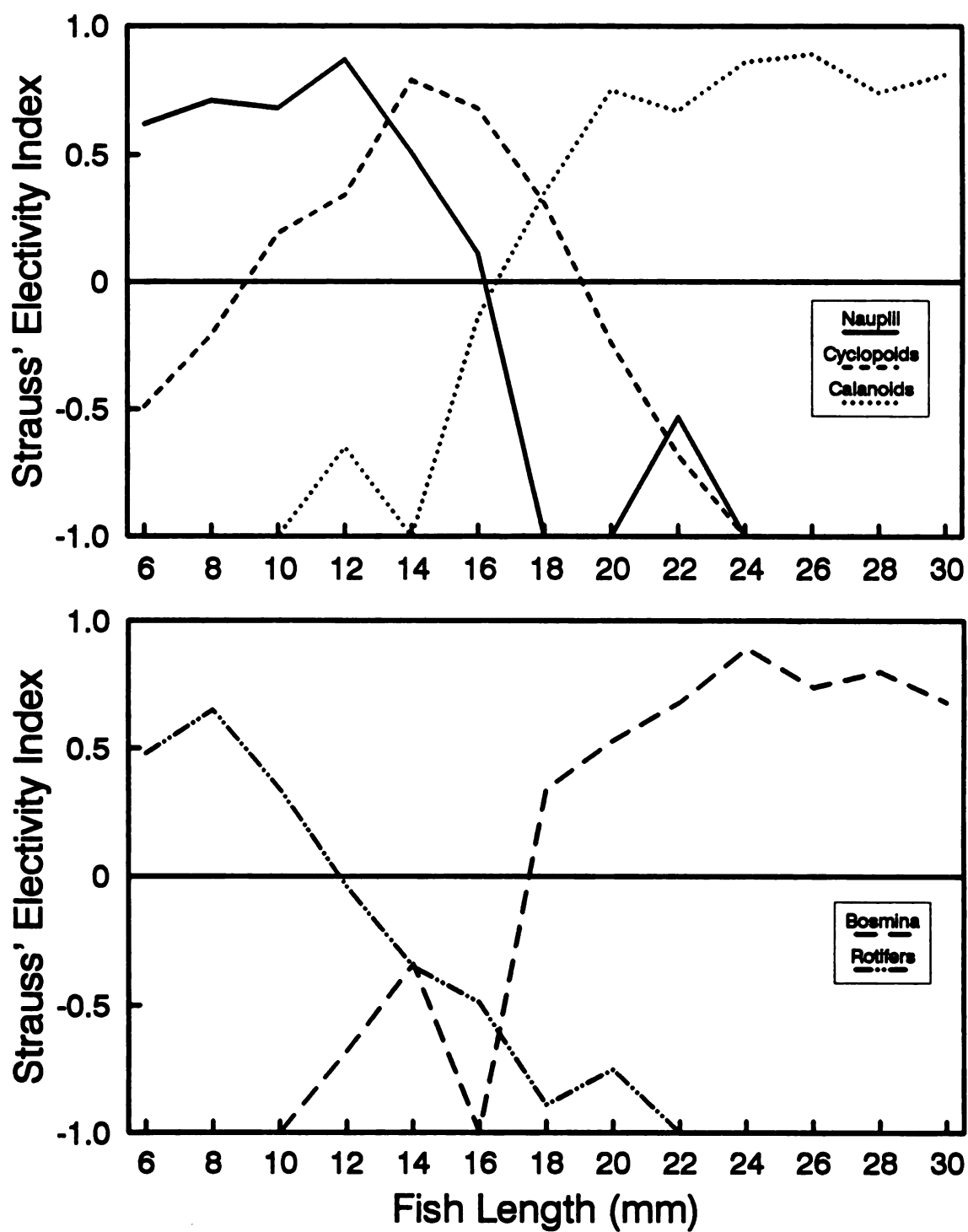


Figure 38. Strauss' electivity indices for taxa consumed by larval rainbow smelt in St. Martin Bay, Lake Huron in 1991.

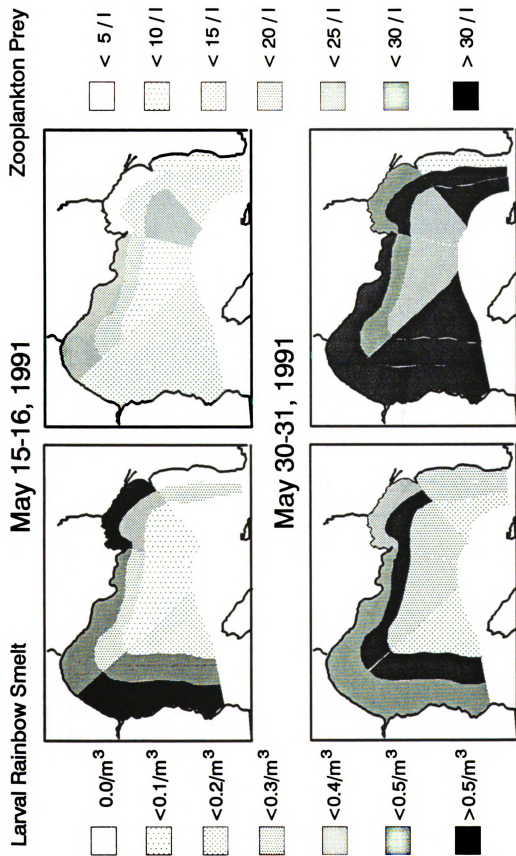


Figure 39. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for May 15-16 and May 30-31, 1991.

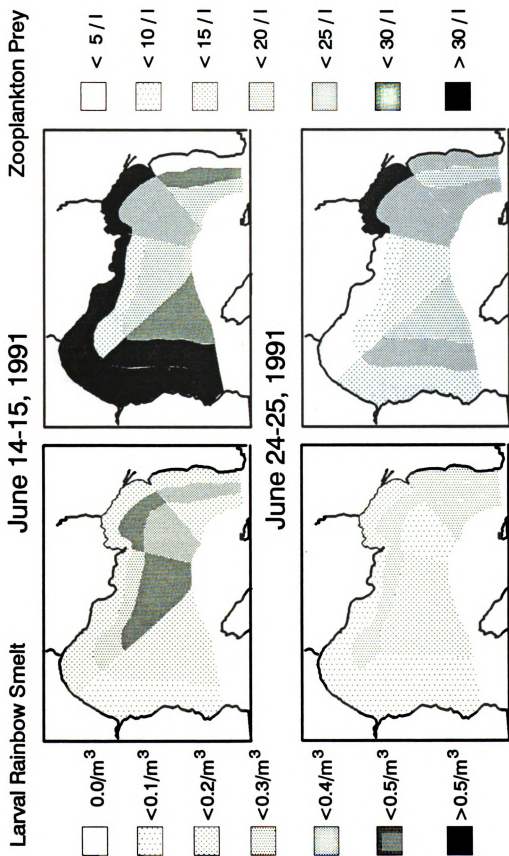


Figure 40. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for June 14-15 and June 24-25, 1991.

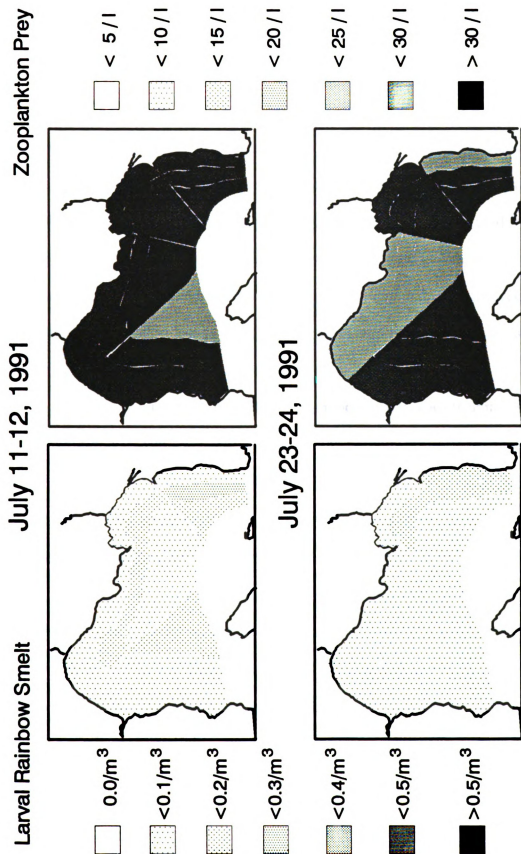


Figure 41. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for July 11-12 and July 23-24, 1991.

frequency distributions indicate high rates of larval growth and a small pulse of smaller, late hatching larvae occurring in mid to late June (Figure 42).

In 1992, low output of larval rainbow smelt from tributaries (approximately 1/3 of 1991 levels, Chapter 2) resulted in low initial densities of larval rainbow smelt (Figure 43). The distribution of larval rainbow smelt did not overlap significantly with high densities of preferred prey species concentrated in the southeast portion of the bay resulting in low survival, and gradual deterioration in the larval densities throughout the bay (Figures 44 and 45). Length frequency distributions indicated low rates of larval growth and a pulse of small, late hatching larvae occurring in late June and early July (Figure 46).

In 1993, moderate output of larval rainbow smelt from tributaries (approximately 2/3 of 1991 levels, Chapter 2) resulted in intermediate initial densities of larval rainbow smelt (Figure 47). The distribution of larval rainbow smelt did overlap significantly with moderate densities of preferred prey species resulting in moderate survival, and gradual decline in the larval densities throughout the bay (Figures 48 and 49). Length frequency distributions indicate moderate rates of larval growth and a significant pulse of late hatching larvae occurring in mid to late June (Figure 50). These larvae comprised a significant proportion of the larval population in the bay during July (Figure 48).

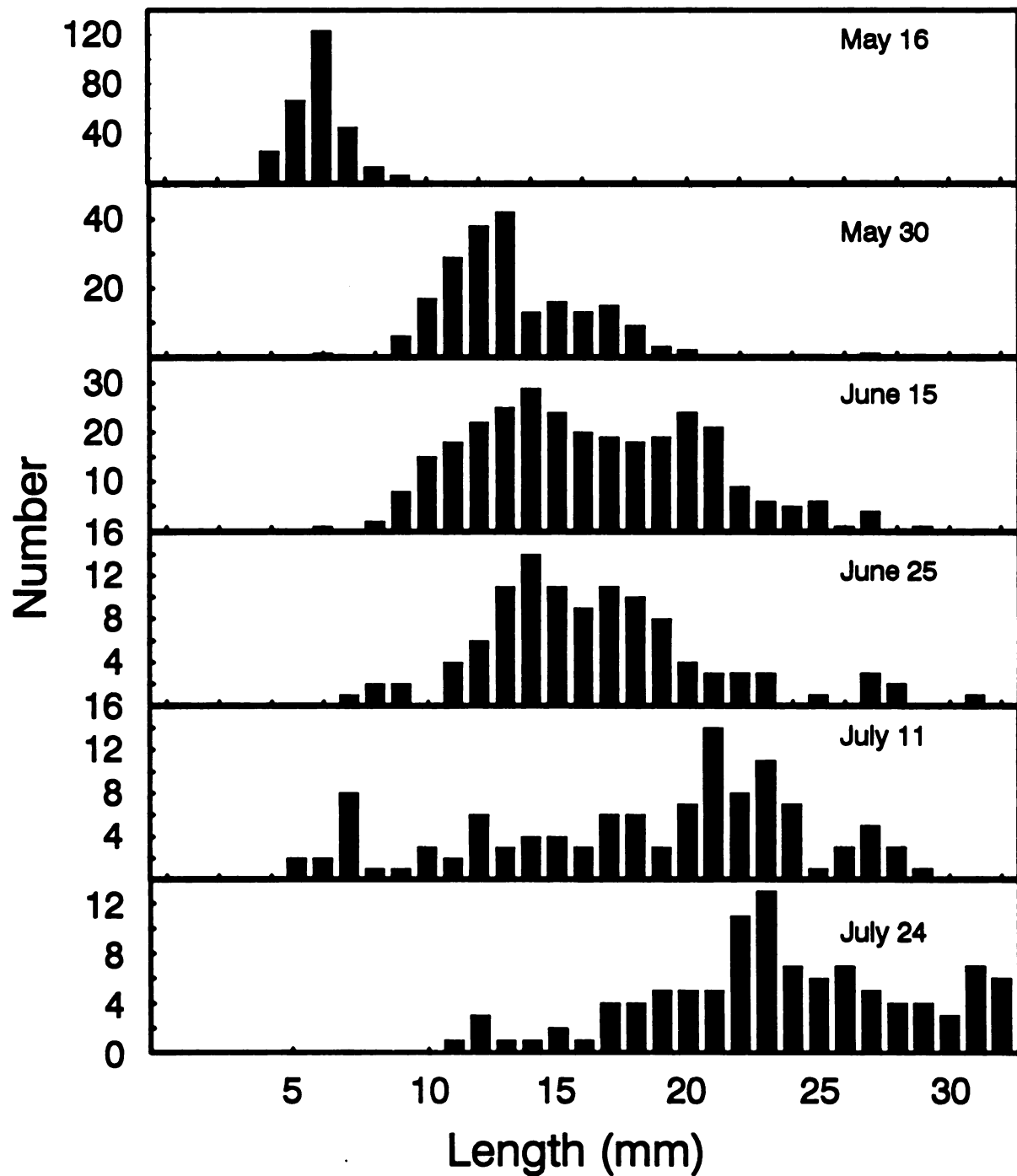


Figure 42. Length frequency distributions of larval rainbow smelt sampled in St. Martin Bay, Lake Huron from mid-May to late-July, 1991.

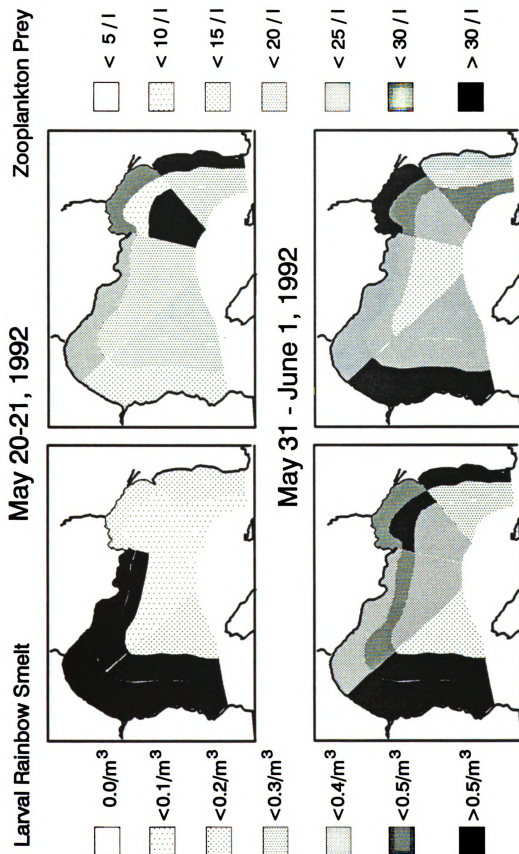


Figure 43. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for May 20-21 and May 31-June 1, 1992.

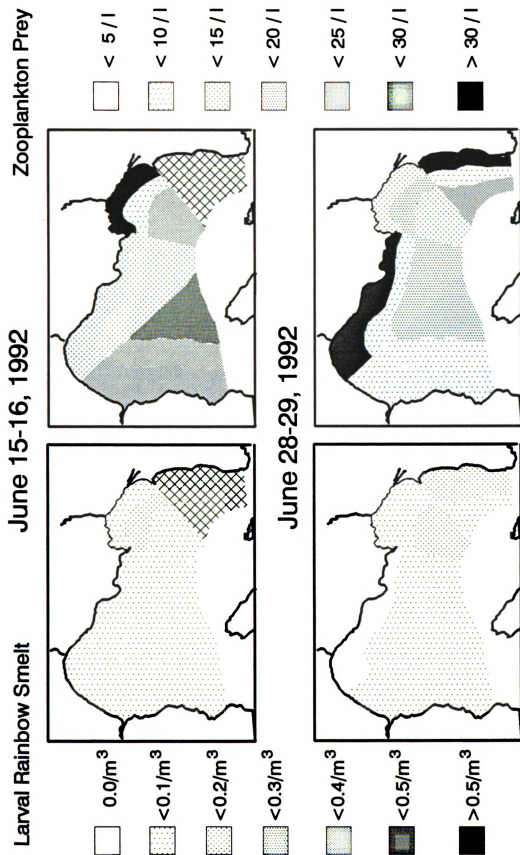


Figure 44. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for June 15-16 and June 28-29, 1992.

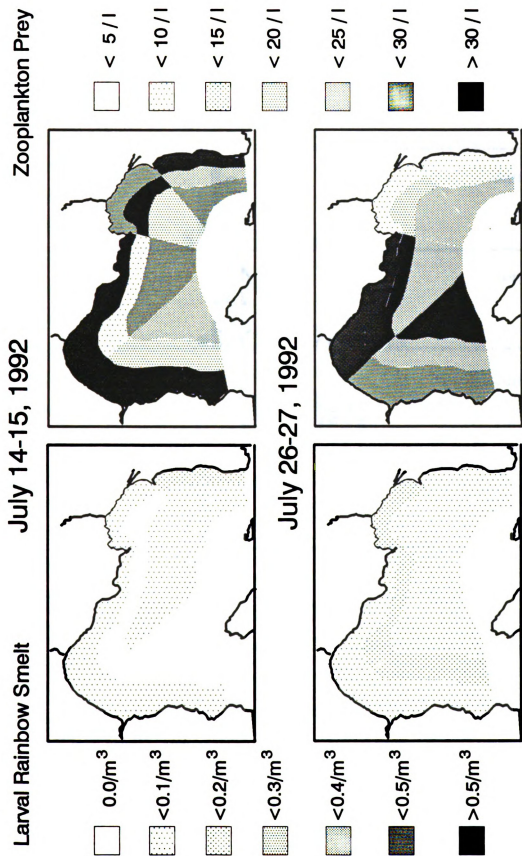


Figure 45. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for July 14-15 and July 26-27, 1992.

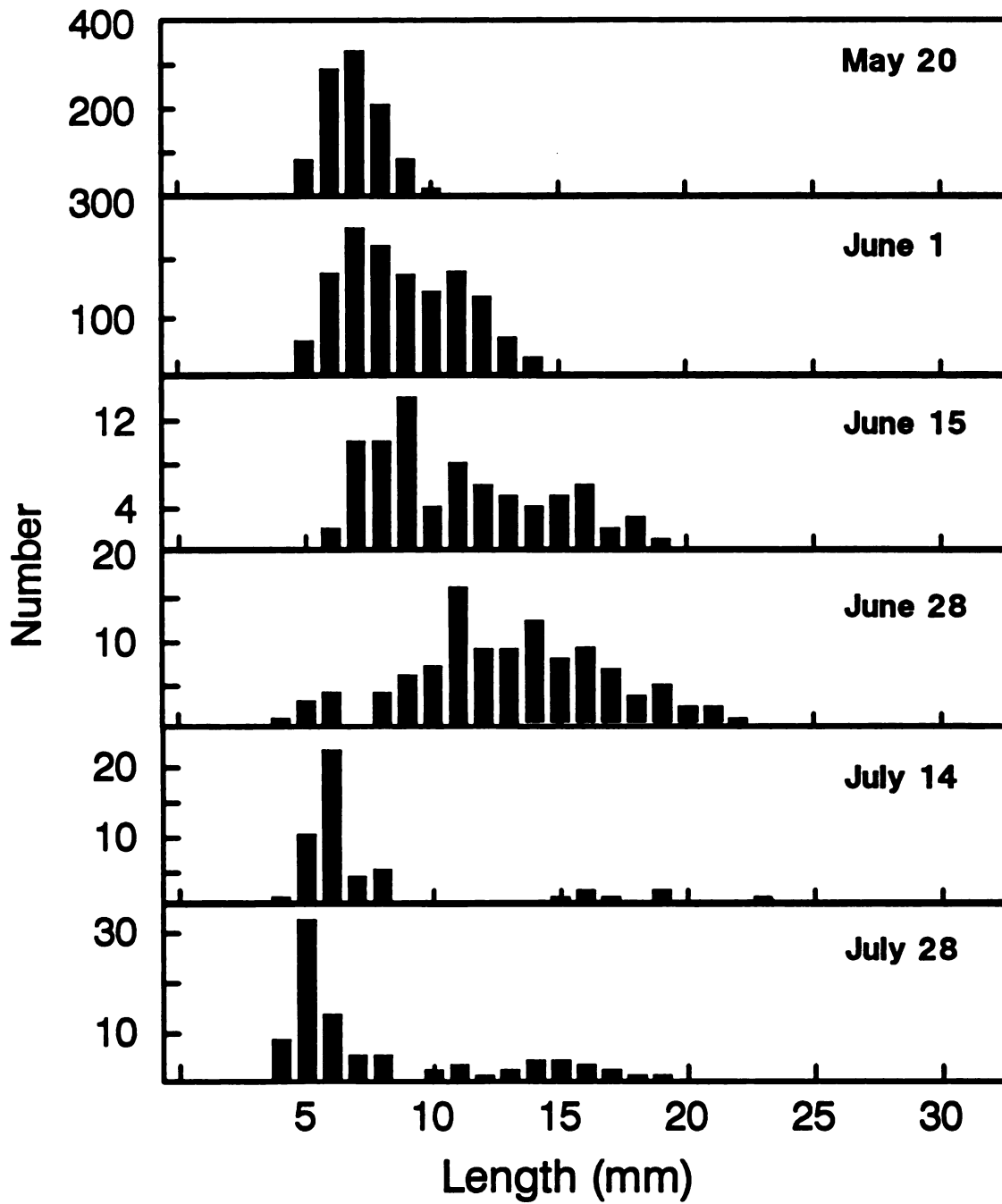


Figure 46. Length frequency distributions of larval rainbow smelt sampled in St. Martin Bay, Lake Huron from mid-May to late-July, 1992.

Growth and Survival Rates

Instantaneous growth rates of the late hatching cohort were higher than the early hatching cohort in 1992 and 1993, but not in 1991 (Table 23). Growth rates for the early cohort were highest in 1991 and lowest in 1992 (Table 23). Growth rates appear to be less variable between years for the late hatching cohort, when compared to the early cohort of larval rainbow smelt.

Instantaneous mortality rates differed between early and late cohorts for 1991 to 1993 (Table 24), and were inversely correlated with the relative growth rates exhibited by these cohorts (Figure 51). In 1991, high growth rates ($G = 0.314 \text{ d}^{-1}$) of the early hatching cohort corresponded with low instantaneous mortality rates ($z = 0.098 \text{ d}^{-1}$). In 1992, the early hatching cohort exhibited low growth rates ($G = 0.182 \text{ d}^{-1}$) and high mortality rates ($z = 0.184 \text{ d}^{-1}$), while the late hatching cohort exhibited intermediate growth rates ($G = 0.251 \text{ d}^{-1}$) and lower mortality rates ($z = 0.169 \text{ d}^{-1}$). In 1993, the early cohort exhibited marginal growth rates ($G = 0.209 \text{ d}^{-1}$) and moderate mortality ($z = 0.137 \text{ d}^{-1}$), while the late hatching cohort demonstrated higher growth ($G = 0.284 \text{ d}^{-1}$) and reduced mortality ($z = 0.126 \text{ d}^{-1}$).

Otolith Derived Hatch Date Distributions

Otolith-derived hatch date distributions indicated differential contribution of tributary vs. lake spawned larval contribution to juvenile recruitment. In 1991, backcalculated hatch dates indicate that the majority of the 1991 year class was composed of fish outmigrating from tributary sources (Figure 52). Later spawned

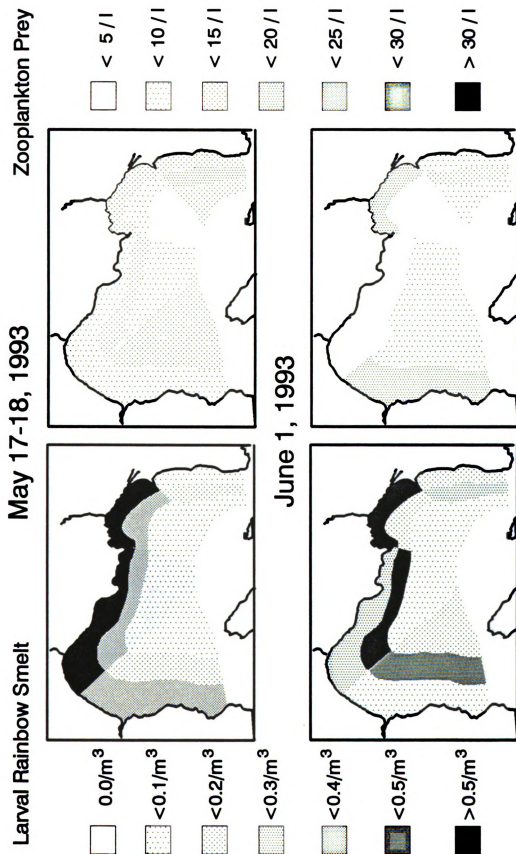


Figure 47. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for May 17-18 and June 1, 1993.

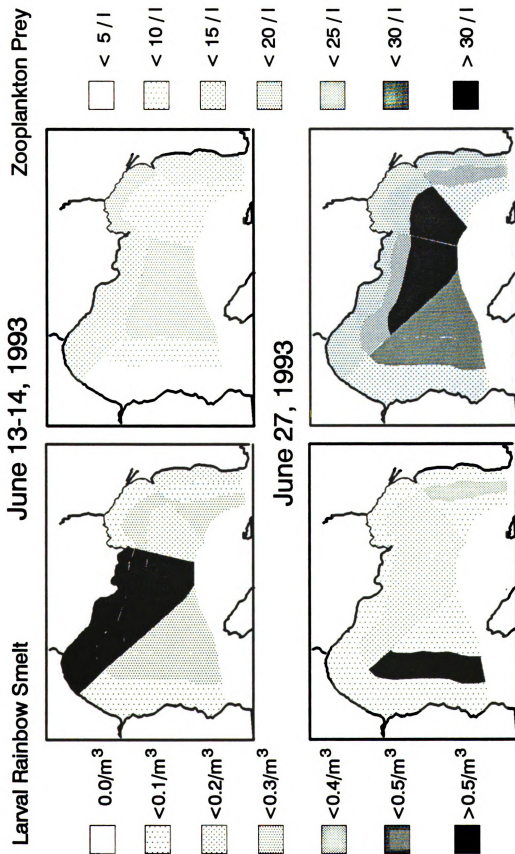


Figure 48. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for June 13-14 and June 27, 1993.

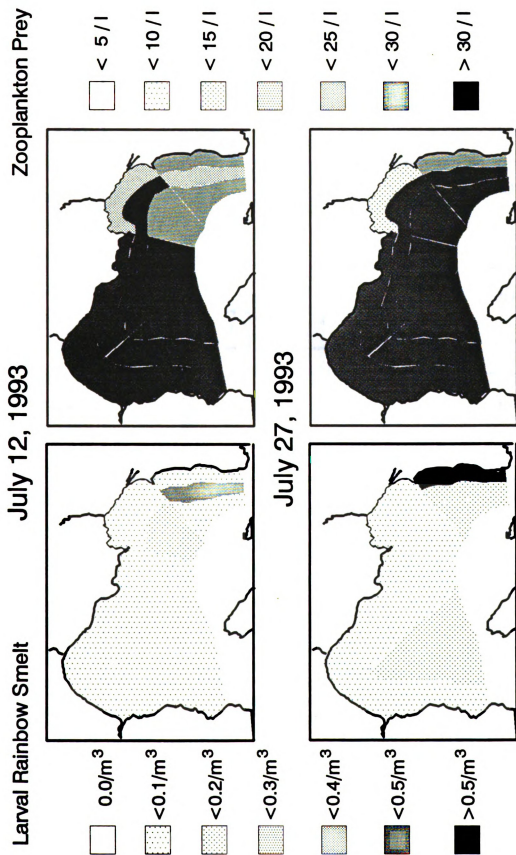


Figure 49. Site specific densities of larval rainbow smelt and zooplankton prey in St. Martin Bay, Lake Huron for July 12 and July 27, 1993.

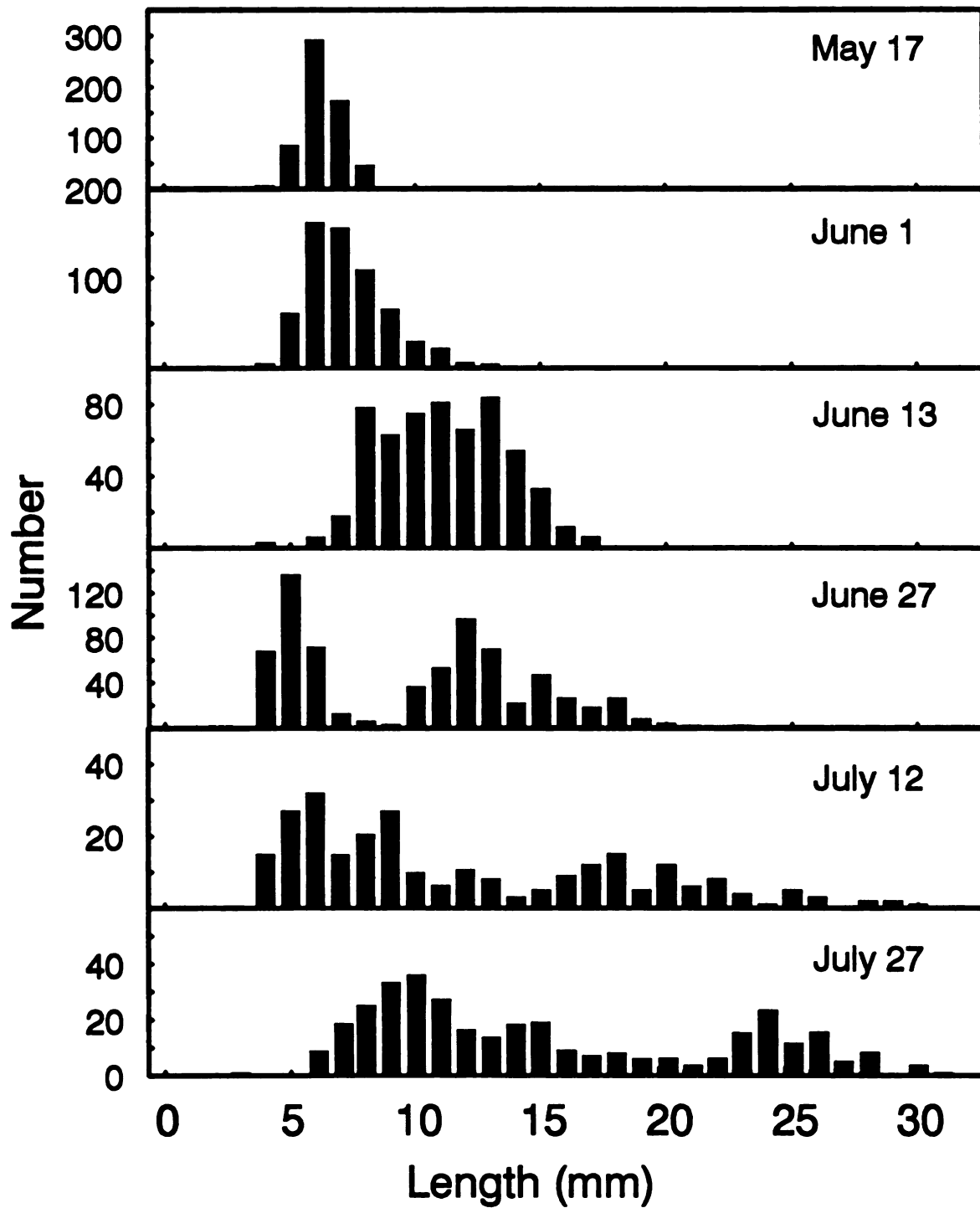


Figure 50. Length frequency distributions of larval rainbow smelt sampled in St. Martin Bay, Lake Huron from mid-May to late-July, 1993.

Table 23. Length-class based estimates of growth for early and late hatching cohorts of larval rainbow smelt in St. Martin Bay, Lake Huron from 1991 to 1993.

Year	Cohort	Instantaneous Growth Rates	Standard Error
1991	Early (May-early June)	0.0314	0.0031
1991	Late (mid June-July)	0.0247	0.0078
1992	Early (May-early June)	0.0182	0.0063
1992	Late (mid June-July)	0.0251	0.0097
1993	Early (May-early June)	0.0209	0.0049
1993	Late (mid June-July)	0.0284	0.0062

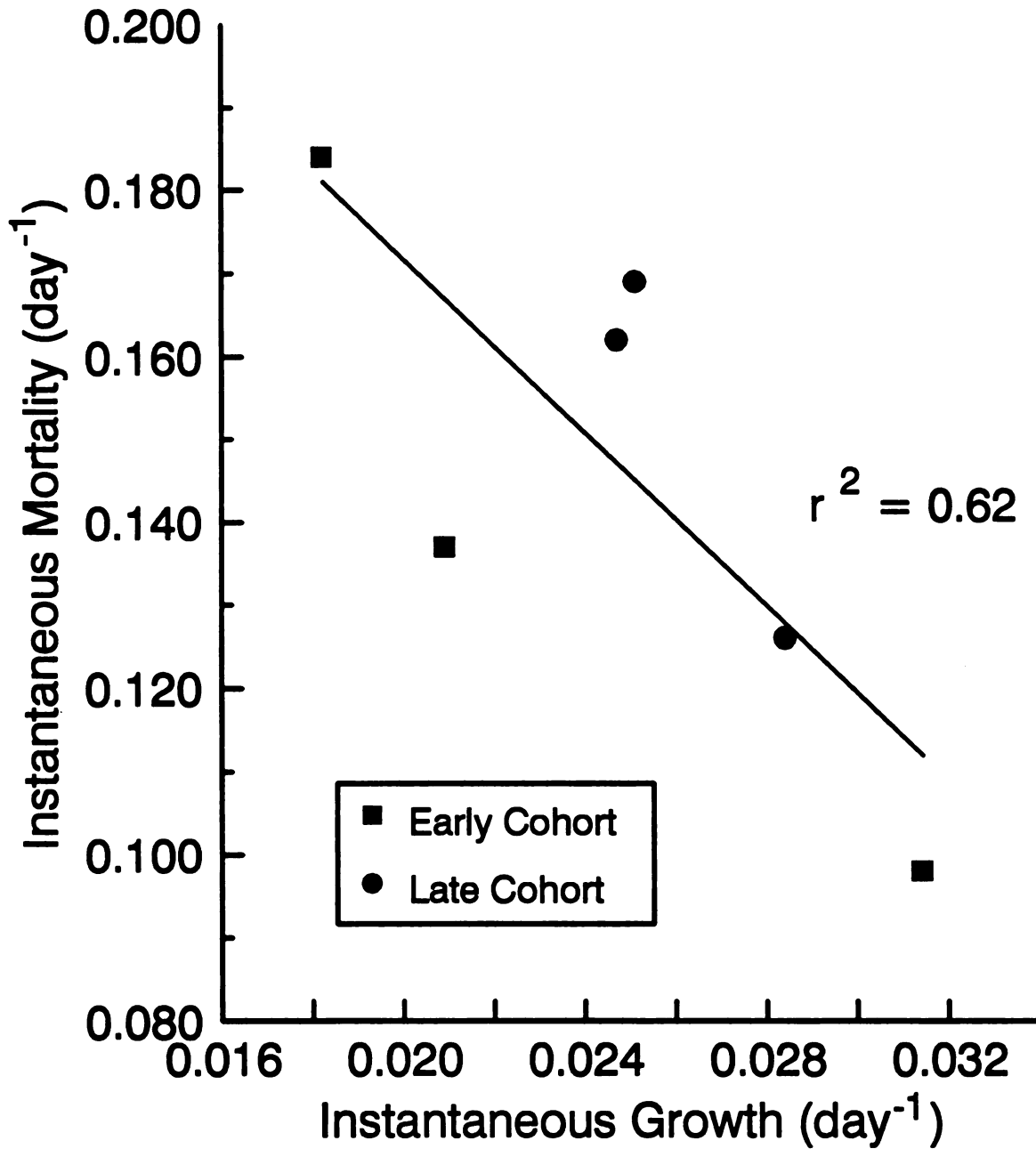


Figure 51. Relationship between instantaneous growth and instantaneous mortality rates for early and late hatching cohorts of rainbow smelt in St. Martin Bay, Lake Huron.

tributary larvae (hatch dates from May 20 to 28, 1991) had higher survival rates than early hatch larvae (May 6 to 15, 1991). Approximately 88% of the backcalculated hatch date distribution occurs during the period of tributary larval outmigration prior to June 1, 1991.

By contrast, the hatch date distribution in 1992 was dominated by larvae hatching from mid-June to mid-July in 1992 (Figure 53). Tributary spawned larvae hatching between May 11 and June 2 experienced poor survival (Table 24) and made a relatively small contribution to the 1992 year class. Larvae with hatch dates after June 5th (the end of tributary outmigration) comprised approximately 65% of the 1992 year class.

In 1993, the hatch date distribution was dominated by larvae hatching during May (Figure 54). The hatch date distribution of recruited juveniles was highly correlated with larval outmigration measured in four St. Martin Bay tributaries, indicating that larval survival of tributary-produced larvae with differing hatch dates was relatively constant. A smaller, but significant group of juveniles was recruited from larvae hatching between June 10th and July 9th, after tributary larval outmigration had subsided. Recruited juveniles with hatch dates before June 5th (end of tributary outmigration) comprised approximately 74% of the 1993 year class.

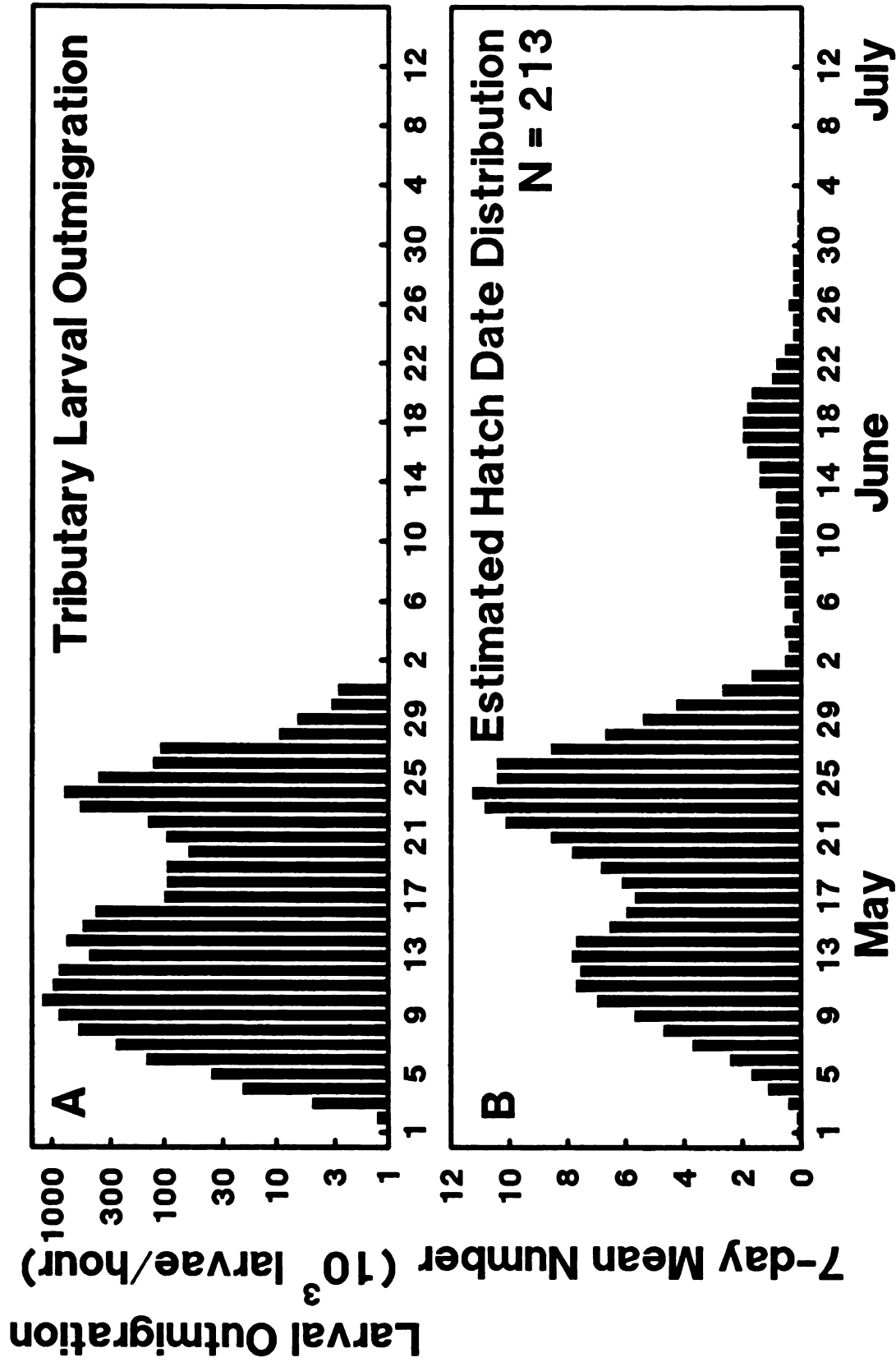


Figure 52. Hatch date distributions for recruited juvenile rainbow smelt sampled in August and September, 1991. Bars represent 7-day mean numbers (± 3.5 days) representing the 95% confidence interval for backcalculated hatch dates.

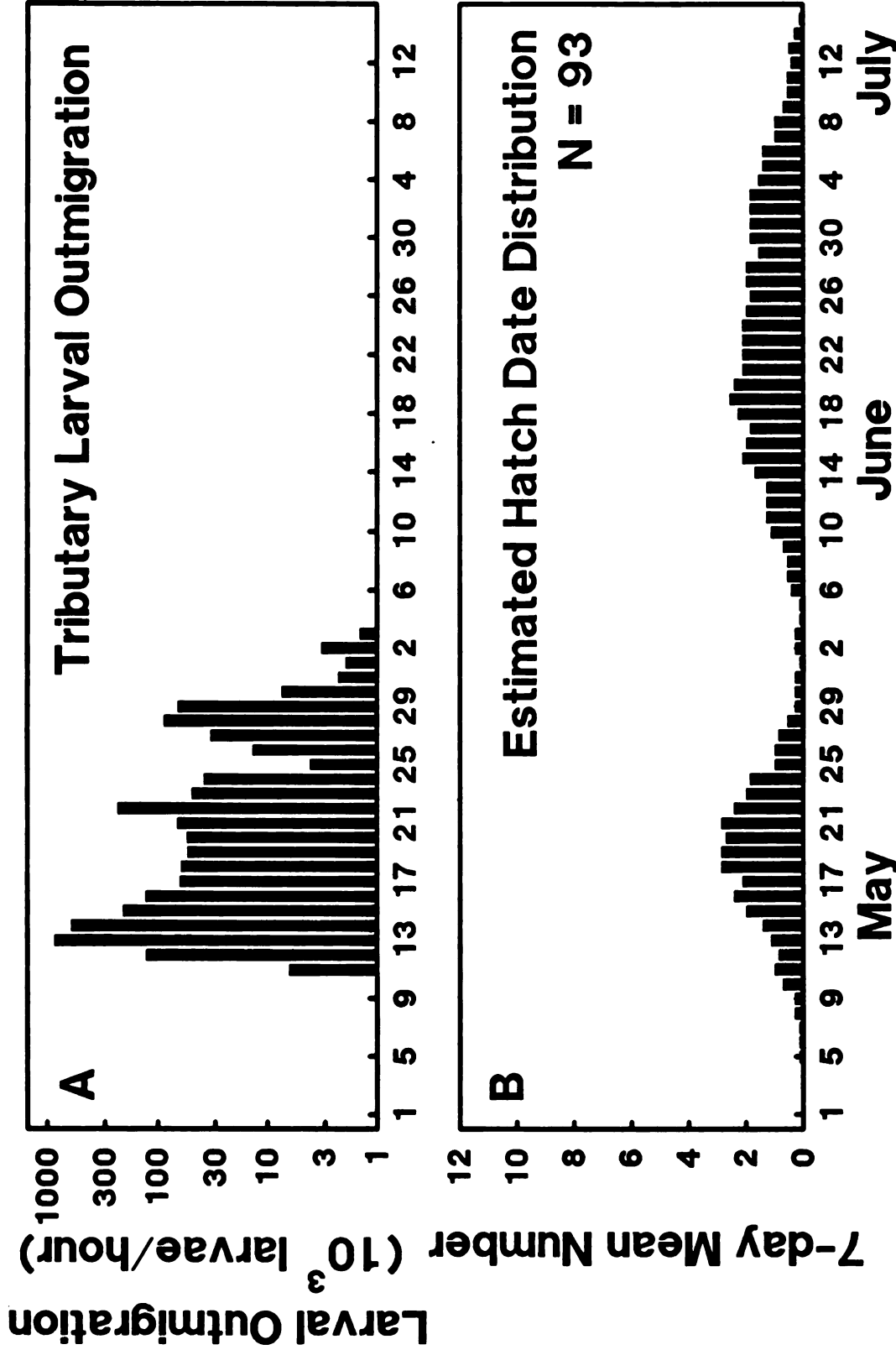


Figure 53. Hatch date distributions for recruited juvenile rainbow smelt sampled in August and September, 1992. Bars represent 7-day mean numbers (± 3.5 days) representing the 95% confidence interval for backcalculated hatch dates.

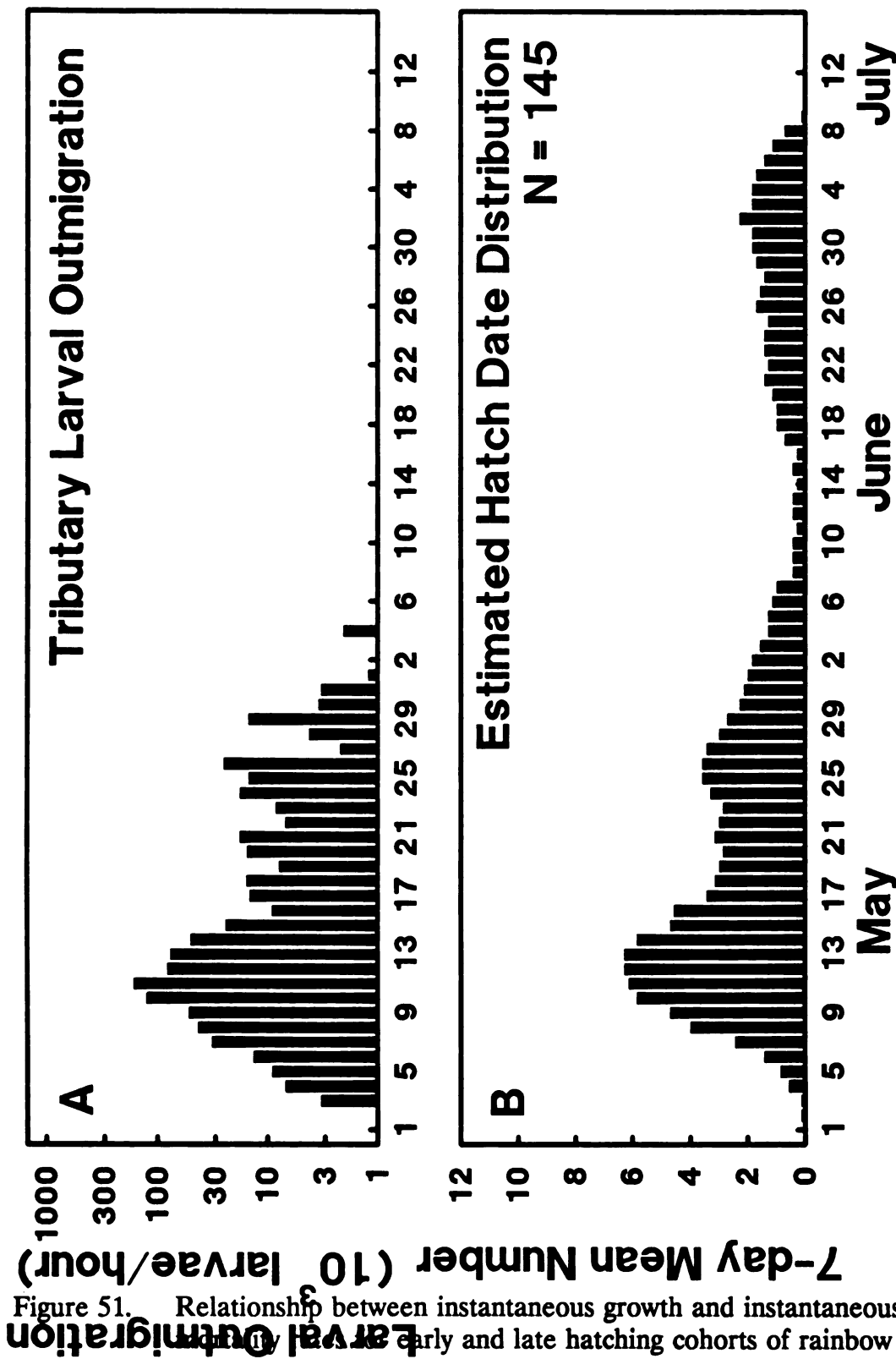


Figure 51. Relationship between instantaneous growth and instantaneous outmigration for early and late hatching cohorts of rainbow smelt in St. Martin Bay, Lake Huron.

Figure 54. Hatch date distributions for recruited juvenile rainbow smelt sampled in August and September, 1993. Bars represent 7-day mean numbers (± 3.5 days) representing the 95% confidence interval for backcalculated hatch dates.

Bottom Trawl Year Class Index

Bottom trawl surveys from May to September indicated that age 0+ and age 1+ rainbow smelt were most abundant in St. Martin Bay. In 1991, age 1+ rainbow smelt were abundant inshore during May and June, but migrated outside of the bay by July (Figure 55). Age 0+ rainbow smelt from the 1991 year class were recruited to bottom trawling gear by mid-July and were most abundant in August 1991 (Figure 55). In 1992 and 1993, age 1+ rainbow smelt remained in St. Martin Bay throughout the summer (Figures 56 and 57). In 1992 and 1993, age 0+ rainbow smelt were not fully recruited to bottom trawling gear until September (Figures 56 and 57) because of relatively slow growth rates (Table 23).

The relative sizes of the 1991 to 1993 year classes of rainbow smelt were indexed by bottom trawl surveys in August and September. In 1991, large numbers of age 0+ juvenile rainbow smelt were captured in bottom trawls and the combined August/September CPUE was 25.0 fish/tow (Table 25). In 1992, relatively few age 0+ rainbow smelt were captured and the combined August/September CPUE was only 2.9 fish/tow (Table 25). In 1993, intermediate numbers of age 0+ juveniles were captured with a combined August/September CPUE of 10.9 juveniles/tow (Table 25). Differences in juvenile recruitment between years were due primarily to variable levels of recruitment from early hatching larval cohorts (Figure 58). While the contribution of early hatching cohorts was highly variable, late hatching cohorts made a relatively constant contribution to juvenile recruitment between years (Figure 58).

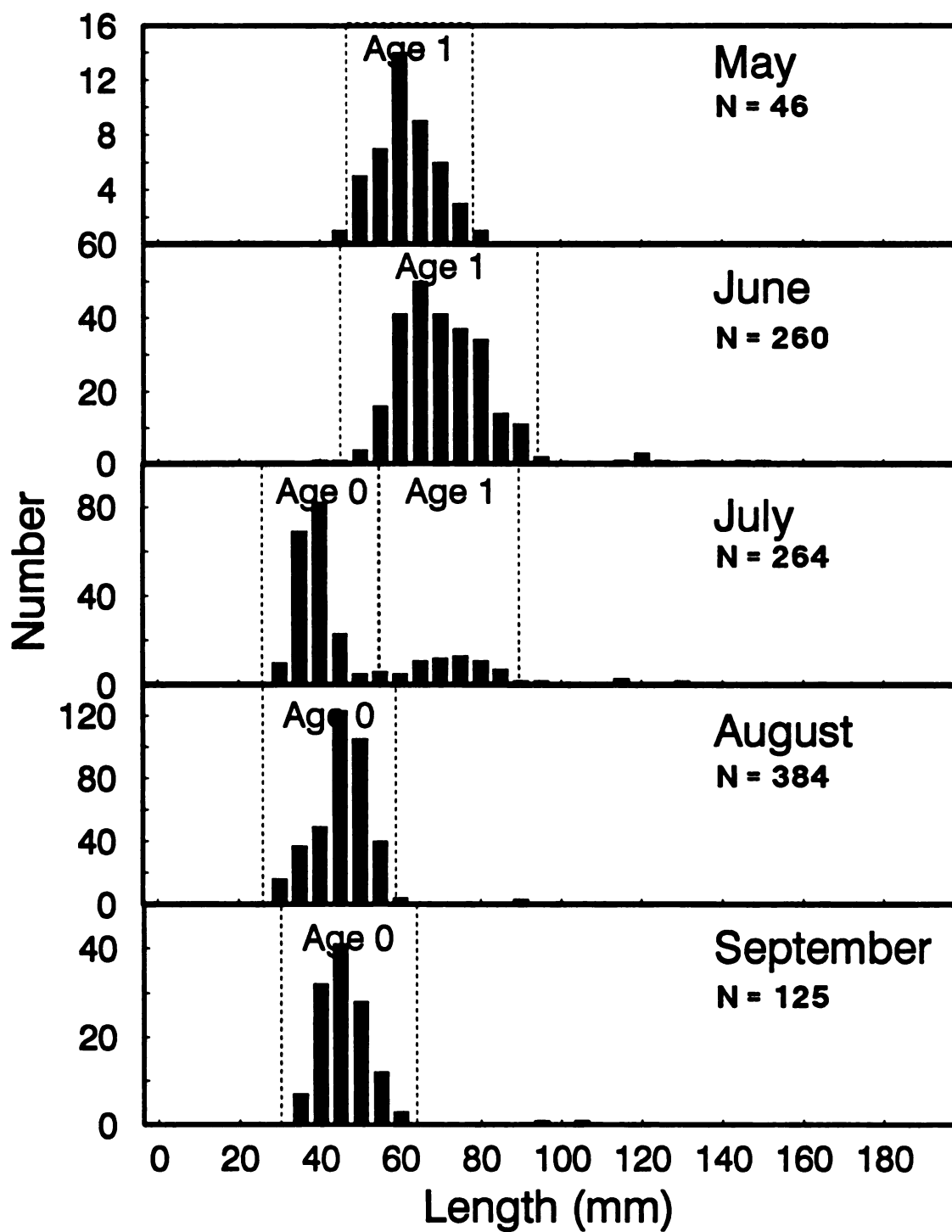


Figure 55. Length frequency distribution of juvenile and adult rainbow smelt sampled during monthly bottom trawl surveys in 1991.

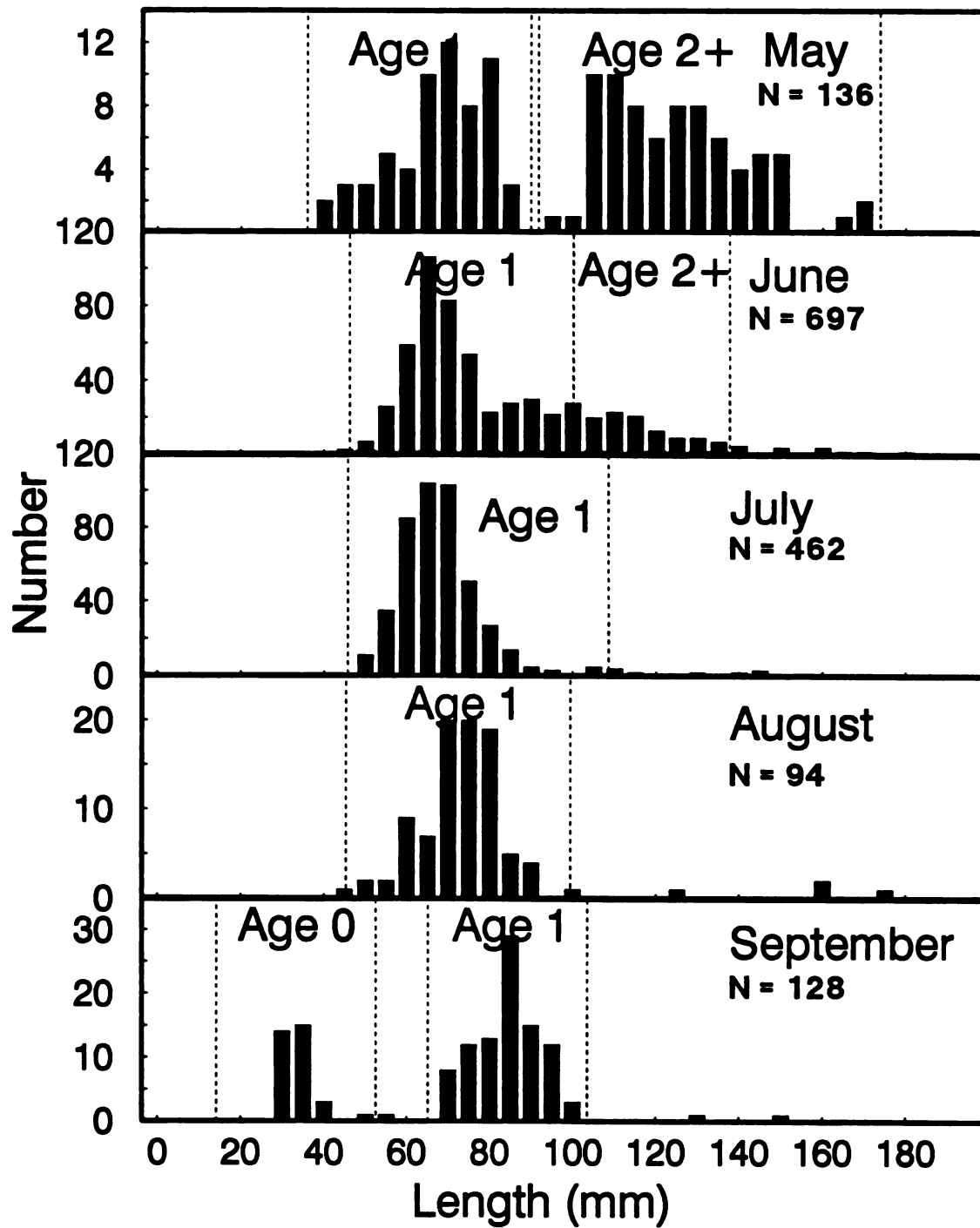


Figure 56. Length frequency distribution of juvenile and adult rainbow smelt sampled during monthly bottom trawl surveys in 1992.

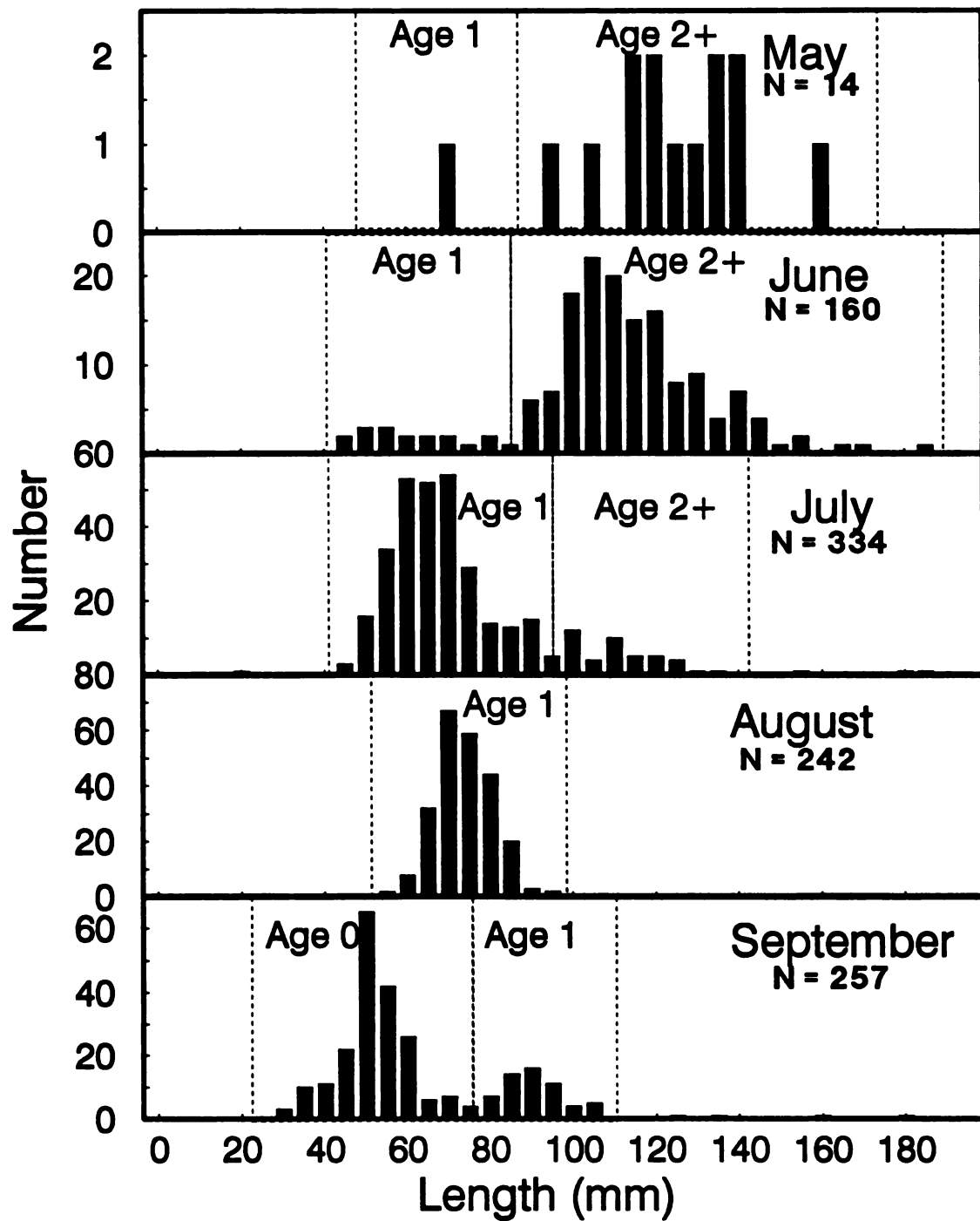


Figure 57. Length frequency distribution of juvenile and adult rainbow smelt sampled during monthly bottom trawl surveys in 1993.

Table 25. Total catch and combined CPUE of age 0+ rainbow smelt indexed using a standardized bottom trawl survey in St. Martin Bay, Lake Huron from 1991 to 1993.

Year	August Age 0+ Catch	August Effort (tows)	September Age 0+ Catch	September Effort (Tows)	Combined CPUE
1991	376	10	123	10	25.0
1992	21	10	34	9	2.9
1993	11	10	196	9	10.9

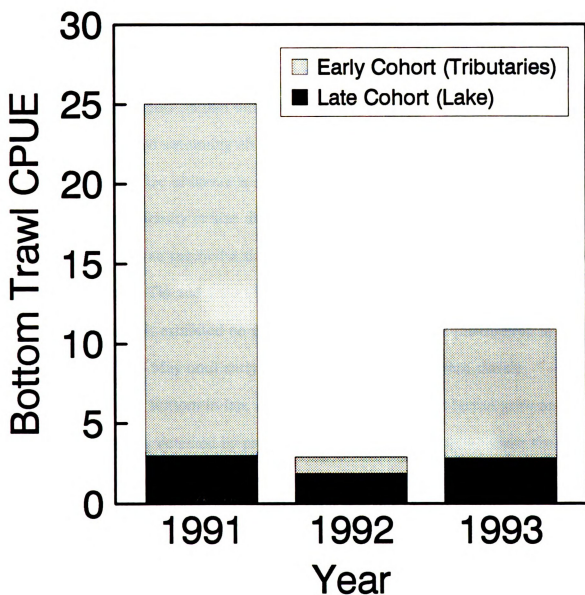


Figure 58. Relative contribution of early and late hatching cohorts to juvenile recruitment in St. Martin Bay, Lake Huron from 1991 to 1993.

Discussion

Diel Patterns in Larval Distribution

Diel differences in the density and size distribution of larval rainbow smelt are most likely a function of vertical migration and net avoidance. The influence of both of these factors on diel differences escalates with increasing larval size because of enhanced swimming ability of larger larvae. In May and early June, when the average size of larvae is less than 10-mm, I found no significant differences in the density or size distributions between day and night samples. However, once larvae reached a size exceeding 10-mm, vertical migration patterns became apparent. Tin and Jude (1983) found similar patterns, reporting that larval rainbow smelt exhibited no particular pattern of vertical distribution in the water column from May until early August, but that age 0+ were closely associated with the bottom in late August and September. As larvae grow and become more easily detected by predators, vertical migration may reduce the risk of predation by visually feeding predators (Miller et al. 1988).

Spatial Patterns Between Depth Contours

During late May and June, larvae appeared to be uniformly distributed across depth contours in the study area. Dunstall (1984) found that densities of rainbow smelt larvae in Lake Ontario were generally greatest in surface waters over the 3-m depth contour immediately after hatching. He found decreasing densities of larval rainbow smelt with increasing depth from the 3.0-m to the 13.0-

m contour indicating dispersal of larvae from shallow water regions. Larval densities in nearshore regions of our study area increased late in the season in 1992 and 1993, indicating an onshore migration of age 0+ rainbow smelt. Tin and Jude (1983) noted a similar pattern in Lake Michigan, reporting higher densities of larval rainbow smelt in nearshore waters in late summer samples.

Vertical Distribution Patterns

I found several consistent trends in the vertical distribution of larvae. Larval densities at the surface depth strata were usually the lowest densities recorded on each sampling date. Highest larval densities were associated with mid-depth strata in May and June, and with near-bottom strata in July and August. Emery (1973) found that rainbow smelt larvae in Georgian Bay, Lake Huron were closely associated with the bottom, and reported that larvae vertically migrated into upper depth strata at night from July to September.

O'Gorman (1983) sampled larval rainbow smelt in nearshore areas (5 to 10-m depths) of western Lake Huron during daylight hours to determine geographic distribution and seasonal occurrence and abundance. Abundances of rainbow smelt were highest from 2 to 6-m beneath the surface with abundances ranging as high as 2.5 larvae/m³. O'Gorman (1983) found that peak abundance of larval smelt in St. Martin Bay (467 larvae/1000 m³) occurred in late May to early June. I observed approximately the same densities in late May to early June in 1992 and 1993, but larval densities in 1991 were approximately three times as

high as were observed by O'Gorman (1983). These differences reflect interannual variation in the year class strength of rainbow smelt in this area.

Size Related Patterns in Larval Distribution

Length-frequency data from larval rainbow smelt collected on 27 July, 1993 demonstrate two important depth-related patterns. First, the mean size and length frequency distribution is shifted toward larger size in the deeper depth strata along all three contours. Second, at the 6.0-m and 8.0-m depth strata on the 10-m contour, the size distribution appears to be bimodal indicating a second cohort of larger larvae. I believe that the smaller size classes (6 to 20 mm) represent larvae hatching from lake spawning, which are spawned later and incubate longer due to colder lake water temperatures. The larger size classes (22 to 30 mm) represent tributary spawned larvae, which hatched in May and early June in St. Martin Bay tributaries.

There are several explanations for size-related patterns in the depth distribution of larval rainbow smelt. Larger larvae may inhabit deeper water as a predator avoidance mechanism. As larvae grow, they become more detectable by visual predators including adult rainbow smelt and alewives (Crowder 1980). Larger size distributions collected in night samples indicate that larger larvae may vertically migrate toward the surface at dusk. Nightly vertical migrations into the upper water column may allow larger larvae to feed on larger zooplankton, which also migrate up in the water column after dark. However, it is difficult to determine whether length frequency differences between day and night samples

are due to vertical migration or gear avoidance by larger larvae during day sampling.

It is unlikely that size-related patterns are due simply to dispersion away from spawning tributaries. The sample sites utilized in this study are located at least 2 km away from primary egg deposition areas and larvae dispersing from these areas will encounter deeper depth contours prior to reaching the shallower areas. In addition, I was unable to detect differences in the mean size of larvae between contours.

Larval Growth Rates

Larval growth rates were related to the spatial overlap of larval rainbow smelt and appropriate prey taxa and size classes. High densities of prey resources in late May and early June resulted in rapid growth of the early cohort of rainbow smelt in 1991. In 1992, low densities of prey availability during the same period and lack of spatial overlap between larval rainbow smelt and prey resources resulted in lower larval growth rates. By late June and July, higher densities of prey resources resulted in higher growth rates for the late hatching cohort. In 1993, moderate densities of prey resources and a high degree of spatial overlap between larvae and prey resources is reflected by intermediate growth rates.

Relative Contribution to Recruitment

Otolith-derived hatch date distributions indicate that 12% to 65% of juveniles contributing to recruitment were hatched after larval outmigration from tributaries had ceased. Other investigators (Tin and Jude 1982) have suggested

that later hatching larvae originate from eggs spawned in lake environments. To reach this conclusion, it is necessary to eliminate other possible explanations for the patterns observed in this study.

The tributaries selected for this study covered a wide range in size and average water temperatures. While other St. Martin Bay tributaries contributed to the larval populations in the bay, it is unlikely that the timing of outmigration occurred later than the four tributaries. Of the study tributaries, Spring Creek consistently had the coldest water temperatures. This tributary hosted the latest spawning runs and latest dates for larval outmigration in all three years. Spot sampling of water temperatures on 7 other St. Martin Bay tributaries (Pine River, Paquin Creek, McCloud Creek, and 4 unnamed tributaries) and 4 tributaries just west of the Straits of Mackinac (Martineau, Rabbit Back, Hoban, and Moron Creeks) demonstrated that Spring Creek had the coldest water temperatures during late April and May. Because spawning, incubation, and hatching of rainbow smelt is controlled by water temperature, it is reasonable to assume that Spring Creek had the latest larval hatch dates of St. Martin Bay tributaries. Because the nearest upcurrent tributaries outside of the St. Martin Bay-Mackinac Straits area are located in Lake Michigan, it is highly improbable that significant numbers of tributary spawned larvae would immigrate from sources outside St. Martin Bay.

The timing of spawning and hatching of lake spawned larvae was not directly measured in this study. However, differences in the timing of spring

warming of tributary and lake areas control the timing of spawning and larval hatching in lake areas. Because the bay warms more slowly than its tributaries, it takes longer for lake areas to reach preferred spawning temperatures causing lake spawning to occur later than tributary spawning. Shoreline seining conducted by personnel from the Chippewa-Ottawa Treaty Fishery Management Authority and bottom trawling conducted for this study during May and early June routinely captured spawning condition fish, sometimes weeks after tributary spawning had ceased. Because the rate of warming during incubation is slower in lake areas, the incubation time of lake spawned eggs is longer than for tributary spawned eggs. Later spawning and longer incubation of lake spawned eggs result in a later and temporally distinct hatching period for these larvae.

Because this study clearly identified the period of larval outmigration from tributaries, it is reasonable to conclude that recruited juveniles with hatch dates after the end of tributary outmigration originated from lake spawned larvae. It is less clear whether juveniles with hatch dates that correspond to periods of larval outmigration originated from tributary or lake spawned fish. However, given temperatures in St. Martin Bay and temperature-incubation duration information from the literature (Hoover 1936; McKenzie 1964; Cooper 1978), it was possible to estimate an approximate spawning period needed by lake spawning fish to have larval hatching temporally overlap with hatching of tributary spawned larvae. For lake spawned larvae to hatch by late May (the end of tributary outmigration), spawning would have to occur in early to mid April when water temperatures

were less than 2 C. Not only has spawning never been documented at temperatures this low, temperatures of 2 C have been shown to cause high mortality of rainbow smelt eggs under laboratory conditions (McKenzie 1964). Therefore, I conclude that juveniles with hatch dates corresponding with periods of tributary outmigration originate from tributary spawned larvae, while juveniles with hatch dates after the end of tributary outmigration represent lake spawned larvae.

Interannual Recruitment Patterns

The strongest year class produced during this study occurred in 1991, when the August/September bottom trawl CPUE of age 0+ juveniles was 25.0 juveniles/tow. Tributary larval production in 1991 was the highest recorded in this study (46 million larvae, Chapter 2), and hatch date distributions indicated that the majority (approximately 88%) of recruited juveniles were recruited from tributary spawned larvae. A weak year class was recruited in 1992 when the bottom trawl CPUE of age 0+ juveniles was only 2.9 juveniles/tow. Tributary larval production in 1992 was the lowest of the three years of the study (13.2 million larvae, Chapter 2), and the majority (approximately 65%) of recruited juveniles were recruited from lake spawned larvae. A moderate year class was recruited in 1993 when the bottom trawl CPUE of age 0+ juveniles was 10.9 juveniles/tow. Tributary larval production in 1993 was at intermediate levels (31.7 million larvae, Chapter 2), and significant contributions of both tributary and stream spawned larvae comprised the 1993 year class.

Based on these observations it appears that, although lake spawned larvae contribute significantly to recruitment, variation in recruitment in the St. Martin Bay system is primarily controlled by the contribution of tributary spawned larvae. The relatively strong 1991 year class was produced as a result of high tributary production of larvae, high growth rates and low mortality rates of this early cohort. In 1992, low tributary production of larvae, low growth rates and high mortality of early hatching larvae resulted in poor recruitment of this cohort. Larvae hatching after the end of tributary outmigration (assumed to be lake spawned fish) had relatively high growth and low mortality rates. Although late hatching larvae represented a significant portion of recruited juveniles relative to early hatching larvae, the overall magnitude of recruitment was low compared to 1991. During the three years of this study, late hatching cohorts made a relatively minor contribution to overall levels of recruitment.

It is important to recognize that the St. Martin Bay area has a relatively large number of tributary areas suitable for spawning by rainbow smelt. In areas where suitable tributaries are less prevalent (central and southwest Michigan coasts) and in onshore areas, the relative contribution of lake spawned larvae to recruitment may be significantly greater than was estimated for St. Martin Bay.

APPENDICES

Appendix 1. Age-length key for spawning rainbow smelt sampled from four tributaries to St. Martin Bay, Lake Huron in 1991.

Length Interval Minimum-Maximum	N	Age Class					
		I	II	III	IV	V	VI
90 - 94	0	-	-	-	-	-	-
95 - 99	0	-	-	-	-	-	-
100 - 104	2	0	100	0	0	0	0
105 - 109	1	0	100	0	0	0	0
110 - 114	6	0	100	0	0	0	0
115 - 119	8	0	100	0	0	0	0
120 - 124	17	0	100	0	0	0	0
125 - 129	25	0	100	0	0	0	0
130 - 134	44	0	98	2	0	0	0
135 - 139	55	0	84	16	0	0	0
140 - 144	57	0	37	63	0	0	0
145 - 149	52	0	16	84	0	0	0
150 - 154	40	0	3	97	0	0	0
155 - 159	27	0	0	100	0	0	0
160 - 164	20	0	0	100	0	0	0
165 - 169	16	0	0	100	0	0	0
170 - 174	13	0	0	62	38	0	0
175 - 179	8	0	0	63	37	0	0
180 - 184	7	0	0	71	29	0	0
185 - 189	8	0	0	13	87	0	0
190 - 194	3	0	0	0	100	0	0
195 - 199	3	0	0	0	67	33	0
200 - 204	2	0	0	0	50	50	0
205 - 209	1	0	0	0	0	100	0
210 - 214	2	0	0	0	0	100	0
215 - 219	2	-	-	-	-	-	-
220 - 224	0	-	-	-	-	-	-
225 - 229	0	-	-	-	-	-	-
230 - 234	0	-	-	-	-	-	-

Appendix 2. Age-length key for spawning rainbow smelt sampled from four tributaries to St. Martin Bay, Lake Huron in 1992.

Length Interval Minimum-Maximum	N	Age Class					
		I	II	III	IV	V	VI
90 - 94	0	-	-	-	-	-	-
95 - 99	2	0	100	0	0	0	0
100 - 104	2	0	100	0	0	0	0
105 - 109	12	0	100	0	0	0	0
110 - 114	15	0	100	0	0	0	0
115 - 119	21	0	100	0	0	0	0
120 - 124	30	0	100	0	0	0	0
125 - 129	55	0	100	0	0	0	0
130 - 134	63	0	100	0	0	0	0
135 - 139	62	0	100	0	0	0	0
140 - 144	66	0	85	15	0	0	0
145 - 149	57	0	32	68	0	0	0
150 - 154	43	0	0	100	0	0	0
155 - 159	27	0	0	100	0	0	0
160 - 164	22	0	0	100	0	0	0
165 - 169		0	0	100	0	0	0
170 - 174	15	0	0	100	0	0	0
175 - 179	15	0	0	100	0	0	0
180 - 184	10	0	0	100	0	0	0
185 - 189	8	0	0	100	0	0	0
190 - 194	11	0	0	36	64	0	0
195 - 199	0	-	-	-	-	-	-
200 - 204	4	0	0	0	50	50	0
205 - 209	1	0	0	0	0	100	0
210 - 214	3	0	0	0	0	100	0
215 - 219	0	-	-	-	-	-	-
220 - 224	0	-	-	-	-	-	-
225 - 229	0	-	-	-	-	-	-
230 - 234	2	0	0	0	0	0	100

Appendix 3. Age-length key for spawning rainbow smelt sampled from four tributaries to St. Martin Bay, Lake Huron in 1993.

Length Interval Minimum-Maximum	N	Age Class					
		I	II	III	IV	V	VI
90 - 94	0	-	-	-	-	-	-
95 - 99	0	-	-	-	-	-	-
100 - 104	5	0	100	0	0	0	0
105 - 109	12	0	100	0	0	0	0
110 - 114	12	0	100	0	0	0	0
115 - 119	22	0	100	0	0	0	0
120 - 124	33	0	100	0	0	0	0
125 - 129	51	0	100	0	0	0	0
130 - 134	71	0	100	0	0	0	0
135 - 139	85	0	99	1	0	0	0
140 - 144	75	0	85	15	0	0	0
145 - 149	64	0	75	25	0	0	0
150 - 154	41	0	10	90	0	0	0
155 - 159	31	0	0	100	0	0	0
160 - 164	27	0	0	96	4	0	0
165 - 169		0	0	80	20	0	0
170 - 174	18	0	0	28	72	0	0
175 - 179	5	0	0	0	100	0	0
180 - 184	3	0	0	0	33	67	0
185 - 189	1	0	0	0	0	100	0
190 - 194	1	0	0	0	0	100	0
195 - 199	0	-	-	-	-	-	-
200 - 204	2	0	0	0	0	100	0
205 - 209	0	-	-	-	-	-	-
210 - 214	0	-	-	-	-	-	-
215 - 219	0	-	-	-	-	-	-
220 - 224	0	-	-	-	-	-	-
225 - 229	1	0	0	0	0	0	100
230 - 234	1	0	0	0	0	0	100

Appendix 4. Length-weight regression equations for male and female rainbow smelt sampled from four Lake Huron tributaries from 1991 to 1993.

Year	Tributary	Sex	Sample Size	Slope	Intercept	R ²
1991	Carp River	Males	423	3.09819	-5.47855	0.9393
1991	Carp River	Females	203	3.10268	-5.47225	0.9237
1991	Carp River	Both	626	3.11895	-5.51783	0.9309
1991	Nunns Creek	Males	560	3.06288	-5.40658	0.9459
1991	Nunns Creek	Females	326	3.18790	-5.67797	0.9023
1991	Nunns Creek	Both	886	3.12502	-5.54100	0.9228
1991	St. Martin	Males	343	3.01161	-5.28419	0.9426
1991	St. Martin	Females	214	3.03524	-5.32282	0.9317
1991	St. Martin	Both	557	3.04470	-5.35111	0.9384
1992	Carp River	Males	344	2.99974	-5.25906	0.9626
1992	Carp River	Females	159	3.16349	-5.58969	0.9719
1992	Carp River	Both	503	3.07002	-5.40323	0.9622
1992	Nunns Creek	Males	305	3.12272	-5.52370	0.9539
1992	Nunns Creek	Females	197	3.06781	-5.40586	0.9304
1992	Nunns Creek	Both	502	3.09283	-5.45966	0.9412
1992	Spring Creek	Males	268	3.01650	-5.30093	0.9574
1992	Spring Creek	Females	233	3.04530	-5.35536	0.9549
1992	Spring Creek	Both	501	3.04686	-5.36273	0.9571
1992	St. Martin	Males	256	2.97060	-5.20203	0.9376
1992	St. Martin	Females	244	3.05210	-5.36942	0.9379
1992	St. Martin	Both	500	3.02675	-5.31897	0.9372
1993	Carp River	Males	315	3.11659	-5.50142	0.9565
1993	Carp River	Females	187	3.15296	-5.57734	0.9053
1993	Carp River	Both	502	3.12956	-5.52844	0.9382
1993	Nunns Creek	Males	333	3.01756	-5.29986	0.9450
1993	Nunns Creek	Females	171	2.92171	-5.10234	0.8792
1993	Nunns Creek	Both	504	2.96847	-5.19757	0.9197
1993	Spring Creek	Males	342	2.97275	-5.20978	0.9331
1993	Spring Creek	Females	139	2.98541	-5.22145	0.9022
1993	Spring Creek	Both	481	3.00615	-5.27709	0.9239
1993	St. Martin	Males	336	3.06545	-5.40618	0.9514
1993	St. Martin	Females	169	2.93061	-5.11680	0.9279
1993	St. Martin	Both	505	3.00312	-5.27284	0.9416

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