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Contributions to the early life histories of alewife (Alosa pseudoharengus) and blueback herring (Alosa aestivalis): Rearing, identification, ageing, and ecology

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Contributions to the early life histories of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*): Rearing, identification, ageing, and ecology

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CONTRIBUTIONS TO THE EARLY LIFE HISTORIES OF ALEWIFE (*Alosa pseudoharengus*) AND BLUEBACK HERRING (*A. aestivalis*): REARING, IDENTIFICATION, AGEING, AND ECOLOGY.

A Dissertation
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by

Edward Norbert Sismour

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This dissertation is submitted in partial fulfillment of
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Doctor of Philosophy

Edward Norbert Sismour

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To my wife, Karen, for sharing my triumphs and disappointments and for longstanding encouragement and support.

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ABSTRACT

Alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*, use the tidal freshwater-oligohaline reach of Chesapeake Bay tributaries for spawning and nursery grounds. Early life histories of these species, collectively known as river herring, are poorly documented for Chesapeake Bay populations. Alewife and blueback herring early life histories were investigated following two lines of research. First, cultured alewife and blueback herring larvae were used to evaluate methods for species identification and to validate the otolith increment method for age determination. For the second component, the distribution, abundance, growth, and hatch date frequencies of river herring larvae captured in the Pamunkey River, Virginia, tidal freshwater reach were analyzed. Potential zooplankton prey distributions and abundances were evaluated for field-collected samples.

Alewife and blueback herring larvae were reared beyond first-feeding in a continuous-flow culture system. River herring larvae hatched from naturally-spawned eggs collected in 1990 were reared to age 16 d, and alewife and blueback herring larvae hatched from artificially-spawned eggs in 1991 were reared to age 32 d and age 37 d, respectively. Meristic and morphometric characters did not differ between species, but diagnostic pigment characters were observed. Blueback herring exhibited one or two melanophores dorsally on the notochord starting at about 11 mm SL, relatively large xanthophores dorsally on the head, and xanthochrome at the caudal fin base. Alewife larvae exhibited paired melanophores laterally along the notochord starting at about 15 mm SL which increased in number with length, contracted xanthophores dorsally on the head, and lacked xanthochrome at the caudal fin base. Other pigment variation was observed. Otoliths of cultured larvae were relatively larger in slow-growing, older individuals than in fast-growing, younger individuals. Growth increments were deposited at rates of 1.16 increments$\cdot d^{-1}$ for blueback herring larvae reared in 1990 and 0.90 increments$\cdot d^{-1}$ for alewife and blueback herring larvae reared in 1991. Estimated deposition rates were influenced by variable microstructural appearance of otoliths, but did not differ statistically from one increment$\cdot d^{-1}$.

River herring larvae were sampled from the Pamunkey River tidal freshwater reach in 1989 and 1990. Yolk-sac larvae of river herring and gizzard shad, a freshwater herring, were captured together suggesting that the larvae coexist in this region. High water velocity in early May 1989 appeared to reduce larval river herring abundance along the mainstem river. High abundances from early to mid-May in two tidal creeks suggests that larvae use these areas briefly, but residence in the creeks may affect survival and growth of larvae and, possibly, year-class abundance. Larval river herring growth, pooled across seasons, was faster in the tidal creeks, 0.46 mm$\cdot d^{-1}$, than in the mainstem river, 0.34 mm$\cdot d^{-1}$. Older larvae, pooled across habitats, grew faster than younger larvae, 0.59 mm$\cdot d^{-1}$ and 0.35 mm$\cdot d^{-1}$. Hatch date frequency distributions identified one group with relatively earlier hatch dates associated primarily with the mainstem river and another group with relatively later hatch dates associated primarily with the tidal creeks. Zooplankton abundances were higher in the tidal creeks than the mainstem river when river herring larvae were abundant.

CONTRIBUTIONS TO THE EARLY LIFE HISTORIES OF ALEWIFE (*Alosa pseudoharengus*) AND BLUEBACK HERRING (*A. aestivalis*): REARING, IDENTIFICATION, AGEING, AND ECOLOGY.

INTRODUCTION

Anadromous fishes account for about 20% of species in tidal freshwater and oligohaline ecosystems compared to 60% freshwater species, 13% brackish water species, and 7% marine species (Odum et al. 1988). However, few species utilize the tidal freshwater-oligohaline reach of coastal plain rivers in the mid-Atlantic region for spawning and nursery habitat as extensively as anadromous herrings. Anadromous herring are part of the tidal freshwater-oligohaline milieu during the first year, and in this milieu is where year classes are established.

The significance of mesohaline and euryhaline estuarine ecosystems (salinity > 5‰) for larval, juvenile, and adult fishes is well documented (Massmann 1963; Wiley et al. 1973; Shenker and Dean 1979; Bozeman and Dean 1980; Dovel 1981; Boesch and Turner 1984). Tidal freshwater ecosystems have not been studied as extensively as estuarine ecosystems farther downstream, and only in the past 10 to 15 years have tidal freshwater and oligohaline ecosystems been investigated intensively. Studies of tidal freshwater and oligohaline ecosystems have shown that: 1) high primary productivity occurs in the tidal freshwater-oligohaline reach (Anderson 1986; Marshall and Alden 1990; Schuchardt and Schirmer 1991; Jones et al. 1992), 2) food webs in marshes and tidal creeks of the tidal freshwater-oligohaline reach may be detritus-based (Odum 1988) and a microbial food web may be a significant component of ecosystem trophodynamics in the Chesapeake Bay region (Sellner 1988), 3) tidal freshwater-oligohaline ecosystems are important nursery grounds for fishes and invertebrates (Mihursky et al. 1982; Rozas and Hackney 1983; Rozas and Odum 1987a, 1987b, 1987c; Rozas, McIvor, and Odum 1988), and 4) biogeochemical transformations significant to estuarine ecology occur in the tidal freshwater-

oligohaline reach (Morris et al. 1978; Biggs et al. 1983; Anderson 1986; Odum 1988; Schuchardt and Schirmer 1992). Although discussing specifically the importance of vascular plant detritus for salt-marsh ecosystem management, a statement by Odum et al. (1972) applies equally to the importance of tidal freshwater and oligohaline ecosystem processes in fisheries and habitat management and states explicitly the need for further understanding of underlying ecological processes:

> "... *if the ecological role of marsh grasses as a basis of an entire detritus-based food web is not recognized, how can the results be predicted when a proposal is made to replace 300 acres of marsh with a housing development?*".

Spawning populations of four anadromous herring species occur in Chesapeake Bay: American shad (*Alosa sapidissima*), hickory shad (*Alosa mediocris*), alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*). Alewife and blueback herring are collectively known as river herring due to similar adult morphologies. Two freshwater herring species, gizzard shad (*Dorosoma cepedianum*) and threadfin shad (*Dorosoma petenense*), also occur in fresh and brackish water reaches of Chesapeake Bay tributaries. Ecologically, herring in tidal freshwater ecosystems are important since relatively few species utilize this region for nursery habitat to the same extent as herring and because these species are prey for numerous other ecologically, commercially, and recreationally valuable species of both terrestrial and aquatic origin (Loesch 1987). Anadromous herrings are exploited by commercial and recreational fisheries making further understanding of their biology and ecology a significant fisheries management issue.

Improved understanding of anadromous herring ecology and of linkages uniting tidal freshwater with adjacent ecosystems (Ward 1989) are necessary for fisheries and habitat management. As human populations in coastal regions increase, improved knowledge of tidal freshwater ecosystems will be essential to balance increased human usage

with habitat requirements for fishes and other species utilizing these ecosystems during some or all of their life-history. The human population in the Chesapeake Bay watershed is expected to increase nearly 20%, from 13.6 million to 16.2 million, by the year 2020 with significant growth projected for Virginia (32% increase) especially in the coastal plain where Virginia's tidal freshwater ecosystems occur (Anon. 1988). Pressure on tidal freshwater ecosystems will increase as municipalities seek additional freshwater supplies and as citizens seek recreational opportunities.

Anadromous herring recruitment studies are limited geographically, primarily New England, with emphasis placed on American shad (Leggett 1977; Crecco and Savoy 1987a), although alewife and blueback herring recruitment has been examined to lesser degree (Havey 1973; Walton 1987; Jessop 1990). Anadromous herring early life histories and the importance of tidal freshwater habitats as nursery grounds for anadromous herring larvae are poorly documented for Chesapeake Bay. Hypotheses explaining anadromous herring recruitment in other areas may not explain, to same degree, recruitment variation for these species in Chesapeake Bay tributaries. Understanding mechanisms affecting larval fish survival is necessary to explain recruitment variation, but little effort has been made to elucidate mechanisms of larval river herring survival in Chesapeake Bay tributaries.

The present research was undertaken to obtain basic biological and ecological information on alewife and blueback herring larvae in the tidal freshwater reach of the Pamunkey River, a southern Chesapeake Bay tributary. A field investigation of larval river herring ecology was conducted to describe and quantify distributions and abundances of alewife and blueback herring larvae and potential zooplankton prey in the Pamunkey River tidal freshwater reach, to quantify larval river herring growth between seasons and locations that may differ as nursery habitat, and to evaluate larval river herring hatch dates in relation to

larval river herring and zooplankton abundances. To accomplish these objectives, studies were made to evaluate methods for identification of alewife and blueback herring larvae and to validate the otolith increment method for age determination. These studies required the development of a technique to rear alewife and blueback herring larvae. Investigations conducted for this research are summarized briefly below.

Inability to rear alewife and blueback herring larvae beyond first-feeding has impeded alewife and blueback herring early life history investigations. Chapter 1 describes a continuous-flow culture system used successfully over a two-year period to rear alewife and blueback herring larvae beyond first-feeding. This chapter documents zooplankton abundances and growth of larvae in the culture system.

Ecological studies of alewife and blueback herring larvae have been hindered by an inability to identify field-collected larvae. Other inquiries do not agree on the usefulness of morphometric or meristic characters for delimiting alewife and blueback herring larvae, and pigment characters had not been investigated using larvae of known taxonomic identity prior to this research. Chapter 2 evaluates the usefulness of morphologic, meristic, and pigment characters for delimiting alewife and blueback herring larvae using specimens reared from artificially-spawned eggs of known identity.

An important aspect of the distribution and abundance of fish larvae is whether vital rates vary between cohorts of larvae. Daily incremental deposition of calcium carbonate in otoliths provides an endogenous chronometer recording larval fish age providing information fundamental to population dynamics assessment. Validation of the otolith increment method for age determination is an essential prerequisite before using the method to estimate ages of field-collected specimens. Chapter 3 validates the otolith increment method for age determination using known-age river herring larvae and examines relationships between otolith size, fish size, and true age.

Aspects of larval river herring ecology and population dynamics in the Pamunkey River tidal freshwater zone in 1989 and 1990 are analyzed in Chapter 4. Distributions and abundances of larvae along the mainstem river and between areas hypothesized to represent distinct nursery habitats are analyzed. Distributions and abundances of zooplankton (rotifers, copepod nauplii and copepodites, and cladocerans) in the mainstem river and between potential nursery habitats also are analyzed. Selected abiotic variables which might influence larval river herring vital rates are evaluated, including temperature, rainfall, river flow, dissolved oxygen, and water transparency. Growth of larvae between the mainstem river and selected tidal creek habitats is also evaluated.

This research provides a foundation for further investigations of larval alewife and blueback herring biology and ecology. Principal contributions of this research include:

1. A method to culture alewife and blueback herring larvae is described. A culture system developed to rear larvae may facilitate experimental studies on river herring larvae by promoting growth beyond first-feeding without elaborate laboratory support. Once able to feed on larger prey which may be more readily cultured (e.g. *Artemia*), river herring larvae may then be transferred to other tanks for study.

2. Characters delimiting alewife and blueback herring larvae are described. Ability to delimit these larvae will facilitate comparative ecological study of these species.

3. The daily otolith growth-increment method for ageing is validated for river herring larvae. A method to identify and enumerate daily growth increments is described and potential sources of error are identified.

4. This research provides fundamental information on the ecology of river herring larvae in a tidal freshwater ecosystem. Improved knowledge of larval river herring ecology will contribute to further understanding of factors affecting year-class success in these species. This research will contribute potentially to fisheries and habitat management and to land-use and water-use planning affecting the Pamunkey River and other coastal plain rivers.

Chapter 1.

Zooplankton Abundances and Growth of Alewife and Blueback Herring Larvae in a Continuous-flow Culture System

ABSTRACT

Alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) larvae do not feed readily when reared in aquaria and they eventually die. A continuous-flow culture system used successfully to rear alewife and blueback herring larvae beyond first-feeding is described. Mean standard length (SL) of blueback herring larvae reared in 1990 was 16.4 mm at age 16 d, and a single larva was 19.6 mm SL at age 24 d. Mean lengths of alewife and blueback herring reared in 1991 were 17.1 mm SL at age 32 d and 14.6 mm SL at age 37 d, respectively. Availability of prey (rotifers, copepodites and nauplii, and cladocerans) appeared to be the primary factor limiting survival and growth of larvae reared in 1991. An ability to rear alewife and blueback herring larvae under controlled conditions may facilitate studies of their early life histories and of factors influencing their survival and growth in the wild. In addition, the continuous-flow system may provide an alternative to *in situ* enclosures for studying the dynamics of fish larvae in tidal freshwater or estuarine ecosystems.

INTRODUCTION

Numerous factors potentially limit larval fish survival in culture. One important factor is prey quality, including suitable size, composition, and density (Houde 1973; Kinne 1977; Hunter 1984). Wild zooplankton offers a wide variety of prey, but fluctuating availability and uncontrolled composition and quality may affect the foraging success of larvae in aquaria (Kinne 1977). Cultured zooplankton provide reliable, controlled prey (Kinne 1977), but culturing requires specialized facilities (Heinrich 1981; Kellogg 1982). Collecting or intensive culturing of zooplankton in sufficient quantity to support large numbers of fish larvae can be difficult and labor-intensive. *Artemia salina* nauplii are used extensively as prey for fish larvae and are relatively easy to culture. However, they are too large for first-feeding larvae of many species (Houde 1973), including alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*. Rearing conditions may affect larval fish survival in culture. Rearing container volume may influence prey consumption, the nutritional condition of larvae (Theilacker 1980; Barahona-Fernandes and Conan 1981), and neurological stimulation which may be essential to proper behavioral development (Blaxter 1969). Additionally, accumulation of pathogens in closed systems may increase larval fish mortality (Blaxter 1968).

Attempts to rear alewife and blueback herring larvae, collectively known as river herring, in the laboratory have had limited success (Mansueti 1956; Norden 1967, 1968; Adams and Street 1969; Cianci 1969; Davis et al. 1972; Loesch and Kriete 1976; Lam and Roff 1977; Schubel et al. 1977; Kellogg 1982). Difficulty in completing successfully the transition from endogenous (yolk) to exogenous nourishment in aquaria appears to be the primary factor inhibiting larval river herring culture

under controlled conditions (Heinrich 1981). However, Heinrich (1981) successfully reared alewife from eggs to the juvenile stage in aquaria using wild zooplankton for prey. Heinrich (1981) collected wild zooplankton which he fed to the alewife larvae twice daily without additional treatment (e.g. sieving), and he supplemented the natural zooplankton with *Artemia salina* nauplii after about 15 days and with laboratory-cultured *Daphnia magna* after 40 days.

Inability to rear alewife and blueback herring larvae using relatively simple techniques has hindered basic early life history studies which have importance for fisheries and habitat management. Methods facilitating active feeding at the time of transition to exogenous nourishment would promote experimental evaluation of these species. In this chapter, I describe the design of a continuous-flow culture system developed to circumvent problems associated with either culturing prey or collecting wild zooplankton and with intensive daily maintenance. The growth of larvae in 1-m^3 tanks of the system is analyzed and is compared to growth of starved larvae maintained in aquaria. Zooplankton concentrations, dissolved oxygen, water clarity, and water temperature in the 1-m^3 tanks and in the Pamunkey River are evaluated and compared to determine whether the 1-m^3 tanks imitated the natural environment.

METHODS

Artificial-spawning of eggs

Adult, ripe-running alewife and blueback herring were collected on tidal freshwater spawning grounds in eastern Virginia (Fig. 1-1). Unfertilized eggs (approximately 30 to 40 mℓ) from two to four females were expressed into a shallow glass dish and fertilized with milt from several males following the dry-method (Piper et al. 1982). The fertilized eggs were poured onto 333-μm mesh nylon screen sieves, rinsed in ambient temperature creek water to remove excess milt, and

transported to the culture facility in coolers in creek water taken from the spawning ground. The culture facility was located within the historical nursery area for *Alosa* spp. near the upper limit of the Pamunkey River estuary (Van Engel and Joseph 1968) (Fig. 1-1).

Rearing facilities

The recirculating system for rearing embryos and yolk-sac larvae

Blueback herring eggs were incubated in 1989 in 0.5-μm filtered Pamunkey River water collected from near the upper limit of the tidal freshwater zone 72 kilometers upstream from West Point, Virginia. Alewife and blueback herring eggs were incubated in 1990 and 1991 in Pamunkey River water obtained at the site of the culture facility 32 kilometer upstream from West Point in the lower reach of the tidal freshwater zone and in water from Herring Creek and Massaponax Creek (Fig. 1-1). Pamunkey River water at the culture facility was very turbid so it was filtered through 5.0-μm polyethylene filters. Herring Creek and Massaponax Creek water samples were not turbid and were filtered through a 35-μm sieve to remove relatively larger debris.

In 1989, blueback herring larvae were hatched from eggs and maintained in a 37.8-ℓ aquarium until all larvae died (Fig. 1-2a). In 1990, a recirculating system was established incorporating two 37.8-ℓ aquaria for rearing embryos and yolk-sac larvae (referred to as rearing aquaria) and a third 37.8-ℓ aquarium as a reservoir (Fig. 1-2b). A filter-pump (Fluval[1]) circulated and filtered the water in the system, and circulation in the rearing aquaria was enhanced using adjustable-flow aquarium pumps[2]. Embryos and yolk-sac larvae were separated from overflow outlets in the rearing aquaria using 333-μm nylon screen. Eggs and yolk-sac larvae were illuminated indirectly by sunlight or by continuous, overhead incandescent light at night. A submersible aquarium heater in the reservoir tank, adjusted for a minimum water temperature of about 17-18 °C, prevented extreme temperature decline.

The continuous-flow system for rearing larvae beyond first-feeding

The continuous-flow culture system water intake consisted of a submersible pump[3] (1000 gallon-per-hour maximum capacity) suspended in a perforated (6.25-mm diameter holes), 208-ℓ plastic barrel. The barrel was suspended from a floating platform to provide constant head pressure on the pump (Fig. 1-3A:1). Vinyl-coated chicken wire surrounded the platform perimeter to a depth of about 1 m. Water was pumped through 15.6-mm diameter hose into the bottom of a sealed 208-ℓ plastic barrel half-filled with one-quarter inch diameter (pea) gravel which served as a coarse filter and settling tank (Fig. 1-3A:2). From an outlet near the top of the barrel, flow was split into two lines which drained into 300-μm mesh nylon bag filters suspended in sealed 208-ℓ plastic barrels (Fig. 1-3A:3). The filtrate drained from the barrels into 1-m^3 conical tanks used for rearing larvae (see below). The settling tank was back-flushed weekly to prevent excessive sediment accumulation which might increase the transfer of sediment to the tanks.

Two 1-m^3 fiberglass tanks were used to rear larvae (Fig. 1-3B:4). Each tank was 80 cm deep at the wall, 100 cm deep at the center, and 120 cm in diameter. Water depth at the center varied from 91 cm to 96 cm depending on the clogging of a wire screen covering the drain holes of a standpipe sleeve (see below). Each tank had a bluegreen vinyl tank liner[4] as a contrasting background to facilitate foraging by larvae (Kinne 1977). In-line valves positioned before the settling tank (not shown in Fig. 1-3) and between the settling tank and nylon filter socks[4] enabled adjustment of flow rate. Flow into each tank was approximately equal averaging about 1.5 $\ell \cdot min^{-1}$ resulting in about 12 hr turnover.

The outlet for each tank consisted of a standpipe with an outer sleeve (Fig. 1-3:5). Each standpipe was 91-cm tall, 50-mm diameter polyvinyl chloride (PVC) pipe inserted through a 100-to-50 mm PVC reducing adapter and fit into the drain adapter of the 1-m^3 tanks. Each outer sleeve was 96-cm tall, 100-mm diameter PVC pipe with several 50-mm

diameter holes near the base covered with 300-μm wire-mesh screen. The outer sleeve forced water to drain from the bottom facilitating circulation and oxygenation throughout the tank, and the reducing adapter prevented larvae from escaping the tank.

The 1-m^3 tanks were subject to ambient environmental conditions (e.g. illumination, rainfall, temperature). Zooplankton entrained in Pamunkey River water established and supplemented zooplankton populations in the tanks and were prey for larvae.

Rearing embryos

In 1990, river herring and gizzard shad, *Dorosoma cepedianum*, yolk-sac larvae were hatched from naturally-spawned eggs; river herring larvae were later identified as blueback herring (Chapter 2). River herring and gizzard shad were delimited based on yolk sac morphology (Lippson and Moran 1974) and were stocked into separate 1-m^3 tanks. In 1991, alewife and blueback herring were hatched from artificially-spawned eggs in 37.8-ℓ aquaria. In both years, larvae were transferred to the 1-m^3 tanks prior to complete yolk absorption. All yolk-sac larvae were transferred to the 1-m^3 tanks in 1990, but a small number of alewife and blueback herring yolk-sac larvae reared in 1991 were maintained in aquaria without food to compare the growth of starved and fed larvae.

In 1991, alewife larvae were reared from 10 April to 13 May and blueback herring larvae were reared from 30 April to 6 June because of differing availability of adults. Alewife larvae were stocked initially into both 1-m^3 tanks (collectively referred to as Tank A) because of uncertainty about zooplankton abundance. When blueback herring were available for stocking, alewife larvae were collected from one of the two 1-m^3 tanks which was then drained, refilled, and stocked with blueback herring (Tank B). By 13 May, all alewife were collected from the other 1-m^3 tank which was then drained, refilled, and maintained as

a larvae-free standard to evaluate changes in zooplankton abundance independent of predation.

Specimen collection

Alewife and blueback herring larvae were collected from the 1-m^3 tanks using a 333-μm mesh net at 3- to 5-day intervals. At least 15 larvae were usually sampled, although as few as 10 larvae were sampled on occasion because of uncertainty in the number of larvae remaining in the 1-m^3 tanks. Larvae were anaesthetized in tricaine methanosulfate (MS-222) immediately upon capture and were measured prior to fixation to avoid error caused by fixative-induced shrinkage. Morphometric measurements, including standard length (SL) and vent length, were made using a Wild M3Z stereo-zoom microscope fitted with a calibrated, 120-unit reticle ocular micrometer and followed Lippson and Moran (1974). Subsamples of larvae were fixed in 5% phosphate buffered formalin (5% PBF) (Markle 1984) or in Bouins solution or were preserved in 95% ethanol for subsequent analyses.

Larval herring growth

Length-at-age data were fitted to the Gompertz growth function (Eq. 1-1) using the FISHPARM computer program (Prager et al. 1987):

$$L(t)=L(0)\exp(G(1-\exp(-gt))) \qquad \text{Eq. 1-1,}$$

where L(0) is the length at hatching. The Gompertz growth function was selected because it potentially describes the relation between weight or length and age for young fishes, and because the parameters have defined biological meaning. The term Gg is the instantaneous rate of growth when t = 0, and g is the instantaneous rate of decrease in the instantaneous rate of growth (Ricker 1975). Mean daily growth was the average estimated daily growth between age-classes.

Larvae maintained in aquaria without food were compared with fed larvae reared in the 1-m^3 tanks of the continuous-flow system. Growth was estimated as the difference between mean standard lengths of larvae at hatching and prior to complete mortality of starved larvae (8 days after hatching). A single sample of starved blueback herring larvae reared in 1991 was obtained 5 days after hatching so the change in length with age was calculated for this group. The difference in mean length-at-age between starved and fed larvae was evaluated using Student's t-test ($\alpha = 0.05$).

Environmental variables

Water temperature, measured using a stem thermometer, and water samples to measure dissolved oxygen were obtained when larvae were sampled in 1991. Water temperature measurements were made near the continuous-flow system intake and in the 1-m^3 tanks, but water samples for dissolved oxygen determination were taken only from the tanks. Dissolved oxygen was determined by modified Winkler titration. Salinity was measured using a refractometer. The difference in water temperature between the river and 1-m^3 tanks was evaluated using Student's t-test.

Zooplankton collection and laboratory methods

Zooplankton was collected from the Pamunkey River near the system intake and in the 1-m^3 tanks in 1991 to evaluate the abundance of potential prey for alewife and blueback herring larvae in both locations. Twenty-liter water samples were obtained from a standard depth of 0.5 m using an impeller-driven pump (RULE, 2000 gallon-per-hour maximum capacity) powered by a 12-volt marine battery. Zooplankton samples were concentrated on a 35-μm sieve, transferred to sample jars, and preserved in 5% PBF. In the laboratory, the samples were adjusted to a standard volume (110 mℓ) and mean relative densities (subsequently called abundances) of rotifers, copepods (nauplii and copepodites), and

cladocerans were estimated from counts made on four 1-mℓ subsamples per collection. Collections were subsampled using a Hensen-Stempel pipet and were dispensed into a Sedgewick-Rafter counting chamber for enumeration using a compound microscope at 40x magnification. Soft-bodied rotifers may have been underestimated due to formalin fixation (Pennak 1989).

Zooplankton samples from the river and the 1-m^3 tanks were compared to determine whether abundances of rotifers, nauplii and copepodites, and cladocerans differed between rearing tanks (with herring larvae and the larvae-free standard) and the Pamunkey River. Zooplankton abundances in the larvae-free standard and in the river were compared to determine whether herring larvae affected zooplankton abundance in the tanks.

Statistical analysis

A Kruskal-Wallis nonparametric ANOVA was used to determine whether zooplankton abundances in the 1-m^3 tanks and the river differed significantly. Spearman's rank correlation coefficient measured the association between zooplankton abundances in the rearing tanks and the river. Statistical analyses were conducted using the microcomputer statistical program package MINITAB (MINITAB 1989).

RESULTS

Rearing alewife and blueback herring larvae

Numerous attempts were made from 1989 to 1991 to rear alewife and blueback herring larvae (Table 1-1). Blueback herring were successfully hatch in 1989 from artificially-spawned eggs incubated in 0.5-μm filtered Pamunkey River water. In 1990, artificially-spawned eggs incubated in 5.0-μm filtered Pamunkey River water failed to hatch due to fungal infestation, but naturally-spawned blueback herring and gizzard shad eggs were hatched successfully in Herring Creek water (Fig. 1-1).

In 1991, artificially-spawned alewife and blueback herring eggs were also hatched successfully in Herring Creek water. One unsuccessful attempt was made to hatch artificially-spawned alewife eggs in Massaponax Creek water. For successfully reared groups of larvae (Table 1-1), hatching success was high and few dead eggs were observed. Mean water temperature in the rearing aquaria during alewife and blueback herring egg incubation in 1991 was 18.8 °C (±1.8 °C).

Yolk sac absorption occurred 2 to 3 days after hatching. Numbers of yolk-sac larvae stocked in the 1-m^3 tanks of the continuous-flow system in 1990 and 1991 were not standardized. No information was available to determine an optimal stocking density which was likely to depend on prey availability at the onset of exogenous feeding. Compared to the abundance of artificially-spawned eggs, fewer naturally-spawned eggs were available due to the small number collected from Herring Creek. Consequently, fewer specimens were stocked into and collected from the 1-m^3 tanks in 1990. A total of 51 blueback herring larvae were collected in 1990, but no gizzard shad larvae survived. In 1991, 280 alewife larvae and 521 blueback herring larvae were collected.

Growth of alewife and blueback herring larvae

Larvae reared in aquaria without food in 1989 and 1991 died after about 8 days, presumably of starvation. Mean standard length of starved larvae increased about 1.0 mm to 1.5 mm compared to 2.2 mm to 5.8 mm for larvae reared in the tanks ($t = -3.09$, one-tail $p = 0.045$) (Table 1-2). Estimated mean growth of starved and fed larvae during this period was 0.2 $mm \cdot d^{-1}$ and 0.5 $mm \cdot d^{-1}$, respectively (Table 1-2).

Growth differed significantly between the three groups of cultured alewife and blueback herring larvae based on 95% confidence intervals of mean standard lengths (Fig. 1-4). Blueback herring larvae in 1990 ranged from 4.3 mm SL at hatching to 19.6 mm SL for a single specimen at age 24 d. Growth was approximately linear from 5 to 16 days after

hatching with a mean rate of about 0.8 mm·d^{-1}. In 1991, growth averaged about 0.4 mm·d^{-1} for alewife larvae and about 0.3 mm·d^{-1} for blueback herring larvae over the entire age range (Table 1-3), but growth was non-linear (Fig. 1-4). Alewife larvae ranged from 3.8 mm SL at hatching to 17.3 mm SL at age 32 d. Growth increased from about 0.1 mm·d^{-1} for age 4 d to age 8 d larvae to about 0.6 mm·d^{-1} for age 27 d to age 32 d larvae (Table 1-3). Blueback herring ranged from 3.9 mm SL at hatching to 14.1 mm SL at age 37 d. Growth decreased from about 0.7 mm·d^{-1} for age 5 d to age 8 d larvae to about 0.3 mm·d^{-1} for age 29 d to age 37 d larvae (Table 1-3). Mean length-at-age of blueback herring larvae did not change significantly between age 21 d and age 29 d (Fig. 1-4). Gompertz growth parameters *G* and *g* were about twice as high and about seven-fold higher, respectively, for blueback herring, 0.117 and 0.087, than for alewife, 0.058 and 0.013. Consequently, the instantaneous rate of growth (*Gg*) was about an order of magnitude greater for blueback herring (0.01 mm) than for alewife (0.001 mm). Growth of cultured alewife and blueback herring larvae is analyzed in further in Chapter 3.

Environmental Conditions

Water temperature in the 1-m^3 tanks and the river ranged from about 13 °C to about 30 °C and from about 16 °C to about 29 °C, respectively (Fig. 1-5). Water temperature in the 1-m^3 tanks was about 18 °C when alewife larvae were stocked and was about 22 °C when blueback herring were stocked. Water temperature in 1991 did not differ significantly between the 1-m^3 tanks and the river ($t = -1.03$, $p = 0.31$, $df = 33$). Dissolved oxygen in the 1-m^3 tanks always exceeded 7 mg·mℓ^{-1}. Salinity in the 1-m^3 tanks was always 0.0‰ (freshwater).

Zooplankton Availability

Zooplankton in river

Rotifer, copepod (nauplii and copepodites), and cladoceran abundances in the Pamunkey River fluctuated in 1991 (Fig. 1-5B to 5D). Maximal rotifer abundance observed in mid-May was about 700 individuals$\cdot \ell^{-1}$. Copepod abundance exceeded 250 individuals$\cdot \ell^{-1}$ from mid- to late May. Maximal cladoceran abundance, observed from late April to early May at about 60 individuals$\cdot \ell^{-1}$, occurred during low rotifer and copepod abundances, about 50 individuals$\cdot \ell^{-1}$.

Zooplankton in culture tanks

Zooplankton abundance without herring larvae

Abundances in the larvae-free standard and the river did not differ for rotifers ($H = 0.03$, $df = 1$, $p = 0.873$; Fig. 1-5B) or for copepods ($H = 0.00$, $df = 1$, $p = 1.000$; Fig. 1-5C), whereas cladoceran abundance was significantly greater in the larvae-free standard ($H = 4.69$, $df = 1$, $p = 0.031$, adjusted for ties; Fig. 1-5D). Correlation between abundances in the larvae-free standard and river was weak for rotifers ($r = 0.429$), copepods ($r = -0.143$), and cladocerans ($r = 0.257$). Rotifer and copepod abundances did not differ between the larva-free standard and the river (rotifers: $H = 0.03$, $df = 1$, $p = 0.873$; copepods: $H = 0.00$, $df = 1$, $p = 1.000$), but cladoceran abundances differed significantly ($H = 4.67$, $df = 1$, $p = 0.031$).

Zooplankton abundance during the culture of alewife

Rotifer abundances during larval alewife development were higher in the 1-m^3 tanks (Tank A) than in the river (Fig. 1-5B). Maximal abundance in Tank A, 682 rotifers$\cdot \ell^{-1}$, and highest observed abundance in the river, 463 rotifers$\cdot \ell^{-1}$, were observed on 13 May. Mean abundance was 169.2 $\pm$ 218.0 rotifers$\cdot \ell^{-1}$ in Tank A and 91.3 $\pm$ 148.1 rotifers$\cdot \ell^{-1}$ in the river. Abundances of rotifers in Tank A and the river did not

differ (H = 0.94, df = 1, p = 0.331) and abundances were strongly correlated (r = 0.983).

Copepod abundances in Tank A and the river were less than 50 copepods$\cdot \ell^{-1}$ and remained stable throughout larval alewife development (Fig. 1-5C). Mean abundances were 22.4 ± 12.3 copepods$\cdot \ell^{-1}$ in Tank A and 17.7 ± 12.4 copepods$\cdot \ell^{-1}$ in the river. Abundances of copepods in Tank A and in river did not differ (H = 1.03, df = 1, p =0.309) and abundances were weakly correlated (r = 0.226).

Cladoceran abundance in Tank A early during larval alewife development were initially higher than the river and were relatively higher than rotifer or copepod abundances, but declined and then fell below abundance in the river (Fig. 1-5D). Maximal abundance in Tank A, 112 cladocerans$\cdot \ell^{-1}$, was observed on 23 April while maximal abundance in the river, 60 cladocerans$\cdot \ell^{-1}$, was observed on 29 April. Mean abundances were 43.7 ± 36.2 cladocerans$\cdot \ell^{-1}$ in Tank A and 27.3 ± 20.5 cladocerans$\cdot \ell^{-1}$ in the river. Abundance of cladocerans in Tank A and the river did not differ (H = 0.86, df = 1, p = 0.354) and were weakly correlated (r = 0.276).

Zooplankton abundance during the culture of blueback herring

Rotifer abundance during larval blueback herring development in the 1-m^3 tank (Tank B) following complete draining and refilling was equivalent initially to abundance in Tank A which had not been drained and refilled. Abundance was higher in Tank B than in the river. Rotifer abundance in Tank B declined then declined while abundance in Tank A and the river increased (Fig. 1-5B). Maximal rotifer abundance in Tank B, 285 rotifers$\cdot \ell^{-1}$, was observed on 13 May and that in the river, 688 rotifers$\cdot \ell^{-1}$, was observed on 17 May. Mean abundances were 140.0 ± 96.3 rotifers$\cdot \ell^{-1}$ in Tank B and 279.0 ± 198.3 rotifers$\cdot \ell^{-1}$ in the river. Abundances in Tank B and the river did not differ (H = 2.96, df = 1, p = 0.085) and were weakly correlated (r = 0.317).

Copepod abundances in Tank B, Tank A and the river were equivalent initially (Fig. 1-5C). However, abundances increased in the river, exceeding 100 copepods·ℓ^{-1}, and in Tank A, to about 40 copepods·ℓ^{-1}, but did not increase in Tank B, about 20 copepods·ℓ^{-1}. Mean abundances were 20.1 ± 6.8 copepods·ℓ^{-1} in Tank B and 110.2 ± 90.2 copepods·ℓ^{-1} in the river. Copepod abundances in Tank B and the river differed significantly (H = 6.80, df = 1, p = 0.009 adjusted for ties) and were uncorrelated (r = 0.100).

Cladoceran abundance was similar initially in Tank B and Tank A but were lower than the river (Fig. 1-5D). However, abundance in the river decreased to a comparable level several days after blueback herring larvae were stocked into Tank B. Abundance in Tank B remained relatively low and stable, ranging from 3 to 12 cladocerans·ℓ^{-1}, while abundance in the river fluctuated, ranging from 0 to 57 cladocerans·ℓ^{-1}. Mean abundances were 7.8 ± 3.9 cladocerans·ℓ^{-1} in Tank B and 23.9 ± 19.6 cladocerans·ℓ^{-1} in the river. Cladoceran abundances in Tank B and the river differed significantly (H = 3.96, df = 1, p = 0.047 adjusted for ties) and were uncorrelated (r = -0.076).

DISCUSSION

Rearing alewife and blueback herring larvae

Egg incubation and embryo rearing

Fungal infestation has been a significant problem in the rearing of alewife and blueback herring embryos (Davis et al. 1972; Schubel et al. 1977). Davis et al. (1972) controlled fungal infestation using either Wardley's fungus remedy or malachite green (0.05-0.1 ppm). Davis et al. (1972) attributed variable hatching rates, from 0% to over 50%, to variability in the ripeness of eggs at fertilization. However, adverse effects from chemical treatment of eggs to control fungus cannot be discounted as a potential factor reducing hatching success (Meyer and Jorgenson 1983). Removal of the adhesive layer may be one method to

reduce pathogenic infestation of adhesive eggs because bacterial, fungal, or viral pathogens adhere to this layer (Krise et al. 1986).

Fungal infestation precluded successful hatching when eggs were incubated in Massaponax Creek water or in Pamunkey River (km 32, 5.0 μm-filtered) water. In contrast, fungal infestations did not occur when eggs were incubated using Herring Creek water or Pamunkey River (km 72, 0.5 μm-filtered) water (Table 1-1). Although filtering Pamunkey River water through 0.5-μm filters might have removed fungal spores, differences in water chemistries of these sources were likely a significant determinant of fungal infestation. In the rearing aquaria, eggs were either attached to sieves or rested on the bottom. Because of large numbers, eggs attached to sieves often were several layers thick and eggs not attached to sieves were often in large clumps. These conditions promoted the rapid growth of fungal mycelia. Chemical treatment of eggs was ruled out due to potential adverse affects on embryo development (Meyer and Jorgenson 1983); formalin, in particular, was not an option as a fungicide. Since no other methods were used to control fungal growth, the inhibition or promotion of fungal infestation in the rearing aquaria was influenced solely by the incubation water.

Rearing larvae beyond first-feeding

Providing nutritionally sufficient high-quality prey that stimulates active feeding appears to be the greatest impediment to rearing alewife and blueback herring larvae under controlled conditions. The continuous-flow culture system described is of a simple design, but it facilitates rearing alewife and blueback herring larvae beyond first-feeding using natural prey under conditions which replicate the nursery zone for these species. This simple, yet effective, design offers a low-cost alternative to intensive zooplankton culture and does not require daily maintenance.

No attempt was made to standardize the number of yolk-sac larvae stocked into the 1-m^3 tanks since survival was likely to be determined by prey densities in the tanks at about the time of first feeding. However, numbers of yolk-sac larvae hatched from artificially-spawned eggs in 1991 may be estimated conservatively based on a few assumptions. Fertilized egg diameter ranges from 1.1 to 1.2 mm for alewife and from 0.9 to 1.2 mm for blueback herring (Wang and Kernehan 1979). Assuming an average unfertilized egg diameter of 0.8 mm for both species, unfertilized egg volume is about 0.002 mℓ. About 30 to 40 mℓ of unfertilized eggs were stripped from several females for each group of artificially-spawned eggs. Assuming 40% to 50% viability of by the time of stocking (few dead yolk-sac larvae were observed in the rearing aquaria), at least 10,000 alewife and blueback herring larvae were stocked into the 1-m^3 tanks in 1991. Accepting this value as a conservative estimate of initial stocking density, then total mortality exceeded 95 percent for both alewife and blueback herring larvae.

Alewife and blueback herring larvae were reared successfully beyond transition to exogenous feeding in this system. Fifty-one blueback herring larvae were collected in 1990 with a single larva surviving to 24 days after hatching, but gizzard shad larvae failed to survive. In 1991, 280 alewife larvae were collected with a maximum age of 32 days and 521 blueback herring larvae were collected with a maximum age of 37 days. Wild zooplankton entrained in Pamunkey River water established and supplemented zooplankton populations in the 1-m^3 rearing tanks and were prey for the cultured herring larvae. The culture system was located in the lower tidal freshwater-upper estuary reach of the Pamunkey River, an area of high turbidity and high productivity, which is in the nursery zone for wild herring larvae, including alewife, blueback herring, and gizzard shad (Chapter 4). Schubel et al. (1977) attempted to rear alewife and blueback herring larvae using a continuous-flow system (Schiemer and Schubel 1974) located in the upper

Potomac River estuary in an area rich in zooplankton, but larvae failed to survive in their system.

Cyclopoid copepods may be abundant in the tidal freshwater zone (McGovern 1991) and are known to be potential predators of larval fishes (Hartig et al. 1982; McGovern and Olney 1988). Two components the continuous-flow system, the settling tank/coarse filter and 300-μm mesh filter socks, were included to reduce the accumulation of suspended debris and sediment in the 1-m^3 tanks and to inhibit passage of wild fish larvae and invertebrate predators of fish larvae. The barrel half-filled with gravel was an effective settling tank removing substantial amounts of sediment and debris. However, the filter socks may have been ineffective at precluding transfer of all fish larvae or relatively large potential predators into the tanks.

Leslie and Timmins (1989) reported that a 250-μm mesh netting retained 100% of an experimental catch of gizzard shad larvae in towed plankton nets, but 6% of the catch was theoretically capable of being extruded. Similar results would be expected for river herring larvae because of morphology virtually identical to gizzard shad larvae (Lam and Roff 1977). Herring eggs with embryos were found adhered to the outer surface of the intake barrel when the system was disassembled in June 1991. Consequently, entrainment of herring eggs and larvae from the river into the continuous-flow system appears probable, but the extent to which entrained larvae survived passage through the system is not known. At the conclusion of the study, each 1-m^3 tank was drained by removing the center stand-pipe and the effluent was filtered through a 333-μm mesh plankton net to capture remaining larvae. No herring larvae were captured after the larvae-free tank was drained. Although this does not prove conclusively that wild herring larvae were excluded from the 1-m^3 tanks, it suggests that contamination by wild herring larvae may have been only a minor problem in that the proportion of wild larvae to cultured larvae was probably low.

The grand mean larval river herring abundance in the Pamunkey River measured from ichthyoplankton collections made in 1989 and 1990 was about 1 to 2 larvae·m^{-3} (Chapter 4), but average abundance was about 0.5 larvae·m^{-3} in early April and about 5 larvae·m^{-3} in late April-early May. These periods correspond to the times when alewife and blueback herring larvae were stocked in the 1-m^3 tanks. Larval river herring abundances in the Pamunkey River provide little basis for establishing initial stocking density for the 1-m^3 tanks. However, the field-study results are consistent with the present study in that fewer feeding larvae were produced in early April than in late April or early May.

Growth of cultured alewife and blueback herring larvae

Estimated average growth rates of herring larvae reared using this system ranged from about 0.3 mm·d^{-1} to about 0.8 mm·d^{-1}. These rates are comparable to other growth estimates for wild or reared alewife larvae. Alewife larvae grow 0.8 mm·d^{-1} in Smith Mountain Lake, Virginia, (Tisa and Ney 1991), and Lake Michigan alewife larvae reared in aquaria grew about 0.5 mm·d^{-1} (Heinrich 1981; Kellogg 1982). Lower growth rates estimated for younger alewife larvae and older blueback herring larvae suggest that cultured larvae may have been at times food limited.

Numbers of yolk-sac larvae used to stock the 1-m^3 tanks were not standardized assuming that larval herring abundance would adjust to the level of available prey at the time of first-feeding. This assumption appears to have been valid as fewer alewife larvae than blueback herring larvae were collected in 1991. First-feeding alewife larvae likely experienced relatively high mortality because of low prey abundances in early April, but fewer larvae in the 1-m^3 tank during times of high prey abundance probably promoted growth. In comparison, first-feeding blueback herring larvae likely experience relatively low mortality because of high prey abundances in late April-early May, but greater survival potentially caused an over-abundance of larvae once prey

abundance declined thereby slowing growth. However, slower growth by older blueback herring larvae might also have been associated with diversion of energy from somatic growth to physiological processes associated with transformation to the juvenile stage.

Average growth rates for starved alewife and blueback herring larvae reared in aquaria for this study and for starved alewife larvae reared by Kellogg (1982) were 0.2 $mm \cdot d^{-1}$. In the present study, starved alewife and blueback herring larvae exhibited an initial increase and subsequent decline in mean length-at-age. Similar growth rates of starved alewife and blueback herring larvae between this study and Kellogg (1982) suggests that endogenous energy reserves derived from yolk may maintain growth at a minimum rate, possibly in association with ontogenetic changes occurring during larval development. Reduced mean length-at-age of starved herring larvae may be associated with chemical changes in the body (Ehrlich 1974; Blaxter and Ehrlich 1974). Shrinkage of starved larvae, in length and wet weight, has been observed for other species (Lasker 1964; Ishibashi 1974). Alternatively, apparent shrinkage of starved larvae may arise from differential mortality of smaller and larger larvae and of slower- and faster-growing larvae. Smaller larvae may tend to die sooner since they may have the least yolk-derived stored energy. Larger, faster-growing larvae then may tend to die since they may exhaust yolk-derived stored energy sooner than slower-growing larvae. The result is an apparent increase followed by a decrease in mean length-at-age.

Zooplankton in the culture tanks

Zooplankton abundance appears to have been an important determinant of larval alewife and blueback herring survival and growth. Conditions in the 1-m^3 tanks of the continuous-flow system closely tracked those in the Pamunkey River. Rotifer and copepod (nauplii and copepodites) abundances in the larvae-free standard were similar to

abundances in the river, but cladoceran abundances in the larvae-free standard were significantly greater than in the river. Cladoceran populations in the tanks possibly thrived under the low-flow conditions and may have benefitted from algal or microbial populations which grew on the tank wall. Similar temporal fluctuations in abundance suggest that zooplankton populations in the tanks and the river responded in like manner to environmental influences. Equivalent or higher zooplankton abundances in the larvae-free standard and lower abundances in 1-m^3 tanks containing herring larvae compared to the abundances in the river suggest that larval herring predation affected zooplankton abundance. However, behavior may have differed in the presence of larval herring with zooplankters remaining nearer the side or bottom to reduce predation risk.

Conclusion

This study shows that alewife and blueback herring larvae can be reared successfully beyond transition to exogenous feeding. The continuous-flow culture system described herein offers the potential for rearing alewife and blueback herring larvae with a relatively minimal expenditure of time and labor, and especially avoids the expense associated with intensive laboratory-culture of zooplankton. Rearing larvae in 1-m^3 tanks circumvents problems associated with detrimental conditions that arise during culture in relatively small aquaria (Blaxter 1968, 1969; Theilacker 1980; Barahona-Fernandes and Conan 1981). Continuous-flow systems, such as described, may facilitate experimental study of alewife and blueback herring larvae as well as larvae of other species. Transfer to tanks maintained under controlled conditions may be possible once larvae are able to ingest larger prey, e.g. *Artemia salina* nauplii, . Additionally, this type of system may provide an alternative to *in situ* enclosures for evaluating the dynamics of larval fishes in tidal freshwater or estuarine ecosystems.

NOTES FOR CHAPTER 1

1. Fluval-303 Power Filter. Rolf C. Hagen Corp., Mansfield, Massachusetts, 02048
2. AquaClear-402 Powerhead. Rolf C. Hagen Corp., Mansfield, Massachusetts, 02048
3. Reliant One, submersible utility pump, model number TSC-130. Wayne Home Equipment, 801 Glasgow Ave, Fort Wayne, IN 46803.
4. Aquatic Ecosystems, 2056 Apopka Blvd., Apopka, FL 32703.

Table 1-1. Summary of the culture of alewife and blueback herring larvae, 1989-1991. Two attempts to rear alewife in 1990 (x2) failed. Temperatures not recorded (NR) are missing.

Year	Species	Source of adults	Water source	Mean water temperature (°C)	Water treatment	Results
1989	Blueback	Pamunkey R.	Pamunkey R. (km 72[1])	20	Filtered (0.5 μm)	Hatch
1990	Alewife (x2)	Massaponax Creek	Pamunkey R. (km 32)	15	Filtered (5 μm)	Fungal infestation, failed hatch
	Blueback	Pamunkey River	Pamunkey R. (km 32)	NR	Filtered (5 μm)	Fungal infestation, failed hatch
	Blueback	Herring Creek[2]	Herring Creek	NR	Filtered (35 μm)	Hatch
1991	Alewife	Massaponax Creek	Herring Creek	21	Filtered (35 μm)	Hatch
	Alewife	Massaponax Creek	Massaponax Creek	18	Filtered (35 μm)	Fungal infestation, failed hatch
	Blueback	Herring Creek	Herring Creek	21	Filtered (35 μm)	Hatch

1. Refers to distance (km) following the Pamunkey River channel upriver from West Point, Virginia.
2. Larvae were hatched from naturally-spawned eggs collected in Herring Creek.

Table 1-2. Comparison of mean standard length-at-age of fed and starved alewife and blueback herring larvae. Starved larvae were reared in 1989 and 1991; fed larvae were reared in 1990 and 1991. Measurements of yolk-sac larvae reared in 1991 are for length-at-hatching of fed and starved groups. Growth was estimated as the increase in length for each group during the first 8 days following hatching divided by age. Starved blueback herring larvae were sampled once at 5 days after hatching in 1991, so this group is used to estimate growth.

Age (days)	Fed			Starved		
	1990 BH	1991 Ale	1991 BH	1989 BH	1991 Ale	1991 BH
0	4.6	3.5	4.0	4.0	3.5	4.0
1	5.3	4.3			4.3	
2			5.1	5.1		5.1
3						
4		5.1		5.4	5.1	
5	7.8		5.2			5.0
6				5.5		
7						
8	10.4	5.8	7.0	5.3	5.0	
Estimated Growth ($mm \cdot d^{-1}$)	0.7	0.3	0.4	0.2	0.2	0.2
Within-group Mean Growth ($mm \cdot d^{-1}$)		0.5			0.2	

Table 1-3. Observed mean standard length-at-age and mean daily growth of cultured herring larvae reared in 1990 and 1991. Growth is the increase in standard length between consecutive age-classes divided by the difference in age (in days). Values in parentheses indicate the mean growth rate of a group across age classes. Values in brackets represent a single specimen. Values highlighted with an asterisk were not included in the calculation of mean growth.

Age (days)	SL (mm)	Growth ($mm \cdot d^{-1}$)	Age (days)	SL (mm)	Growth ($mm \cdot d^{-1}$)	Age (days)	SL (mm)	Growth ($mm \cdot d^{-1}$)
1990 Blueback			1991 Alewife			1991 Blueback		
0	4.6		0	3.5		0	4.0	
1	5.3	0.7	1	4.3	0.8	2	5.1	0.5
5	7.8	0.6	4	5.1	0.3	5	5.2	0.0
8	10.4	0.9	8	5.4	0.1	8	7.0	0.7
11	12.9	0.8	12	6.9	0.3	13	9.9	0.6
16	16.4	0.7	14	7.2	0.2	17	11.8	0.5
[24	19.6]	0.4*	18	9.2	0.5	21	12.5	0.2
			21	11.5	0.8	25	12.2	-0.1*
			24	12.9	0.5	29	12.5	0.1
			27	14.1	0.4	34	13.6	0.2
			32	17.1	0.6	37	14.6	0.3
		(0.8)			(0.4)			(0.3)

Figure 1-1. Map of capture locations of ripe-running alewife and blueback herring and location of the culture facility. Alewife were collected from Massaponax Creek (Al), a tributary of the Rappahannock River, in 1990 and 1991. Blueback herring were collected from the mainstem Pamunkey River (km 72) in 1989 (not shown) and from Herring Creek (BH), a tributary of the James River, in 1991. The culture facility was located near the upper limit of the Pamunkey River estuary (CF), about 32 km upstream from West Point, Virginia.

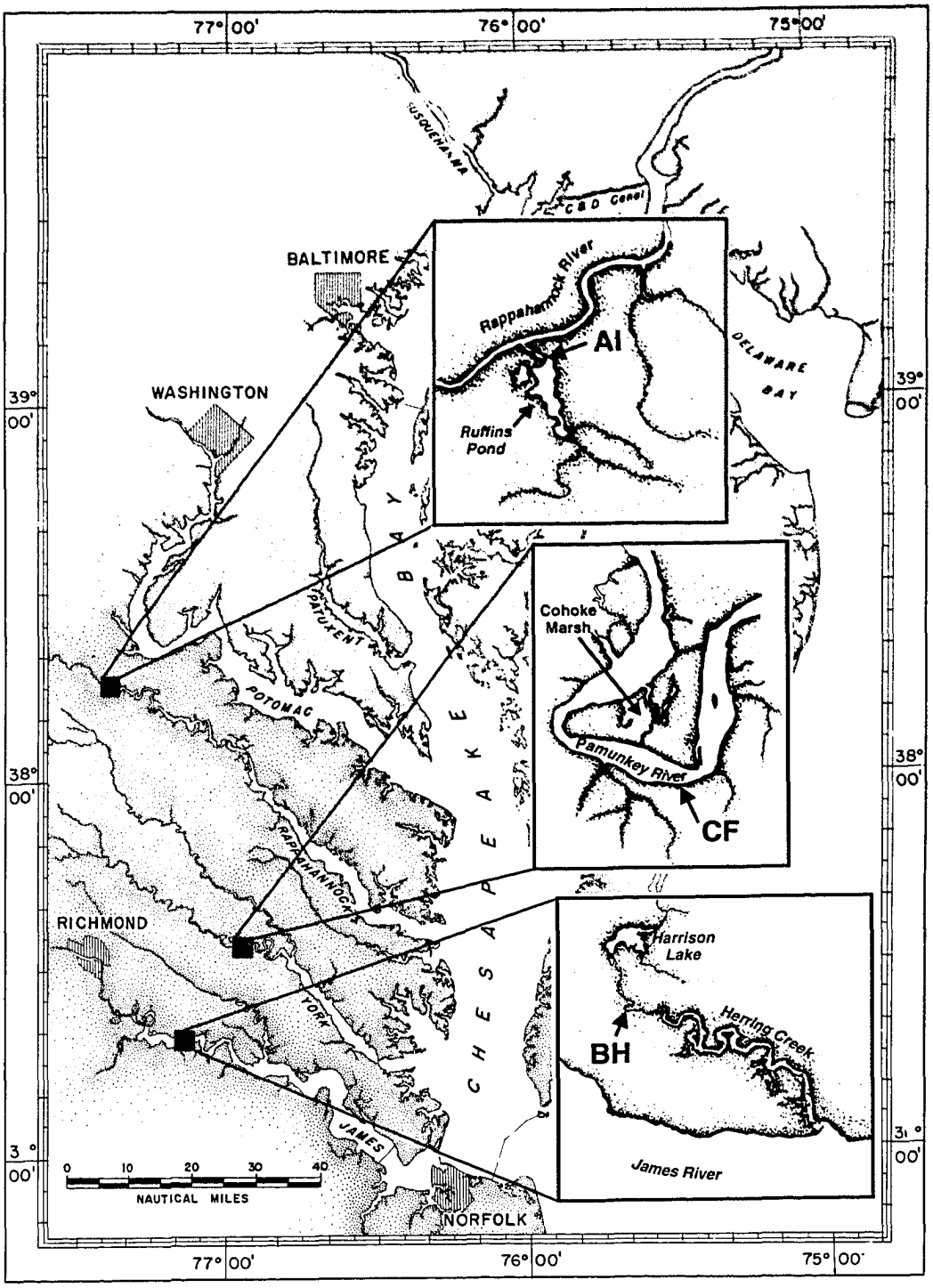


Figure 1-2. Aquaria for rearing eggs and embryos in 1989 (A) and in 1990 and 1991 (B).

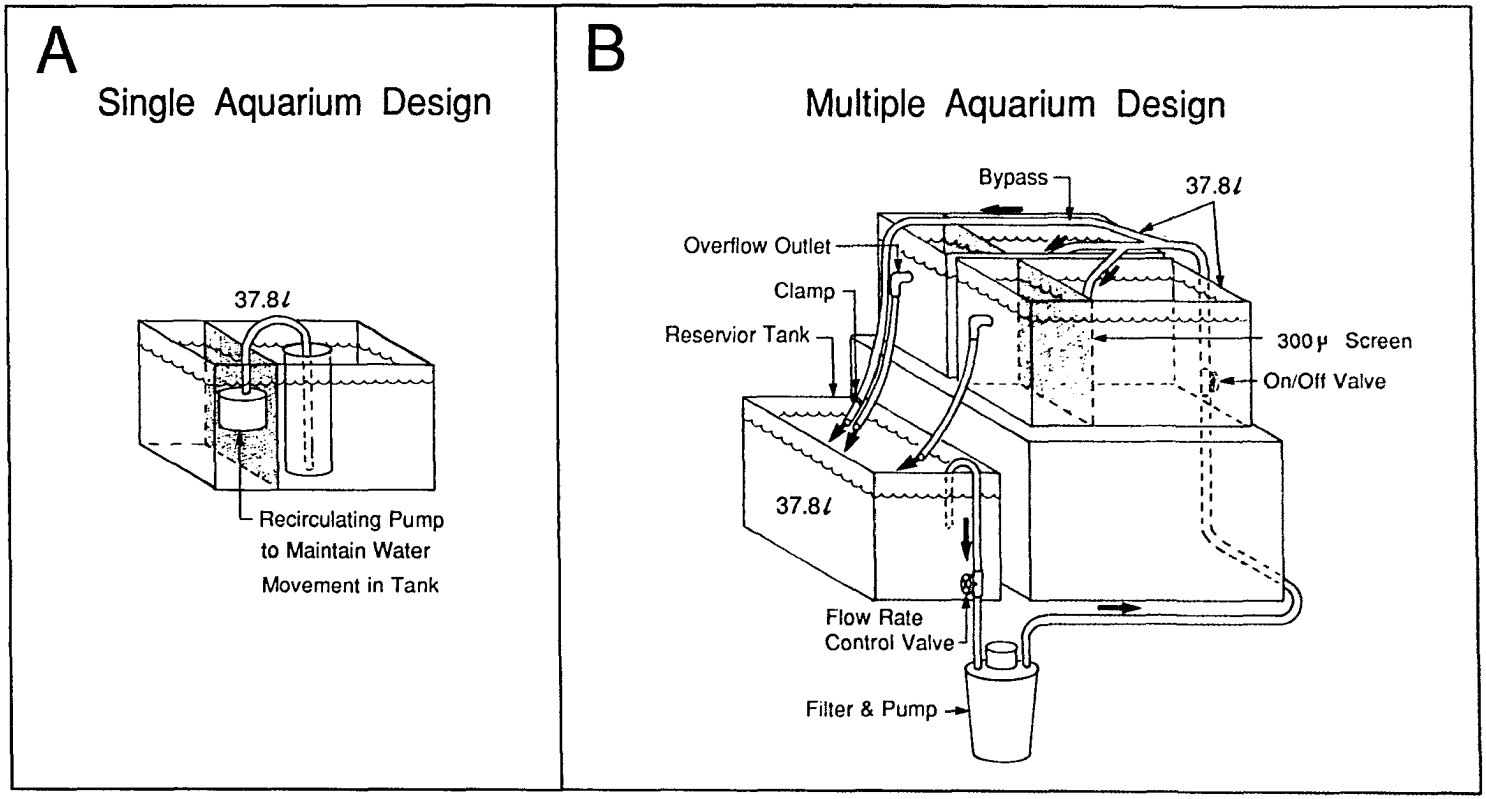
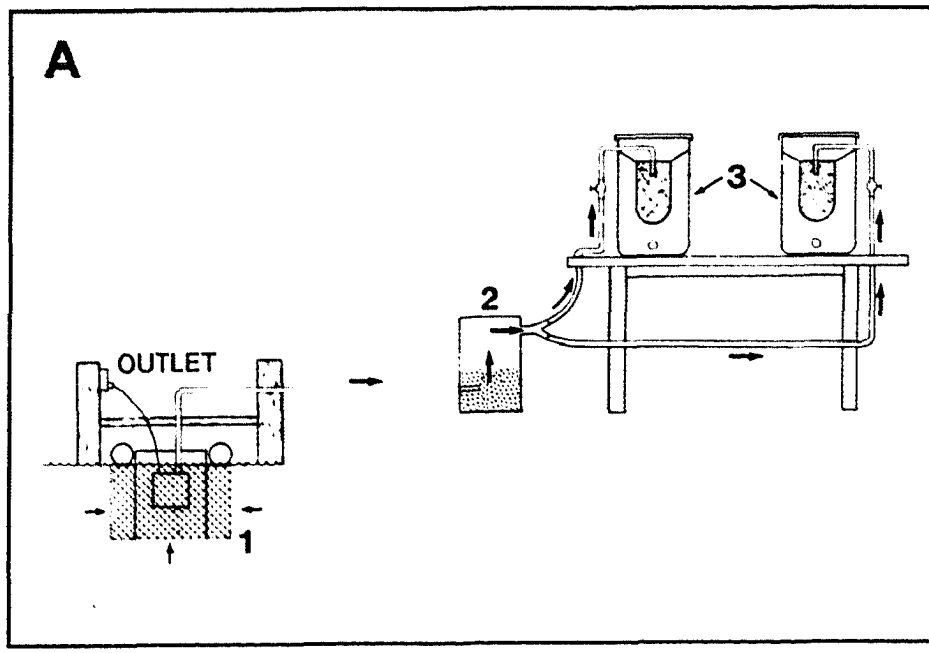


Figure 1-3. The continuous-flow culture system: A) water intake and delivery system, and B) rearing tanks and overflow assembly. Components of the system are referred to by number: 1) water intake, 2) course filter/settling tank, 3) 300-μm filter socks, 4) large-volume tanks, and 5) an overflow assembly. See Methods for descriptions of each component.



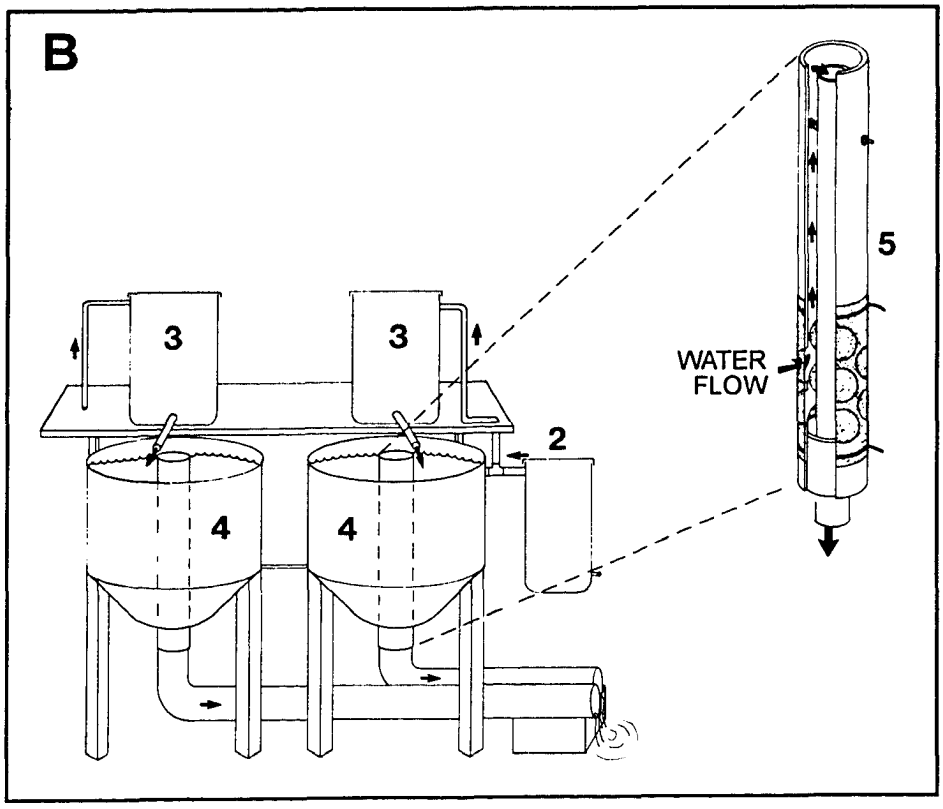


Figure 1-4. Growth of alewife larvae and blueback herring larvae showing mean length-at-age and 95% confidence intervals: blueback herring, 1990 (o) and 1991 (+), and alewife, 1991 (□). Symbols designate mean lengths-at-age, and error bars indicate the 95% confidence limits. The dotted line for 1990 blueback herring shows the increase in length-at-age between age 16 d larvae and a single, age 24 d larva. The age 24 d larva was not included in the fitted growth curve.

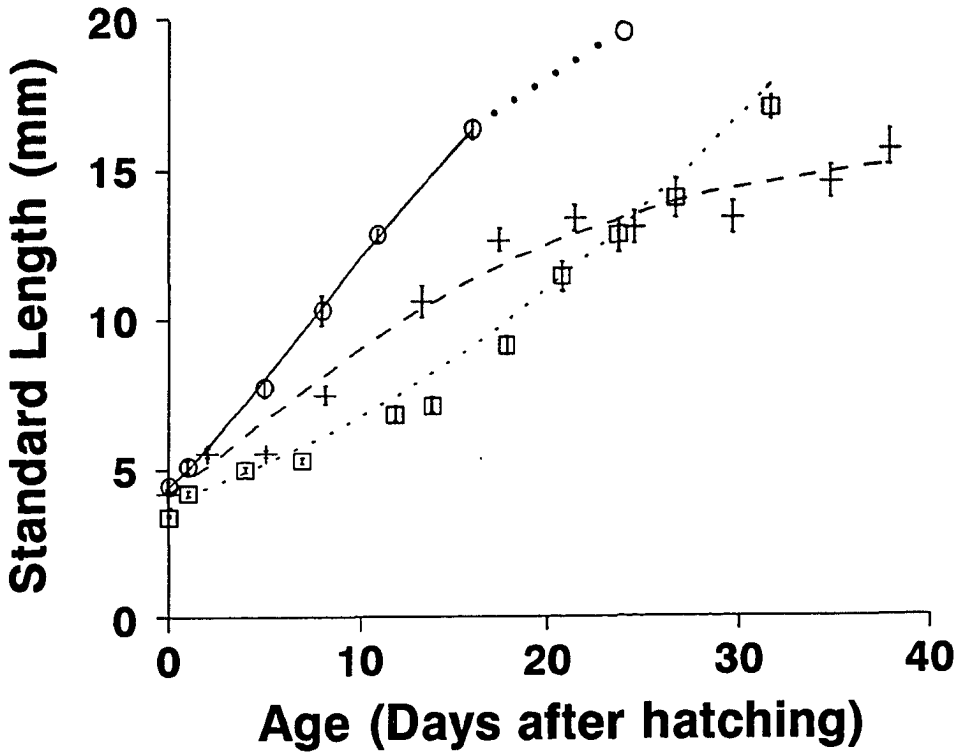
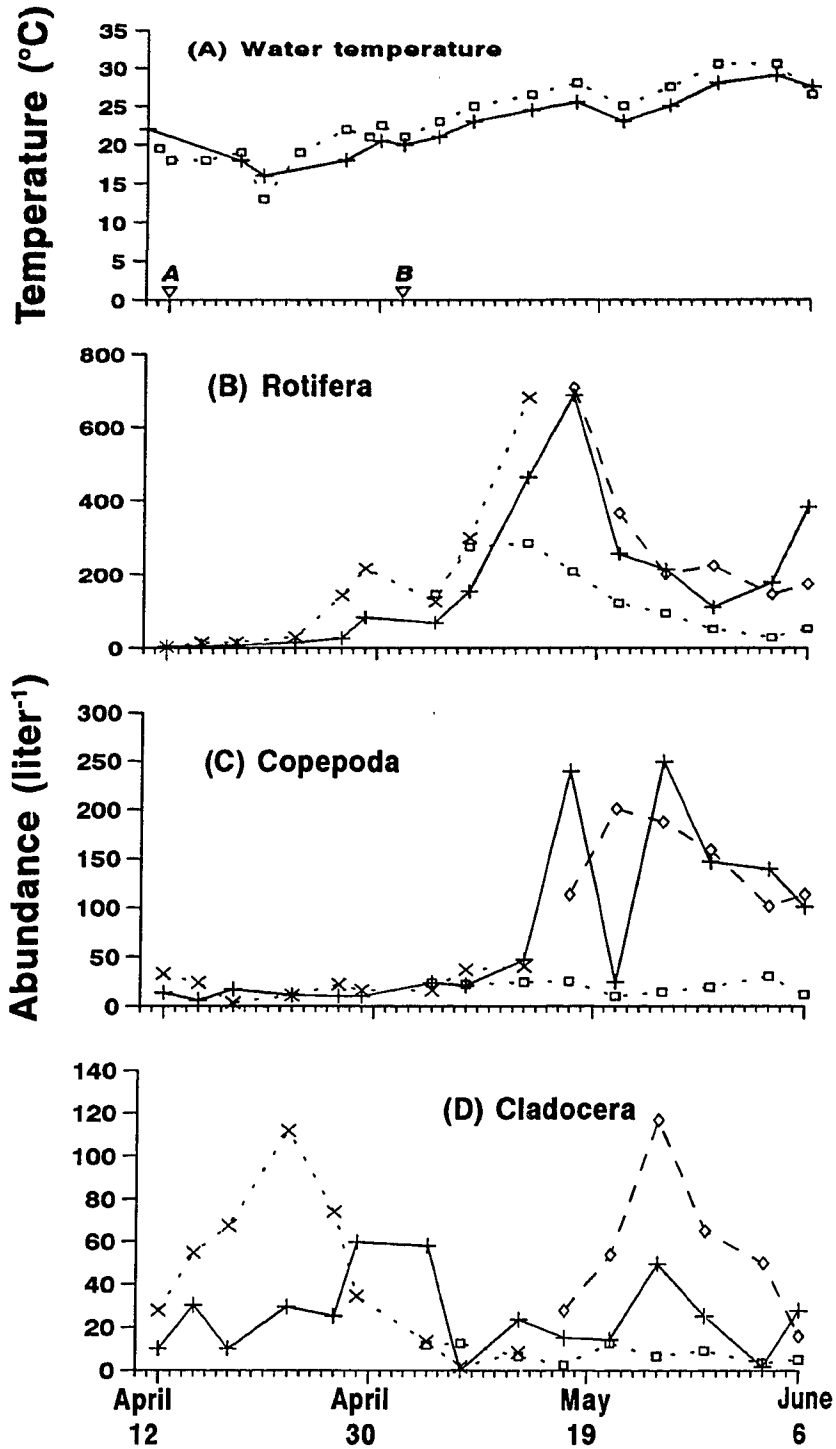


Figure 1-5. Water temperature (°C) and zooplankton abundances (number·ℓ^{-1}) during larval alewife and blueback herring in 1991: A) water temperature in the Pamunkey River (+) and in 1-m^3 tanks (□) of the continuous-flow system (*A*: alewife larvae stocked into large-volume tanks, *B*: blueback herring larvae stocked into large-volume tanks); B) rotifer abundances in the river and 1-m^3 tanks; C) copepod abundances (nauplii and copepodites) in the river and 1-m^3 tanks; and, D) cladoceran abundances in the river and 1-m^3 tanks. Legend for plates B-D: Pamunkey River (+), 1-m^3 tanks containing alewife (×) and blueback herring (□) larvae, and 1-m^3 tank as a larva-free standard (◇).



Chapter 2.

Characteristics of the Early Life Stages of Cultured Alewife (*Alosa pseudoharengus*) and Blueback Herring (*A. aestivalis*) Emphasizing Identification of Larvae

ABSTRACT

Alewife, *Alosa pseudoharengus*, larvae and blueback herring, *A. aestivalis*, are described from specimens hatched from eggs of known taxonomic identity and reared in outdoor tanks. No differences were observed in egg morphology nor in the meristics and morphologies of larvae. Pigmentation of yolk-sac larvae and preflexion larvae did not differ between the species, although melanophores at the base of the caudal fin-fold dorsal to the tail were more common in blueback herring. Following notochord flexion, melanophores along the dorsal midline posterior to the dorsal fin developed earlier and were more numerous in alewife larvae as compared to blueback herring larvae. Diagnostic pigment distributions were observed between postflexion larvae of the two species. In alewife, paired melanophores that increased in number with age were found along the lateral surface of the notochord at the level of the nape, and contracted xanthophores were scattered on the dorsal surface of the head. In blueback herring, one or two melanophores occurred on the dorsal surface of the notochord at the level of the nape, xanthophores covered the dorsal surface of the head over the brain, and xanthochrome occurred at the base of the caudal fin. Other differences in xanthic pigmentation were also identified.

INTRODUCTION

Accurate identification of eggs and larvae is an essential element of early life history studies of fishes. Powles and Markle (1983) state: "Minor errors in identification of larval fishes can lead to major misinterpretations of ecological and taxonomic phenomena." For some groups (e.g. Clupeidae), larvae possess few morphometric characters which can be used to identify species. Numbers of myomeres or vertebrae have been suggested to be the primary taxonomic character for identifying larvae of closely related species, including clupeid larvae (Berry and Richards 1973; McGowan and Berry 1983). Total myomere counts for preflexion clupeid larvae can be difficult to obtain, however, due to indistinct separation of myomeres anterior to the cleithrum or posterior to the vent (Russell 1976).

Morphometric and meristic characters of some clupeid larvae appear to vary regionally which may limit their usefulness for determining species identity, especially when characters for larvae from one region are used to identify larvae from other regions (Bosley and Conner 1984). For example, total numbers of myomeres and vertebrae of larval blueback herring, *Alosa aestivalis*, and larval gizzard shad, *Dorosoma cepedianum*, in the Santee-Cooper River, South Carolina, do not differ, but are significantly greater than those of larval threadfin shad, *D. petenense* (Bulak 1985). Santucci and Heidinger (1986) reported greater total myomere numbers in gizzard shad larvae as compared to threadfin shad larvae, and they show regional variation in total myomere numbers for both species. Taber (1969 cited by Lam and Roff 1977), however, found no difference in total numbers of myomeres and vertebrae for threadfin shad and gizzard shad in Lake Texoma, Oklahoma. In other cases, such as among marine clupeids, species identification of larvae of sympatric

congeners may not be possible based solely on meristics and morphometrics and may be based upon supplemental data, such as date and location of capture (Houde and Fore 1973; Richards et al. 1974; Funes-Rodríguez and Esquivel-Herrera 1985). Species identification is simplified with complete formation of adult characters, such as dorsal-, caudal-, and anal-fin rays and gillrakers (Berry and Richards 1973; McGowan and Berry 1983).

Anadromous populations of alewife (*A. pseudoharengus*) and blueback herring are distributed along the eastern seaboard of North America. Blueback herring occur from Florida to New Brunswick and Nova Scotia, and alewife occur from South Carolina to Newfoundland and Labrador (Loesch 1987). These species support significant commercial and recreational (primarily dip-net) fisheries. These species also are prey for numerous aquatic and terrestrial predators (Loesch 1987). The initiation of spawning by these species is temperature-dependent beginning earlier (December-February) in southern populations and occurring later (May-June) in northern populations (Loesch 1987). Alewife spawning precedes blueback herring spawning by three to four weeks, but there is considerable overlap in their spawning seasons (Loesch 1987). Tidal and nontidal reaches of coastal rivers along eastern North America are utilized for spawning and nursery habitat by alewife and blueback herring, and eggs and larvae of these species likely intermix during their freshwater residency (Dovel 1971; Lippson and Moran 1974; Marcy 1976; Wang and Kernehan 1979; Boreman 1981). Knowledge of the early life histories of alewife and blueback herring is limited by the inability to reliably identify the eggs and larvae of these species when collected in ichthyoplankton samples. A method for species identification would facilitate the analysis of the ecologies and population dynamics of alewife and blueback herring larvae.

The usefulness of meristic and morphologic characters for identifying alewife and blueback herring larvae is unresolved. Chambers

et al. (1976) suggested that alewife and blueback herring larvae may be delimited by the postdorsal-to-preanal myomere number and by the snout-to-vent length as a percentage of standard length (SL). In contrast, Cianci (1969) found no significant differences in meristic or morphometric characters of larvae of these species. In addition, other studies which compare alewife or blueback herring larvae to gizzard shad and threadfin shad larvae provide indirect evidence that alewife and blueback herring larvae lack significant meristic and morphometric variation (see Discussion). Juvenile and adult characters useful for identifying these species are present by about 20 mm SL (Dovel et al. 1965; Wang 1970).

Pigmentation patterns are useful for the identification of larval fishes and to establish taxonomic relationships between species groups (Berry and Richards 1973; Ahlstrom and Moser 1976; McGowan and Berry 1983). Descriptions of pigment patterns in alewife and blueback herring larvae are, at present, limited to preflexion larvae and to late-stage postflexion larvae and early juveniles at transformation. Pigment patterns of alewife and blueback herring larvae between flexion (about 9-11 mm SL) and transformation (about 15-20 mm SL) have not been described.

In this study, selected morphometric and meristic variables as well as pigment characters were examined and evaluated for their usefulness in delimiting cultured alewife and blueback herring larvae.

METHODS

Alewife and blueback herring larvae were hatched from artificially-spawned eggs of known taxonomic identity and were reared to age 32 days and to age 37 days (Chapter 1). Water temperatures in aquaria during egg incubation were approximately 17 °C to 20 °C for alewife and approximately 19 °C to 22 °C for blueback herring. Daytime water temperatures experienced by larvae in the outdoor tanks ranged

from about 13 °C to about 23 °C for alewife and from about 21 °C to about 28 °C for blueback herring. Eggs were sampled during embryo development, and yolk-sac larvae were maintained in the aquaria and were sampled at hatching and at least once before the yolk was completely absorbed. Larvae were transferred prior to complete yolk absorption to 1-m^3 tanks of a continuous flow-through system. The system, which was located outdoors, utilized a pump to deliver water and entrained zooplankton from the Pamunkey River, Virginia, to two tanks in which larvae were reared (Chapter 1).

Larvae were collected from the tanks at irregular intervals ranging from 3 to 5 days throughout their development using a plankton net. Captured larvae were concentrated in the cod-end jar of the net and gently poured into a small (125 mℓ) glass jar to facilitate observation. They were then transferred using a plastic pipet into a petri dish containing a solution of tricaine methanosulfate (MS-222). The amount of MS-222 needed to anaesthetize larvae was initially determined by placing a few larvae in the petri dish and adding small amounts of MS-222 with a laboratory microspatula until larvae stopped moving. With experience, the amount of MS-222 necessary to anaesthetize larvae was estimated without trial. No attempt was made to measure the amount of MS-222 used in the anaesthetic solution since the MS-222 concentration was diluted as larvae were transferred to the petri dish. Small amounts of MS-222 were added to the petri dish when larvae began to revive.

Standard length (SL) and snout-to-vent length (SVL) were measured for the anaesthetized larvae following the definitions of Lippson and Moran (1974) using a Wild M3Z dissection microscope with a 120-unit graduated ocular micrometer. Larvae were measured to the nearest 0.5 micrometer unit at one of three magnifications: 6.5x, 10x, or 16x. Measurements were later converted into millimeters using calibration factors determined for each magnification. Anesthetized larvae used in

this study were fixed either in 5% phosphate buffered formalin (PBF) (Markle 1984) or preserved in 95% ethanol (EtOH). Formalin-fixed specimens were transferred through an increasing series of 20%, 45%, and 70% EtOH for long-term preservation (Lavenberg et al. 1983). Specimens preserved in 95% EtOH were transferred twice to fresh 95% EtOH at 24 hr intervals to prevent the dissolution of otoliths.

Snout-to-vent length to standard length ratios (SVL/SL) were calculated using measurements made on anesthetized larvae to eliminate potential error caused by fixative-induced shrinkage. The number of myomeres between the dorsal-fin insertion and anal-fin origin (postdorsal-preanal myomere count) were enumerated using fixed and preserved specimens. Prior to formation of dorsal-fin pterygiophores, the dorsal-fin insertion was defined as the myomere where the posterior margin of the dorsal-fin anlage joined the body. The anal-fin origin was defined as the first myomere posterior to the vent.

Melanophore and xanthophore distributions and morphologies were examined to identify pigment characters of potential value for taxonomic classification of larvae. Melanophores and xanthophores were classified as contracted if they appeared as round spots, stellate if they appeared with short protrusions, or reticulate if they appeared with dendritic protrusions (Giese 1982). For yolk-sac and preflexion larvae, the term 'supracaudal' referred to the region of dorsal fin-fold adjacent to the tail. The odds ratio and the associated 95% confidence interval were calculated to quantify the likelihood that an alewife larva would demonstrate supracaudal pigment (Agresti 1990).

Illustrations of formalin-fixed larvae were prepared with the aid of a camera lucida. Illustrations of alewife and blueback herring postflexion larvae emphasize ontogenetic change in pigmentation. Morphological and osteological characteristics, such as position and number of myomeres and the number and position of fin rays were illustrated as observed on specimens that were not cleared and stained.

Xanthochrome was unstable in fixed and preserved larvae. It gradually faded over several weeks in specimens fixed in 5% PBF and was rapidly extracted from specimens preserved in 95% EtOH. A method (e.g. photography) to record permanently the distribution of xanthochrome in anesthetized larvae was not available for this study.

Wild herring larvae may have been entrained in water pumped from the river and it appears likely that some wild larvae may have been introduced into the outdoor tanks despite efforts to prevent this, including the use of 300-μm mesh nylon bag filters (Chapter 1). Leslie and Timmins (1989) estimate that an experimental extrusion rate of 6% is theoretically possible for gizzard shad larvae retained in 250-μm mesh nylon netting. Alewife, blueback herring, and gizzard shad larvae are of similar shape and size; consequently, it is probable that wild alewife, blueback herring, or gizzard shad larvae entrained in water by the system intake may have passed through the bag filters. The SVL/SL ratio differs between alewife and gizzard shad larvae, with alewife larvae characterized by a ratio less than 0.85 (Lam and Roff 1977). On the assumption that this difference delimits *Alosa* spp. and *Dorosoma* spp., only alewife and blueback herring specimens with SVL/SL ratios less than 0.85 were used to describe pigment patterns to minimize the possibility of confounding pigment patterns of alewife and blueback herring larvae with pigment patterns of gizzard shad larvae. Larvae considerably smaller and developmentally less advanced compared to other larvae collected from the outdoor tanks for any sampling date were not included for the description of pigment patterns to minimize the inclusion of wild specimens of any species.

RESULTS

Eggs and Yolk-sac Larvae

Unfertilized and fertilized eggs of alewife and blueback herring were golden yellow. Fertilized eggs of both species readily adhered to

one another and initially to nylon sieves used to rinse eggs during artificial spawning. Alewife eggs remained adhered together but detached from the sieves after several hours. In contrast, blueback herring eggs were highly adhesive and remained adhered to the sieve throughout embryonic development.

Alewife and blueback herring yolk-sac larvae were transparent at hatching with average standard lengths of 3.8 mm and 3.9 mm. Pectoral-fin buds and the saccular and lagenar otoliths were present in both species. The yolk of both species was segmented. Oil droplets embedded within the yolk were not observed but occurred between the yolk and the periblast. Yolk-sac larvae of both species possessed unidentified structures associated with the periblast which may be sites for oil storage (Fig. 2-1), but the chemical composition of these structures was not determined. These structures were easier to observe in specimens preserved in 95% EtOH, which caused the yolk to dehydrate and contract away from the periblast, as compared to anesthetized or formalin-preserved specimens.

Pigment, present in both species from hatching to about 24 hr after hatching, consisted of dermal melanophores associated with myosepta along the lateral body surface, below the pectoral-fin buds, on the nape, and occasionally on the head. The eyes of yolk-sac larvae of both species were unpigmented at hatching, except for golden to bronze pigment along the dorsal margin, and were completely pigmented by the second day after hatching. Melanophores were distributed along the ventral surface of the yolk sac and along the gut. No consistent differences in the distribution or numbers of melanophores on the ventral surface of the yolk sac were apparent between the two species. Melanophores in the supracaudal region were observed in yolk-sac larvae of both species.

Larvae

Meristics and Morphology

Dorsal-fin anlagen were observed in alewife larvae ranging in size from 5 to 10 mm SL, and in blueback herring larvae of 7 mm SL (only 2 specimens). Within size-classes of larvae, dorsal-fin pterygiophore counts were higher in blueback herring larvae as compared to alewife larvae up to about 12 mm SL (Table 2-1). Pterygiophore counts in both species were similar (alewife: 15-17; blueback herring: 16-18) in larvae ranging from 14 to 19 mm SL. Anal-fin anlagen were observed in alewife larvae ranging from 9 to 13 mm SL (Table 2-2). In comparison, anal fins of blueback herring larvae had developed several pterygiophores by 10 mm SL (Table 2-2). Anal-fin pterygiophores were not observed in alewife larvae until 11 to 12 mm SL. In larvae from 13 to 19 mm SL, anal-fin pterygiophores ranged in number from 14 to 19 for blueback herring and from 10 to 20 for alewife (Table 2-2).

Sixty-four alewife larvae from 6 to 18 mm SL and 68 blueback herring larvae from 6 to 14 mm SL were examined to determine the diagnostic value of the postdorsal-preanal myomere count for identifying these larvae. The postdorsal-preanal myomere count ranged from 5-11 for alewife and from 6-10 for blueback herring, and decreased in number as standard length increased (Table 2-3). Both species were characterized by a mode of 9 postdorsal-preanal myomeres.

Alewife larvae (n=169) from 6 to 18 mm SL had SVL/SL ratios ranging from 0.77 to 0.89 compared to blueback herring larvae (n=205) from 6 to 17 mm SL which had SVL/SL ratios ranging from 0.77 to 0.88 (Table 2-4). The modal values of the SVL/SL ratio for alewife and blueback herring larvae were 0.83 and 0.84.

Pigmentation: Preflexion Larvae

Ventral margin and gut

A single row of melanophores appeared either as a solid or fragmented line of pigment anterior to the cleithrum. Two rows of melanophores appeared either as solid or fragmented lines of pigment posterior to the cleithrum. These rows diverged from a common origin at the cleithrum to a position between the gut and the myomeres, and ended between the 14th to 17th myomeres. Among alewife preflexion larvae, the junction of the two rows of pigment at the cleithrum had an angular appearance and the rows of pigment were relatively straight as they diverged from the cleithrum (Fig. 2-2). Among blueback herring preflexion larvae, the rows of pigment diverged in a shallow arc and their junction at the cleithrum appeared rounded (Fig. 2-2). These differences were consistent among some preflexion larvae with complete patterns, but the pattern was incomplete in most preflexion larvae examined. Two rows of melanophores along the ventral surface of the gut, again appearing as either solid or fragmented lines of pigment, began between the 12th and 15th myomere and ended at the vent. Scattered melanophores occurred posterior to the vent along the ventral surface in preflexion larvae of both species. This pigmentation was maintained in postflexion larvae, but became less prominent in larger specimens.

Caudal region

Supracaudal melanophores were more frequent in alewife preflexion larvae (89%) than in blueback herring preflexion larvae (8%). The odds ratio calculated for the observed frequencies was 89.9 (95% C.I.=40.4 to 164.0) indicating that, on average among the cultured specimens, an alewife preflexion larva was about 90 times more likely to have supracaudal pigment than a blueback herring preflexion larva. When present, these melanophores were observable until notochord flexion.

After flexion, pigmentation in this region increased causing the supracaudal melanophores to become indistinct.

Pigmentation: Postflexion Larvae

Except for melanophores associated with the gut, the posterior ventral margin, and the supracaudal region, few melanophores were observed on preflexion larvae of either species. With the onset of flexion, melanophores increased in number on the head and epaxial surface of the body, along the dorsal margin, and on the dorsal and lateral surfaces of the gut in both species. Yellow pigment was observed in anesthetized postflexion larvae, it gradually deteriorated in specimens fixed in 5% PBF after several weeks, and it was rapidly extracted from specimens preserved in 95% EtOH. The gradual fading of yellow pigment in formalin-fixed specimens and its rapid extraction in ethanol suggests that it is lipochrome and is generically known as xanthochrome. The occurrence of xanthochrome in alewife larvae was noted initially, but its distribution was not examined in detail until different xanthochrome distributions were observed in blueback herring larvae. Xanthochrome distributions of alewife larvae previously fixed in 5% PBF were then reexamined. Although xanthochrome pigment in formalin-fixed alewife larvae gradually decreased with time, observed distributions of xanthochrome were consistent between anesthetized and formalin-fixed alewife larvae. Observed xanthochrome distributions were consistent within species. Xanthochrome distributions observed in alewife and blueback herring larvae are summarized in Table 2-5.

Head

Pigmentation in the head region of both species began with the development of subdermal reticulate melanophores associated with the otic bullae and the ventral surface of the brain (Figs. 2-3A and 2-4A). With increased size, dermal melanophores developed on the dorsal surface

of the mandible and maxilla, on the head, and on the epaxial surface of the body in both species. Melanophores on the head of alewife postflexion larvae initially were typically contracted or stellate (Fig. 2-5), but those on the head of blueback herring postflexion larvae typically were stellate or reticulate (Fig. 2-6). With increased length, reticulate dermal melanophores developed on the head of larvae of both species.

Xanthophores were observed on the head of larvae in both species beginning at about 11 to 12 mm SL. Among blueback herring larvae, xanthophores on the head were relatively large and reticulate, and eventually covered the dorsal surface of the head above the brain. Beginning at about 13 mm SL, xanthic pigment was observed along the ascending process. In contrast, scattered, contracted xanthophores developed on the dorsal surface of the head of alewife larvae, and xanthochrome was not observed along the ascending process.

Dorsal mid-line and epaxial surface

Qualitative differences in the distribution and density of melanophores between the two species were most prevalent along the dorsal mid-line, especially posterior to the dorsal fin. Melanophores were initially absent along the dorsal mid-line in early postflexion larvae of both species (Figs. 2-3A and 2-4A). Two parallel rows of melanophores along the posterior dorsal mid-line were observed earlier in blueback herring postflexion larvae (Figs. 2-3B and 2-3C) as compared to alewife postflexion larvae (Figs. 2-4B and 2-4C). With ontogeny, the two parallel rows of melanophores developed in both blueback herring and alewife postflexion larvae extending from the nape to the caudal fin (Figs. 2-3D and 2-4D, respectively). Melanophores along the dorsal mid-line were typically reticulate in both species, but they were frequently larger and more numerous in blueback herring postflexion larvae (Figs. 2-3B to 2-3D) yielding an appearance of darker pigmentation as compared

to alewife postflexion larvae of similar standard length (Figs. 2-4B to 2-4D).

Xanthochrome was observed at the base of the dorsal fin and along the dorsal mid-line of blueback herring postflexion larvae beginning at about 14 mm SL, but it was not observed in these areas in alewife larvae (Table 2-5). Xanthophores developed on the epaxial body surface of alewife postflexion larvae beginning at about 15 mm SL, but they were not observed on the epaxial surface of blueback herring larvae.

Caudal fin

Melanophores on the caudal fin appeared to be more numerous in many blueback herring larvae, but the abundance of melanophores varied and could not be used as a trait for identifying species. On the other hand, the occurrence of xanthochrome on the caudal fin was diagnostic. Xanthochrome was observed as a yellow patch at the base of the caudal fin in blueback herring postflexion larvae beginning about 11 to 12 mm SL, but it was never observed on the caudal fin of alewife larvae.

Internal pigment

The distribution of melanophores along the notochord at the level of the nape was diagnostic for blueback herring and alewife larvae larger than 11 mm SL. In alewife larvae, melanophores developed in pairs on the lateral aspects of the notochord beginning at about 15 mm SL and increased in number with increasing length (Fig. 2-5). Pairs of melanophores ranged in number from one to three in most alewife postflexion larvae examined. Notochord pigment of blueback herring develcped as early as 11 mm SL and appeared most often as a single, large, reticulate melanophore, but occasionally as two large, reticulate melanophores (Fig. 2-6). Melanophores were found to be distributed along the lateral and dorsal surfaces of the notochord in specimens of

both species which appeared to have been undergoing or had completed transformation to the juvenile stage.

Xanthophores were observed in blueback herring postflexion larvae dorsal and ventral to the vertebral column beginning about 13 mm SL. Xanthic pigment ventral to the notochord was observed only in a single alewife of about 16 mm SL.

Diurnal expression of xanthochrome

Xanthophores were observed in an expanded condition only during daylight hours. A small number of blueback herring postflexion larvae were sampled on one occasion at night and all lacked xanthochrome, whereas larvae of similar size sampled during the day possessed xanthochrome.

DISCUSSION

Meristics and morphology

Identification of the early life stages of alewife and blueback herring larvae is problematic. Eggs and yolk-sac larvae of these species observed for this study were indistinguishable. Eggs, yolk-sac larvae, and preflexion larvae of these species have been previously described and are illustrated in numerous publications (Kuntz and Radcliffe 1917; Norden 1967; Lippson and Moran 1974; Jones et al. 1978; Wang and Kernehan 1979; see also Cianci 1969). Characteristics suggested to potentially delimit alewife and blueback herring yolk-sac larvae, including the differential appearance of oil droplets (Lippson and Moran 1974), melanophore distribution on the ventral surface of the yolk sac (see descriptions in Jones et al. 1978), and eye pigmentation at hatching (Cianci 1969) were not found to differ between alewife and blueback herring yolk-sac larvae examined for this study. Other characters (e.g. biochemical traits) may be required to delimit the early life stages of these species.

The usefulness of meristic or morphologic characters for identifying alewife and blueback herring larvae had not been resolved prior to the present study. Cianci (1969) found no significant meristic or morphometric variation between alewife and blueback herring larvae reared from eggs of known taxonomic identity, and his results were confirmed by Marcy (1976). In contrast, Chambers et al. (1976) hypothesized that several meristic and morphologic characters of larvae of these species differ based on an evaluation of field-collected herring larvae sampled from locations where either gravid alewife or gravid blueback herring adults were captured in gillnets. Larvae which they classified as blueback herring had significantly more postdorsal-preanal myomeres and a larger SVL/SL ratio (11 to 13 myomeres and about 0.87) compared to larvae which they classified as alewife (7 to 9 myomeres and about 0.82) (Chambers et al. 1976). The two groups of larvae also differed in the number of preanal myomeres and in the ratios of vent-to-urostyle length and vent-to-tail length to standard length (Chambers et al. 1976). All morphometric measurements used by Chambers et al. (1976) are associated with gut length such that a longer gut yields greater preanal and postdorsal-preanal myomere counts and higher SVL/SL ratios. As a result, no additional information is obtained using the ratios of vent-to-urostyle length or vent-to-tail length to standard length for identifying these species that is not provided by using the SVL/SL ratio.

Other studies do not support the hypothesis that alewife and blueback herring larvae are characterized by significant meristic or morphometric variation. Lam and Roff (1977) compared alewife larvae with gizzard shad larvae from Lake Ontario, and Bulak (1985) compared blueback herring larvae with gizzard shad and threadfin shad larvae from the Santee-Cooper river system of South Carolina. The SVL/SL ratio is the only characteristic which Lam and Roff (1977) identified which delimits alewife and gizzard shad less than 16 mm SL. According to Lam

and Roff (1977), the SVL/SL ratio for larvae less than 16 mm SL ranges from 0.78 to 0.85 for alewife and from 0.85 to 0.88 for gizzard shad, and the SVL/SL ratios of alewife and gizzard shad of at least 16 mm SL ranges from 0.78 to 0.82 and from 0.75 to 0.86. Blueback herring less than 14 mm SL examined by Bulak (1985) were characterized by 11 or fewer postdorsal-preanal myomeres (range: 5-11) compared to 10 or more (range: 10-14) for gizzard shad of the same length.

Bulak (1985) suggested that Chambers et al. (1976) may have reversed the identification of their alewife and blueback herring groups. The findings of Lam and Roff (1977) and Bulak (1985), when considered together, suggest that Chambers et al. (1976) may have compared river herring larvae to gizzard shad larvae. The results of Lam and Roff (1977) and Bulak (1985) support Cianci's (1969) conclusion that morphometric and meristic characters of alewife and blueback herring larvae do not differ significantly.

The present study confirms that alewife and blueback herring do not exhibit significant meristic or morphometric variation useful for delimiting field-collected specimens of these species. The frequency distributions of both the postdorsal-preanal myomere count and the SVL/SL ratio for these two species overlapped extensively so that discrimination of the two species was not possible using either of these characteristics. The results indicate that the postdorsal-preanal myomere count and the SVL/SL ratio are of little value as diagnostic traits. The percentage of alewife and blueback herring larvae with SVL/SL ratios greater than 0.85 was 1.8% and 5.3%, respectively, which suggests that a small number of wild gizzard shad larvae might have been introduced from the river into the tanks of the continuous-flow system.

The ontogeny of dorsal- and anal-fin pterygiophores differed between alewife and blueback herring larvae examined for this study. However, it was not possible to determine whether differences in ontogeny of dorsal- and anal-fin pterygiophores between these species

were due to variation in developmental timing or to developmental plasticity as affected by water temperature during the development of embryos and larvae since the two species were not reared simultaneously.

Pigmentation

Alewife and blueback herring preflexion larvae show the general pigmentation pattern characteristic of clupeid larvae (Russell 1976; Moser 1981) with pigment occurring at the interface of the gut and myomeres and along the ventral mid-line. Ripple et al. (1982) reported that ventral pigment patterns of field-collected preflexion herring larvae identified as alewife and blueback herring based on the criteria of Chambers et al. (1976) were highly variable and did not delimit the two groups. In the present study, slight differences in the appearance of ventral pigment were noted in a number of larvae (Fig. 2-2). Because ventral pigment patterns were usually incomplete, these differences could not be confirmed for use in identifying preflexion larvae.

Supracaudal melanophores are present in alewife preflexion larvae from Lake Michigan (Norden 1967) and the Connecticut River (Cianci 1969). Mansueti (1956) did not mention whether supracaudal melanophores occur in alewife preflexion larvae from the upper Chesapeake Bay. Cianci (1969) noted that supracaudal melanophores are absent in blueback herring preflexion larvae from the Connecticut River. Kuntz and Radcliffe (1917) did not mention specifically whether supracaudal melanophores occur in blueback herring preflexion larvae, but these melanophores are evident in an illustration of a preflexion larva they identified as a blueback herring (Fig. 99, Kuntz and Radcliffe 1917).

Supracaudal melanophores were observed in both alewife and blueback herring preflexion larvae examined for this study. Although more prevalent among alewife preflexion larvae, supracaudal pigment should not be used exclusively to delimit these species in field collections since it is not diagnostic and its frequency in field-

collections of larvae is likely to vary. The frequency of supracaudal pigment in a group of preflexion larvae reared in 1990 from naturally-spawned eggs collected from Herring Creek, a tidal freshwater tributary or the James River, Virginia, was 29% (unpublished data). Alewife are not known to spawn in Herring Creek so these larvae were most likely blueback herring, and the relatively low frequency of supracaudal pigmentation supported this identification.

Pigmentation features described by Wang (1970) for older larvae and for early juveniles of alewife and blueback herring are similar to pigmentation observed among alewife and blueback herring larvae reared in this study, although some differences were noted. Wang (1970) described late-stage postflexion alewife larvae and early-stage alewife juveniles (15-20 mm SL) as having two rows of melanophores along the dorsal mid-line from the nape to the caudal peduncle as well as melanophores on the epaxial body surface. Wang (1970) also described early-stage juvenile blueback herring (20 mm SL) as having two rows of melanophores along the dorsal mid-line from the dorsal fin insertion to the caudal peduncle and lacking melanophores on the epaxial body surface. In this study, both species developed two parallel rows of pigment along the dorsal mid-line from the nape to the caudal peduncle and both developed pigment on the epaxial surface. In both regions, pigmentation was heavier in blueback herring larvae than in alewife larvae.

Several of the pigment characters analyzed for this study differed between alewife and blueback herring larvae. Pigment characters which delimited postflexion larvae developed as early as about 11 to 12 mm. Melanophore distribution on the notochord at the level of the nape was diagnostic. This diagnostic pigmentation as well as other differences in melanophore distribution or morphology, such as occurred along the dorsal mid-line posterior to the dorsal fin, and in xanthophore distribution and morphology may assist in species identification of

field-collected specimens prior to development of juvenile and adult characters.

Use of xanthic pigment distributions as diagnostic taxonomic criteria for identifying wild larvae is limited by relatively rapid deterioration of xanthochrome following fixation and preservation. Xanthochrome is a generic term for a number of carotenoid-derived lipochromes, varying in color (e.g. red, yellow, or orange), which often function as oxygen free-radical scavengers and are chemically unstable (Florey 1966). Antioxidants, such as butylated hydroxytoluene (BHT), may slow the xanthochrome deterioration in fixed and preserved specimens (Waller and Eschmeyer 1965; Berry and Richards 1973; D. Smith, Smithsonian Institute, Division of Fishes, personal communication.).

Identifying wild larvae based on reared larvae

The identification of field-collected larvae based on descriptions of reared specimens may be of some concern since reared and wild larvae often show differences which arise as a consequence of the rearing environment. Different feeding regimes, behaviors, activity levels, and rearing conditions often lead to differences in nutritional condition, chemical composition, and morphology between reared and wild larvae (Blaxter 1975; Theilacker 1980). Rearing conditions resulting in low food availability or overcrowding may lead to increased frequencies of pigment abnormalities and bitten fins, as well as to the establishment of size hierarchies in populations of reared larvae of some species (Shelbourne 1965; Blaxter 1975). The expression of variable pigment patterns between reared larvae and wild larvae may be a function of the rearing environment, especially the lighting and temperature regimes. Shelbourne (1965) suggests that chromatophore development may be a sensitive process which might be easily disrupted by conditions associated with some rearing environments.

Various studies have produced conflicting results regarding the expression of different morphologies and pigment patterns between reared and wild fishes. Laboratory-reared larvae may be more heavily pigmented and may exhibit greater meristic variation as compared to wild larvae (Powles and Markle 1984). Johnson et al. (1986) found that the meristics and morphologies of hatchery-reared and wild American shad, *A. sapidissima*, juveniles did not differ, but hatchery-reared specimens exhibited greater pigmentation as compared to wild specimens (Johnson and Loesch 1983). In comparison, Lau and Shafland (1982) reported that reared and wild larval snook (*Centropomis undecimalis*) did not differ in morphology or pigmentation patterns, but that reared larvae might exhibit anomalous dorsal- and anal-fin ray counts.

In the present study, larvae were reared in outdoor tanks (1-m^3) to minimize the effect of rearing container size on larval development and behavior (Theilacker 1980). Rearing conditions experienced by these larvae during their development in these tanks imitated the natural environment of the Pamunkey River (Chapter 1). Rearing conditions are suggested to have had minimal influence on pigment patterns of the reared alewife and blueback herring larvae. Pigment patterns might have been influenced to some degree by seasonal increases in temperatures and lighting associated with the transition from spring to summer. Since larvae of the two species were not reared simultaneously, they did not experience precisely the same conditions during development.

Melanophores 'expand' or 'contract' as a physiologic response to environmental factors (Fujii 1969; Faber 1980; Mansfield and Mansfield 1982; Langsdale 1993), and they may also expand when larvae are anaesthetized (Langsdale 1993). Changes in the physiological state of melanophores would result in qualitative variation in relative pigmentation intensity, in relative size of melanophores, and in relative distribution of pigment. Intraspecific pigmentation variation, as caused by fluctuations in the physiologic condition of melanophores,

might render qualitative pigmentation differences irrelevant for species identification of larvae if intraspecific variation exceeds interspecific variation. In the present study, differences in pigment patterns involved unique distributions of melanophores on the notochord, different ontogenies of melanin pigment along the posterior dorsal mid-line, and unique distributions and ontogenies of xanthophores. The appearance of these different pigment characters was consistent among reared larvae of each species suggesting that environmentally-induced variation may not have been an important factor determining the degree of pigmentation of larvae. This also suggests that errors due to possible contamination of collections with wild larvae was minimized.

The usefulness of diagnostic and qualitative pigment characters for identifying wild alewife and blueback herring larvae remains to be determined. I have collected herring larvae from the Pamunkey River, Virginia, which possessed the 'alewife' pigment pattern and I have seen herring larvae collected from the Rappahannock River, Virginia, (Dr. W. Wieland, Mary Washington College, Fredericksburg, Virginia) which possessed the 'blueback herring' pigment pattern. These preliminary observations suggest that pigment characters may facilitate the identification of wild alewife and blueback herring larvae.

Ecological significance of xanthic pigment

Carotenoids have various physiological roles in animals. Physiological roles of β-carotene, for example, include provitamin A (retinol) activity, protection against photo-oxidation and photosensitization, and modification of the immune response and melanogenesis in humans (Kornhauser et al. 1989). In addition to similar physiologic roles of carotenoids in fishes, xanthochrome may have secondary functions including species recognition and predator avoidance. Unique distributions of xanthic pigments occur in larvae of

a number of marine species (Berry and Richards 1973; D. Smith, Smithsonian Institute, Division of Fishes, personal communication).

Larvae of many fish species are transparent at hatching and remain so throughout most of the larval stage as a mechanism to reduce predation risk from visual predators. At small body size, transparency enables light to pass through the body with minimal impedance, thereby reducing contrast with background illumination. With ontogeny, the opacity of larvae increases due to increased size and pigmentation of the eyes, increased complexity of the internal body structure, increased path-length of light through the body, the proliferation of melanophores, and the amount of food in the gut (Langsdale 1993). Increased opacity enables visual predators to detect potential prey, and strategies to off-set increased visibility would be advantageous for larval clupeids. The proliferation of melanophores to reduce the body area available to refract or reflect light may reduce the stimulus to visual predators of larval fishes (Moser 1981; Langsdale 1993). The development and proliferation of xanthophores may be an analogous strategy of larvae to reduce visibility, especially in turbid, coastal waters where yellow light is the least attenuated component of the visible light spectrum (Pickard and Emery 1982). This suggests that unique xanthophore distributions may be useful for delimiting larvae of other morphologically similar species in these ecosystems.

Pigment as an aid for identifying clupeid larvae

Pigment patterns have been suggested to be of little value for identifying larvae of clupeid species (Russell 1976). However, pigment patterns may aid the identification of larvae of some species groups prior to development of complete osteological characteristics or when meristic and morphometric characters overlap (Hettler 1984; Kendall et al. 1984). This study suggests that pigment characters can delimit postflexion larvae of two closely related clupeid species, and supports

the use of pigment characters as valid taxonomic criteria for delimiting species of postflexion clupeid larvae. Further studies are necessary to determine the significance of pigment characters as taxonomic criteria for identifying field-collected larvae of other clupeid species.

Table 2-1. Dorsal-fin pterygiophore counts for alewife and blueback herring larvae. Table values indicate the number of larvae observed with the specified number of pterygiophores or in which the dorsal-fin anlagen (A) has developed.

Standard Length (mm)	Species	Dorsal-fin Pterygiophore Number															
		A	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
5	Blueback																
	Alewife	1	1														
6	Blueback																
	Alewife	1															
7	Blueback	2															
	Alewife	2															
8	Blueback				1	1											
	Alewife				1												
9	Blueback																
	Alewife	1					2	3									
10	Blueback										4	1	2				
	Alewife	2						1	2								
12	Blueback												3	5	3	2	
	Alewife										1		1				
13	Blueback												1	1	6	6	3
	Alewife								1				4	1			
14	Blueback														3	4	
	Alewife													3	1		
15	Blueback															3	4
	Alewife													1			

Table 2-1 (continued)

Standard Length (mm)	Species	Dorsal-fin Pterygiophore Number															
		A	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
16	Blueback																
	Alewife													3	1		
17	Blueback																2
	Alewife															4	
18	Blueback																
	Alewife															2	
19	Blueback																
	Alewife															1	

Table 2-2. Anal-fin pterygiophore counts for alewife and blueback herring larvae. Table values indicate the number of larvae observed with the specified number of pterygiophores or in which the anal-fin anlagen (A) has developed.

Standard Length (mm)	Species	Anal-fin Pterygiophore Number																	
		A	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
9	Blueback																		
	Alewife	1																	
10	Blueback							1	1	2			2	1					
	Alewife	1																	
11	Blueback													1	1				
	Alewife	1				1													
12	Blueback											4	1	4	1		2		
	Alewife		1											1					
13	Blueback												3	4	2	7	2		
	Alewife	1							3		1			1					
14	Blueback														1	3	3		
	Alewife													2	1	1			
15	Blueback															2	4	1	
	Alewife															1			
16	Blueback																		
	Alewife														1	2		1	
17	Blueback																2		
	Alewife																3	1	
18	Blueback																		
	Alewife																	1	1
19	Blueback																		
	Alewife																	1	

Table 2-3. Postdorsal-preanal myomere counts of alewife and blueback herring larvae. Table values indicate the number of larvae observed with the specified myomere count.

Standard Length (mm)	Species	Postdorsal-Preanal Myomere Count						
		5	6	7	8	9	10	11
6	Alewife						1	
	Blueback				1	1	1	
7	Alewife					2		
	Blueback				1	7	2	
8	Alewife					1	1	
	Blueback					1	1	
9	Alewife				1	1		2
	Blueback					3	1	
10	Alewife					2	4	
	Blueback				1	4	2	
11	Alewife					1	5	1
	Blueback			1		5		
12	Alewife			1		1	4	1
	Blueback			4	5	5		
13	Alewife			2	1	10		1
	Blueback			6	7	3		
14	Alewife			1				
	Blueback		1	4	1			
15	Alewife			3		2		
	Blueback							
16	Alewife		1	2	3			
	Blueback							
17	Alewife	1	3		1			
	Blueback							
18	Alewife		2		1			
	Blueback							

Table 2-4. Snout-to-vent length/standard length (SVL/SL) ratios for alewife and blueback herring larvae. Table values indicate the number of larvae observed with the specified SVL/SL ratio.

Standard Length (mm)	Species	Snout-to-Vent Length/Standard Length Ratio (x 100)												
		77	78	79	80	81	82	83	84	85	86	87	88	89
6	Alewife				1	5	10	6	1	3				
	Blueback						3	6	5					
7	Alewife						5	9	5	2				
	Blueback							3	9	3				
8	Alewife						4	2	5	1		1		
	Blueback							2	3	1	1			
9	Alewife							10	3	3				
	Blueback						1	4						
10	Alewife						1	4	3					
	Blueback						1	7	8	3				
11	Alewife							5	6	3				
	Blueback						2	4	8	4	1	1		
12	Alewife						3	5	3	2	1			
	Blueback						1	3	13	14	4	1	1	
13	Alewife					1	2	2	6	3				1
	Blueback						1	18	14	4	1			
14	Alewife							2	3	1				
	Blueback				1	8	15	6	3		1			
15	Alewife						1		2					
	Blueback		1	2	3	5	1							
16	Alewife					3	2	3	1	1				
	Blueback					1								
17	Alewife	1		5	1		2	1						
	Blueback	1	2											
18	Alewife		5	5	2	2								
	Blueback													

Table 2-5. Summary of xanthophore distributions in cultured alewife and blueback herring larvae. 'Absent' and 'Present' indicates diagnostic characters, 'Not observed' indicates uncertainty regarding character state. Standard length (SL) indicates size at which a character was first observed, although not all specimens may have exhibited the character at that size.

Xanthophore distribution	Alewife	Blueback Herring
Dorsal surface of head	Dermal; small, contracted or stellate; scattered; observed beginning at about 11 mm SL	Dermal; large, reticulate; covers brain; observed beginning at about 10-11 mm SL
Base of caudal fin	Absent	Present; observed beginning at about 10-11 mm SL
Epaxial surface of body	Dermal; observed beginning at about 15 mm SL	Not observed
Base of dorsal fin and along dorsal midline	Not observed	Dermal; observed beginning at about 14 mm SL
Nape	Dermal; small, contracted or stellate; observed beginning at about 18 mm SL	Not observed
Dorsal to vertebral column	Not observed	Internal; present initially as spots which coalesce into solid line with development; observed beginning at about 12-13 mm SL
Ventral to vertebral column	Internal; observed only in the caudal region of a single specimen, 15.6 mm SL	Internal; observed only in caudal region; observed beginning at about 12-13 mm SL
Snout	Not observed	Dermal; follows ascending process; observed beginning at about 13 mm SL

Figure 2-1. Illustration of a 2-day old alewife yolk-sac larva emphasizing unidentified structures (U) associated with the periblast (P). Structures also identified include: eye (E), heart (H), otoliths (O), yolk (Y), pectoral fin bud (F), myomeres (M), and the epiblast (Ep). The illustration was copied from a photomicrograph of a yolk-sac larvae that was fixed and preserved in 95% EtOH. The alcohol caused the yolk to dehydrate and withdraw from the membrane which facilitated observation of the unidentified structures. These structures also were observed in blueback herring yolk-sac larvae.

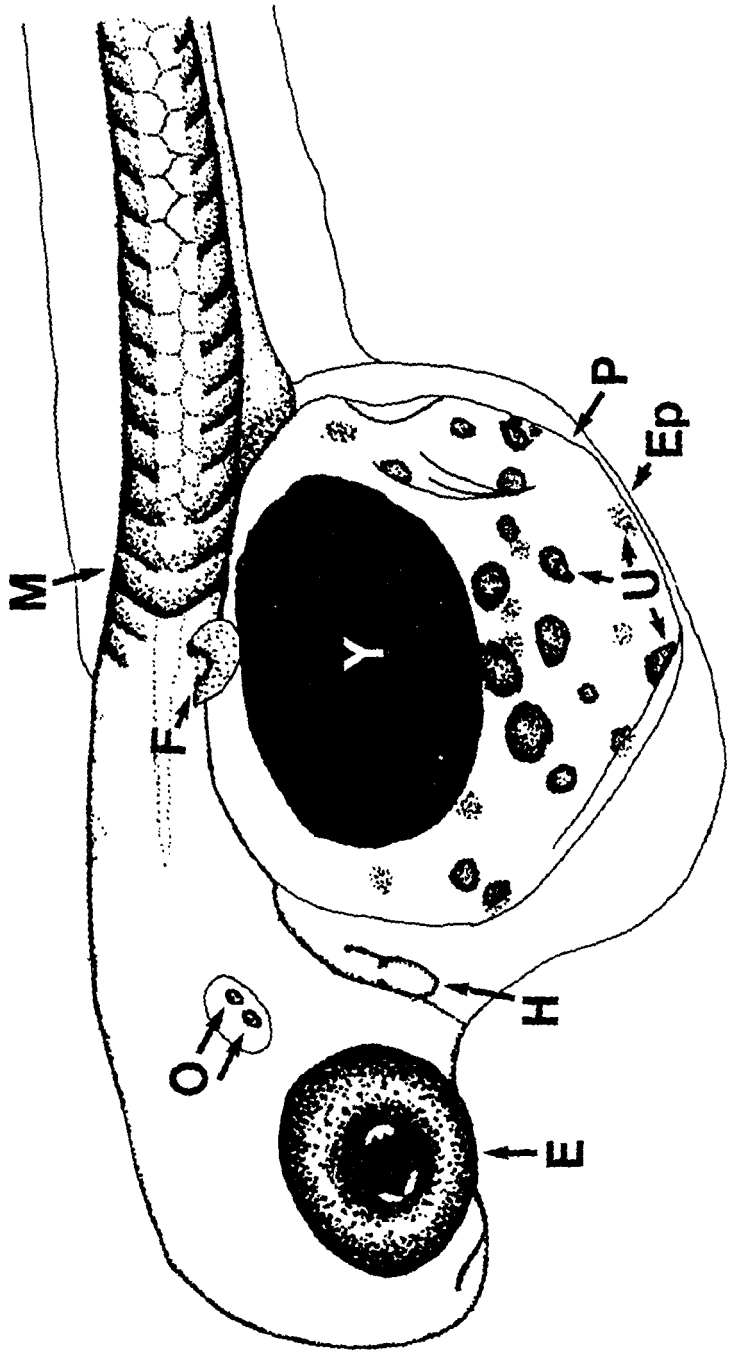
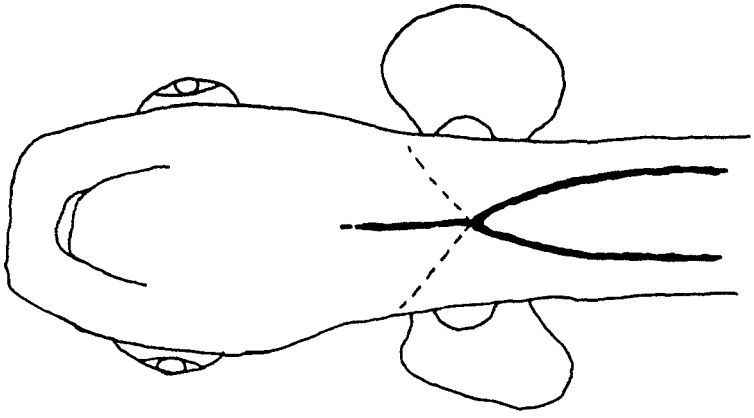


Figure 2-2. Generalized ventral pigment patterns for alewife (*left*) and blueback herring (*right*) preflexion larvae. Most larvae examined lacked sufficient pigment to complete either pattern.



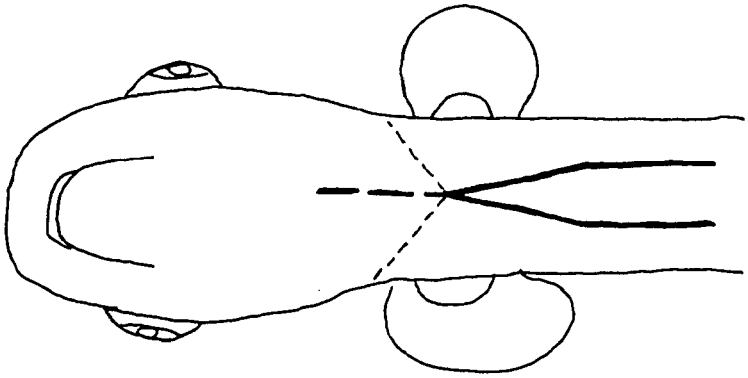


Figure 2-3A. Blueback herring larva, 10.1 mm SL.

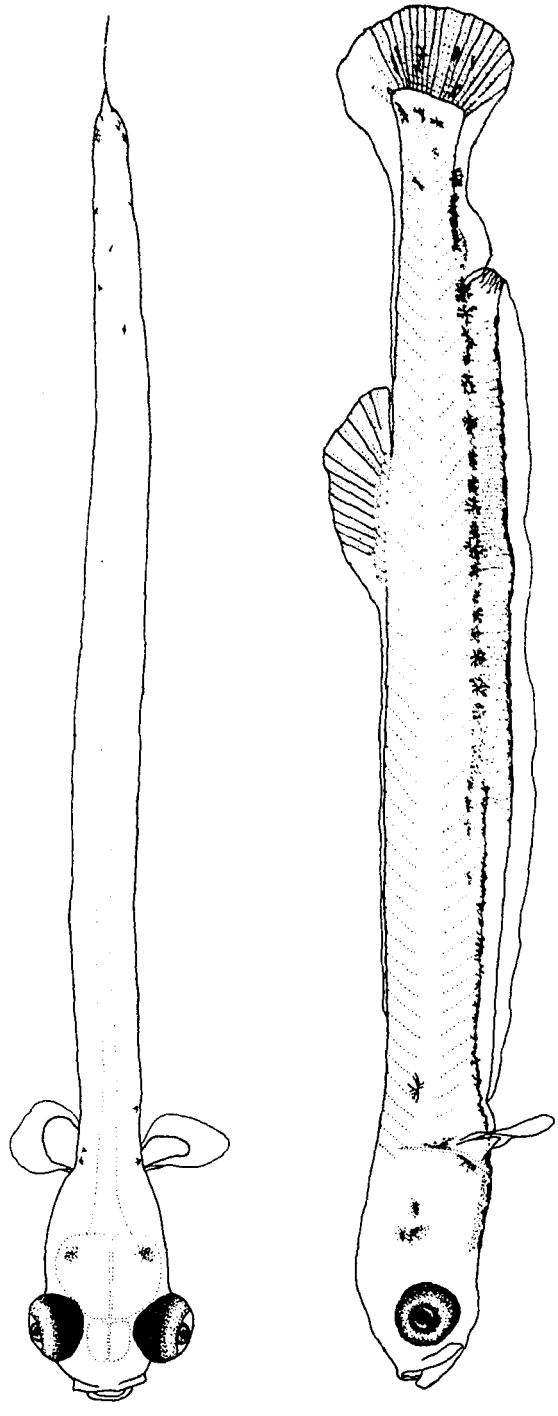


Figure 2-3B. Blueback herring larva, 11.6 mm SL.

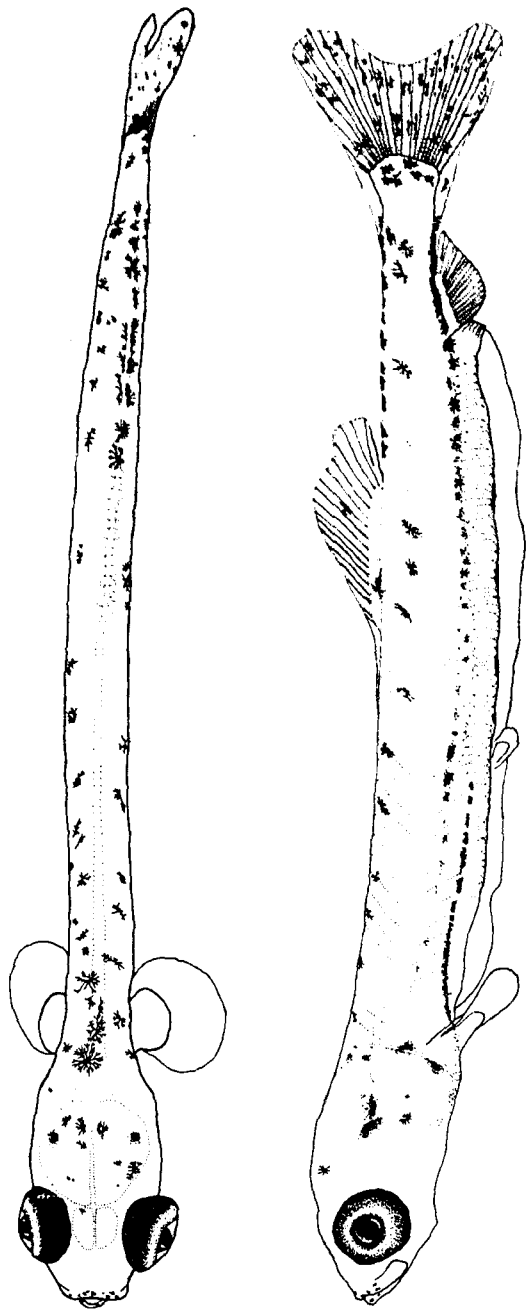


Figure 2-3C. Blueback herring larva, 13.5 mm SL.

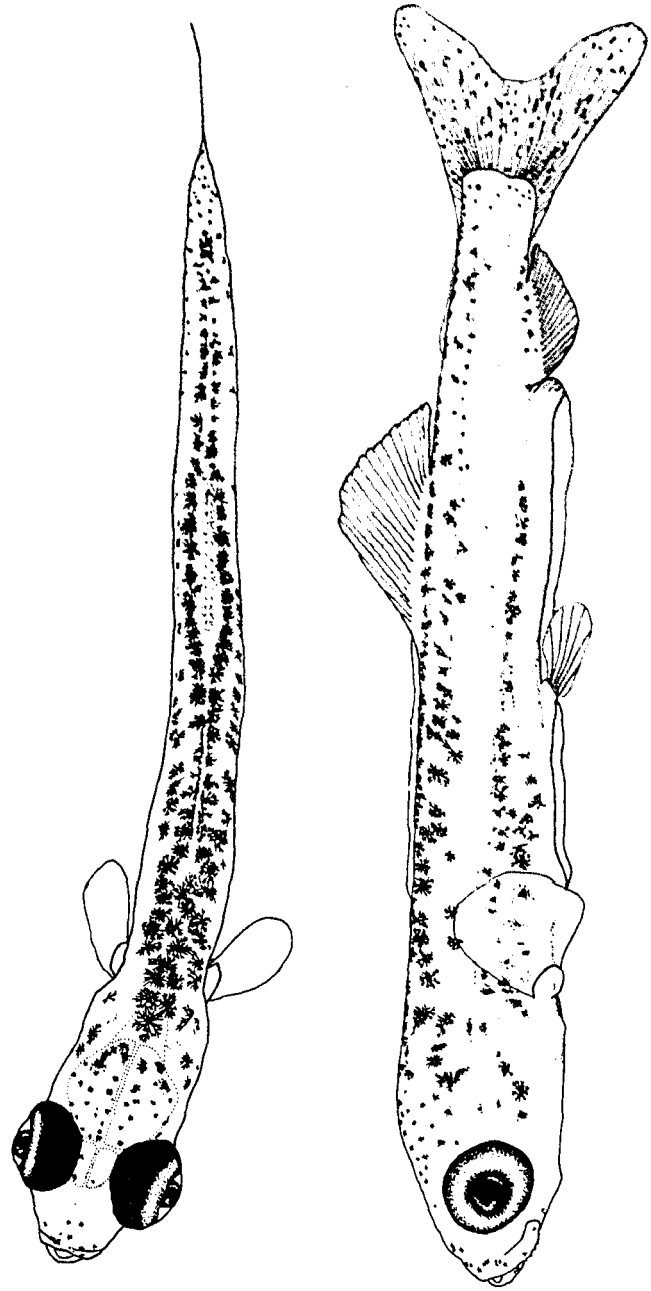


Figure 2-3D. Blueback herring larva, 17.1 mm SL.

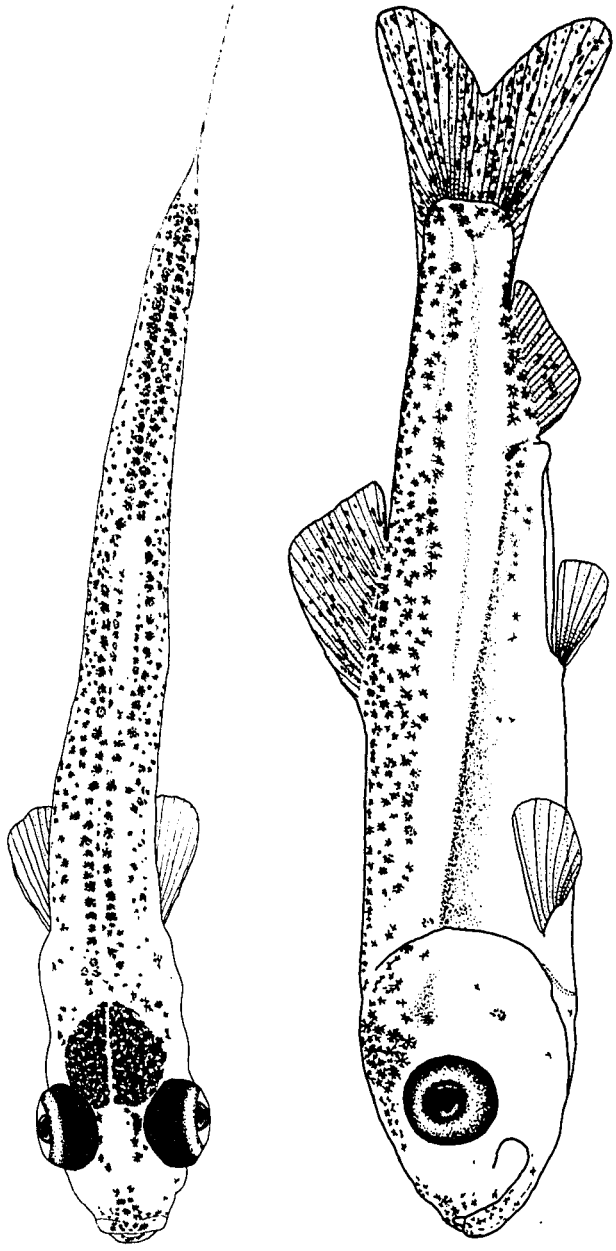


Figure 2-4A. Alewife larva, 11.4 mm SL.

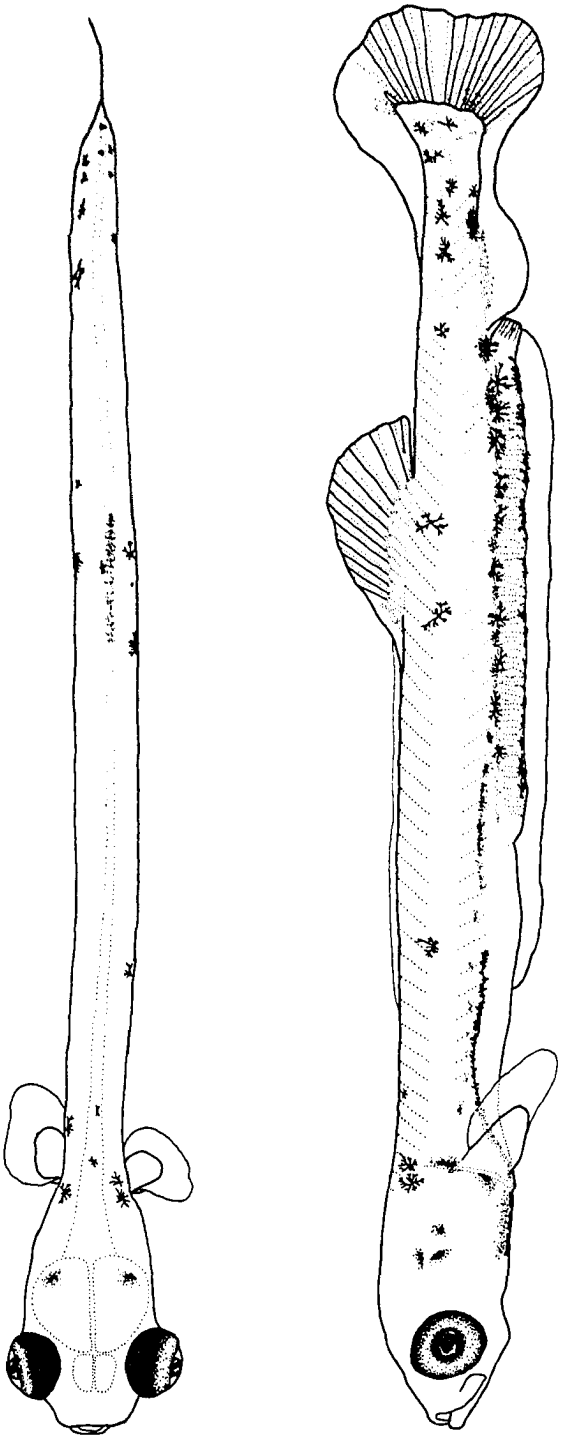


Figure 2-4B. Alewife larva, 13.3 mm SL.

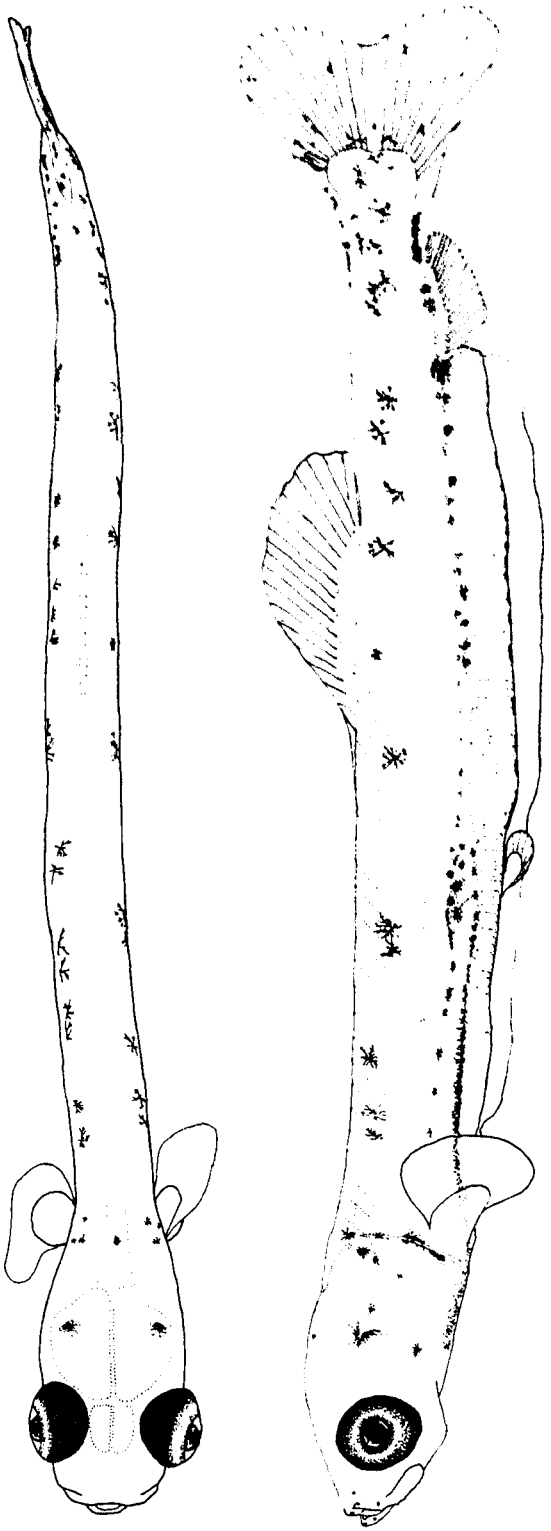


Figure 2-4C. Alewife larva, 15.2 mm SL.

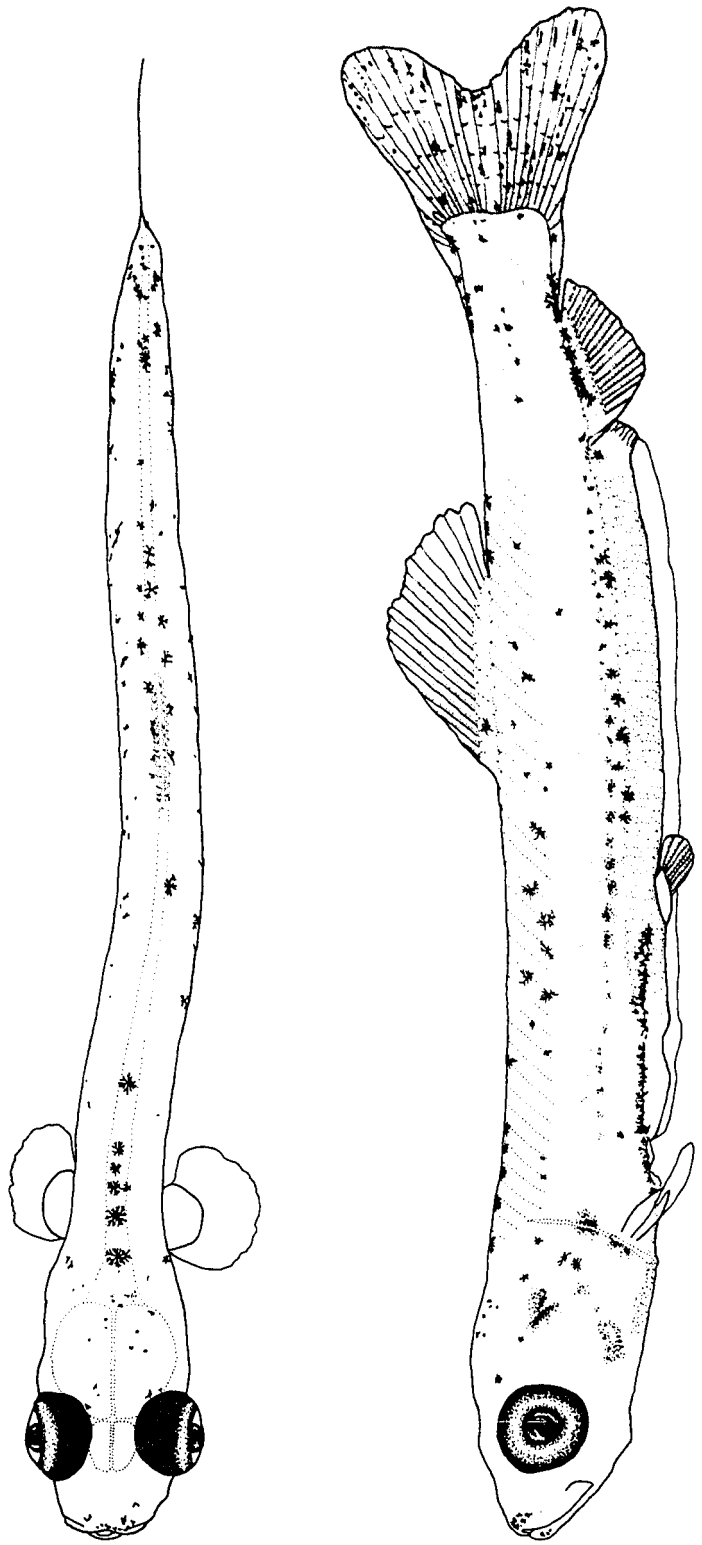


Figure 2-4D. Alewife larva, 17.8 mm SL.

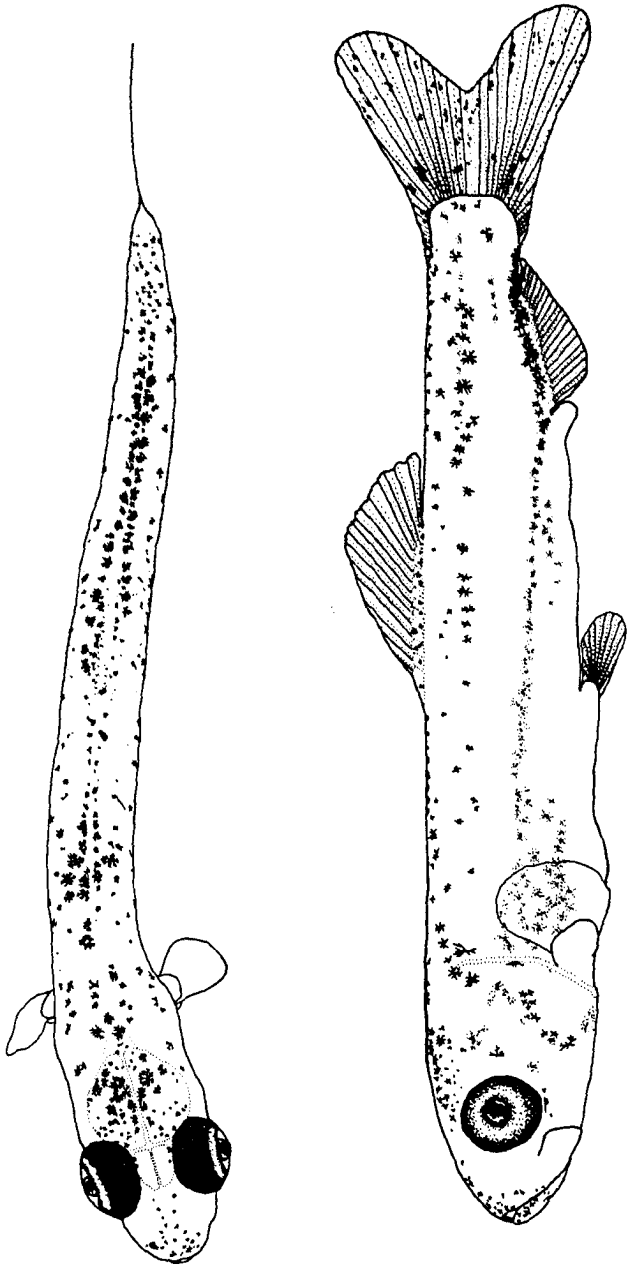


Figure 2-5. Pigmentation of the head (dermal) and notochord (internal) of alewife larvae. The number of melanophores along the lateral surface of the notochord: A) a single pair commonly was observed at about 15 mm SL, and B) 3 pairs were commonly observed at about 17 mm SL. An illustration of a single larva (15.5 mm SL) was modified to show the increase in the number of melanophores that occurred during ontogeny.

Figure 2-6. Pigmentation of the head (dermal) and notochord (internal) of blueback herring larvae. Two alternative patterns observed among specimens are illustrated: A) single melanophore pattern, and B) double melanophore pattern. The occurrence of the single and double melanophore patterns were independent of standard length. An illustration of a single larva (11.8 mm SL) was modified to show both pigment patterns.

Chapter 3.

Daily otolith increment deposition and relationships between otolith size, fish size, and true age in cultured blueback herring (*Alosa aestivalis*) and alewife (*A. pseudoharengus*) larvae.

ABSTRACT

The daily increment method for age determination may be valuable for aiding ecological and biological investigations of anadromous alewife and blueback herring, but validation of the technique is prerequisite to such applications. Otolith increment deposition and relationships between otolith size, fish size, and true age were evaluated in known-age alewife and blueback herring larvae reared from eggs. Ages ranged from 1 to 16 days and from 1 to 34 days for blueback herring larvae and from 1 to 32 days for alewife larvae. Larvae preserved in 95% ethanol did not shrink, but tissue clearing in 1% potassium hydroxide increased standard length. Estimated standard length before preservation was predictable from standard length following preservation. Otolith size was relatively larger in slower growing, older larvae than in faster growing, younger larvae. Daily growth-increment number better estimated true age than total increment number or increment number proximal to the yolk-absorption check. Estimated age at first-increment deposition ranged from about 1 day after hatching for blueback herring to about 3 days after hatching for alewife. Estimated increment deposition rates were equal to or slightly less than one increment per day following yolk absorption. This study is the first to validate the daily increment method for ageing alewife and blueback herring larvae.

INTRODUCTION

Calcified tissues in fishes, including bones (e.g. cleithra, vertebrae, fin rays and spines), scales, and otoliths, encode information about individual growth history through the cyclical, incremental deposition of calcium carbonate. Age and growth information inferred from incremental growth units of calcified tissues is fundamental for assessment and management of fish stocks (Ricker 1975; Gulland 1983). Unlike in adult fishes, otoliths are the only calcified structures in larval fishes available to encode age and growth history (Radtke 1989).

Daily increments in otoliths were discovered by Pannella (1971, 1974). Brothers et al. (1976) and Strushaker and Uchiyama (1976) confirmed the presence of daily growth increments in larvae and juveniles of a number of species and found it possible to estimate ages of young fishes. Since Pannella's discovery, daily growth increments have been found in otoliths of larvae, juveniles, and adults of many fishes (Campana and Neilson 1985; Jones 1986, 1992).

Otolith microstructural analysis potentially enables detailed evaluation of larval fish ecology, population dynamics, and factors influencing year-class strength (Brothers 1981; Methot 1983). The daily increment method enables accurate and precise age estimation and, when applicable, is the preferred method for age determination compared to traditional methods (Campana and Neilson 1985; Jones 1986, 1992).

Daily growth increments are analogous to annular growth increments in otoliths and other calcified tissues of adult fishes, but they differ in their mechanism of formation. Annular growth increments form in response to seasonal changes in metabolism and growth with relatively wide zones laid down during rapid somatic growth and relatively narrow

bands laid down when somatic growth has slowed or ceased. A daily growth increment consists of an incremental zone and a discontinuous zone (Mugiya et al. 1981). The incremental zone is formed by calcium carbonate deposited as twinned aragonite crystals in a protein matrix (Gauldie and Nelson 1990; Degens et al. 1969), while the discontinuous zone is comprised solely of organic matrix (Watabe et al. 1982). Increment deposition is entrained by an endogenous circadian rhythm (Rosa and Ré 1985; Campana 1984), but daily deposition may be disrupted by altered photoperiod, starvation, or water temperature (Tanaka et al. 1981; Karakiri and von Westernhagen 1989; Lagardére 1989). The role of endocrines in otolith growth increment deposition, and in calcium metabolism of fishes in general, is poorly understood (Simkiss 1974; Campana and Neilson 1985; Mugiya and Oka 1991).

Validation of the otolith growth-increment method for age determination is a necessary prerequisite to the application of this technique for otolith microstructural analysis in wild larvae (Beamish and McFarlane 1983, 1987; Campana and Neilson 1985). Validation can be accomplished by various techniques. Rearing larvae from eggs is preferred so that true age is known (Campana and Neilson 1985; Geffen 1987). Alternatively, chemicals or manipulation of the rearing environment (e.g. food, temperature, light) can be used to mark the otoliths. Sequential sampling of a population in which age-specific mortality or age-specific migration do not occur is the last method (e.g. Strushaker and Uchiyama 1976, Essig and Cole 1986). Information obtainable by validation studies include: 1) identification of daily growth increments, subdaily increments, and an appropriate counting path, 2) increment deposition rate, 3) age at first increment formation, and 4) nucleus or yolk-absorption check diameter which may aid the identification of the first growth increment. Lack of validation may introduce systematic error into age and growth analyses.

Application of the otolith increment method for age and growth analysis of anadromous alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*, larvae is limited. Essig and Cole (1986) used otolith growth increments to compare methods for estimating larval alewife mortality rates, and they suggested that growth increments were deposited daily based on corresponding increases in the mean growth increment number and the elapsed number of days between sampling events. The difference between average increment count and known age for five blueback herring larvae which survived in enclosures in the Chowan River, North Carolina, ranged from -6 to +3, prompting O'Rear (1983) to conclude that increments formed daily and could be used to age blueback herring larvae. While these studies support the hypothesis of daily increment deposition, validation of the otolith increment method has not been accomplished for alewife and blueback herring larvae.

Validation of the otolith increment method for ageing alewife and blueback herring larvae has been limited by an inability to rear and maintain these species either in the laboratory. For the present research, alewife and blueback herring were reared from naturally- and artificially-spawned eggs through the larval stage (Chapter 1). Otolith microstructure for known-age alewife and blueback herring larvae was evaluated and analyzed to test the hypothesis of daily increment deposition in the sagittal otoliths. Additional objectives included estimation of the larval herring age and otolith size at first increment formation. Preliminary analysis of larval herring growth relative to conditions experienced in the tanks of the continuous-flow system was reported in Chapter 1. In this chapter, larval herring growth will be analyzed further to evaluate relationships between fish size, otolith size and age, and between somatic growth and otolith growth. Effects on larval herring standard length caused by ethanol preservation and clearing in 1% potassium hydroxide (Brothers 1987) are also examined.

METHODS

Larval herring culture

Alewife and blueback herring larvae analyzed for the present research were reared beyond first-feeding in 1-m^3 tanks of a continuous-flow system (Chapter 1). Methods for rearing alewife and blueback herring larvae are summarized briefly. Blueback herring larvae were reared from naturally-spawned eggs in 1990, and alewife and blueback herring larvae were reared from artificially-spawned eggs in 1991. In both years, embryos were incubated in 37.8-ℓ aquaria illuminated by indirect sunlight during the day and by an incandescent light at night. Water temperature ranged from about 17 °C to 22 °C during embryo development, and hatching occurred about 48 to 72 hr after fertilization. Yolk-sac larvae were transferred prior to complete yolk absorption to the 1-m^3 tanks. In 1991, alewife larvae were reared earlier than blueback herring larvae due to earlier availability of ripe-running adults. Alewife larvae were stocked in the 1-m^3 tanks in early April while blueback herring larvae were stocked in early May and, as a result, the two groups experienced somewhat different environmental conditions and prey abundances during development (Chapter 1). Blueback herring larvae were reared in 1990 to a maximum age of 24 d (a single specimen). In 1991, alewife larvae were reared to a maximum age of 32 d and blueback herring larvae were reared to a maximum age of 37 d in 1991 (Chapter 1). Otolith microstructure was analyzed for blueback herring larvae only up to age 34 d.

Larvae were collected from the 1-m^3 tanks using a 333-μm mesh plankton net at 3- to 5-day intervals throughout development. Larvae were immediately anaesthetized in tricaine methanosulfate (MS-222) and were measured for snout-to-vent length and standard length (SL) following Lippson and Moran (1974) using a Wild M3Z stereo-zoom dissection microscope fitted with a 120-unit reticle ocular micrometer. Lengths were measured to the nearest 0.5 reticle unit at 6.5x, 10x, or

16x magnification and were converted to millimeters using calibration factors. Larvae were preserved in 95% ethanol (EtOH) followed by two changes with fresh 95% EtOH at 24 hr intervals to prevent otolith dissolution. Measured larvae were identified and stored individually, and subsamples of unmeasured larvae were preserved in groups.

Otolith Dissection

Larvae were remeasured prior to otolith dissection to analyze the effect of preservation on standard length. Remeasurement of preserved larvae was often difficult, especially for severely contorted smaller larvae. Larvae cultured in 1990 were straightened, when necessary, and remeasured. Length remeasurements followed the curvature of the lateral body axis for larvae which could not be completely straightened. Following remeasurement, a larva was immersed in 1% potassium hydroxide (KOH) (Brothers 1987) to clear soft tissues and enhance otolith visibility for dissection. Larvae were rinsed briefly in water following clearing. Clearing also rehydrated larvae so that they were flexible and could be easily straightened. Consequently, preserved specimens reared in 1991 were first cleared in 1% KOH to reduce handling time during length remeasurement.

After clearing and length remeasurement, a preserved larva was positioned on a glass microslide in a water droplet and the sagittae were teased from surrounding tissues using microprobes. Initially, sagittae were initially cleaned in bleach to remove adhering tissue but this practice was eventually abandoned because it required excessive time and did not improve the resolution of otolith microstructure. Dissected otoliths were transferred to a clean microslide, rinsed in water, air dried, and mounted to the microslide. Non-spherical otoliths were mounted medial side down. Otoliths for specimens reared in 1990 were mounted using cyanoacrylate adhesive and were covered with histologic grade mounting media and a glass coverslip supported by thin

nylon thread. This technique frequently caused bubble formation beneath the coverslip which made evaluating otolith microstructure difficult or impossible. Otoliths exposed by air pockets were re-embedded in mounting medium following removal of the coverslip, but otoliths were often crushed during coverslip removal. Consequently, sagittae from specimens reared in 1991 were embedded only in mounting media without a coverslip. Otoliths were dissected initially from alewife and blueback herring larvae which had been measured while anaesthetized, but otoliths from larvae which had not been measured prior to preservation were dissected later to replace destroyed otoliths.

Otolith Analysis and Increment Counting

Otolith measurements and growth-increment counts were made using an Olympus BH2 compound light microscope interfaced to a microcomputer through a video image analysis system. Polarizing light and filters were used to improve the contrast of otolith microstructure on the video monitor. Measurements and counts were made at 300× to 1250× magnification. Otolith measurements included the maximum diameter, the maximum radius along the maximum diameter, the yolk-absorption check diameter, and growth-increment count. The yolk-absorption check was identified based on appearance and size as determined from otolith diameter in late-stage yolk-sac larvae. Increment counts were made in the posterior region of non-spherical otoliths.

Data Analysis

Comparison of live and preserved standard length

The median sign test was used to test the hypothesis that standard length measurements made on larvae when anesthetized and following preservation and clearing did not differ by analyzing the numbers of larvae with differences in standard lengths less than, equal to, or greater than the median difference in standard length. Linear

regression analysis was used to determine whether standard length following preservation and tissue clearing varied as a function of live standard length. Analysis of covariance (ANCOVA) was used to determine whether the relationship between preserved standard length and live standard length differed between alewife larvae and blueback herring larvae reared in 1991 since both groups were cleared in 1% KOH prior to remeasurement. Estimated live standard lengths were predicted from preserved standard length using functional regression. Estimated live-length was compared to observed live-length using linear regression to determine whether the two measures differed. Estimated live standard lengths for 1991 alewife and 1991 blueback herring larvae were used in all subsequent analyses to facilitate comparisons between the three groups of cultured larvae.

Somatic Growth

The relationship between standard length and true age was analyzed using linear regression. The 1991 alewife and 1991 blueback herring groups were subdivided into two categories, <age 18 d and ≥age 18 d, to compare larvae reared in 1990 and 1991 over a comparable age range and to improve fit to the linear model. Diagnostic tests were used to determine the appropriateness of linear regression models for evaluating this relationship (see below).

Otolith size, fish size, and true age relationships

Relationships of otolith size (maximum diameter) with fish size (estimated live standard length) and true age were analyzed using linear regression analysis. Otolith size was transformation using the natural logarithm to linearize the relationships with fish size and age. Relationships between otolith size and fish size and between otolith size and true age were analyzed to determine whether variation in otolith size was explained by fish size or age. Otolith growth as

determined by otolith size-age and otolith size-fish size relationships was plotted against somatic growth and analyzed using linear regression to evaluate the otolith growth-somatic growth relationship.

Otolith microstructure

Verification of daily growth increments

Increment counts made on sagittae from 78 otolith preparations selected randomly from the available otolith preparations were used to determine whether all observed increments or a subset of observed increments were deposited daily. Counts made on each sagitta included the total increment number, the total increment number proximal to the yolk-sac absorption check, and the number of growth increments defined as daily based on qualitative microstructure appearance. Increments defined as daily were characterized by prominent discontinuous zones and relatively uniform widths (Campana 1992; see Results). For each specimen, either the left or right sagitta was selected randomly for each of two readings. If either sagitta was missing then the other was always read. The relationship between mean increment number and true age for each culture group was analyzed using linear regression.

Comparison of left and right sagittae

Thirty-one otolith preparations were selected randomly from the available otolith preparations and were analyzed to determine the significance of differences between left and right sagittae. Preparations with an unreadable or missing sagitta were replaced by a another, randomly selected preparation. Otolith measurements and increments counts were made twice. T-tests were used to determine the significance of differences in increment number and morphologic measurements between left and right sagittae.

Precision of Age Estimates

All otolith preparations were read twice, non-sequentially, by the author without knowledge of specimen identity. Otoliths were randomized prior to each reading, and either the left or right sagitta was selected randomly for each reading. If only a single sagitta was available, then it was always read. Daily increments were identified by qualitative appearance of discontinuous zones and relative increment widths. However, all observed discontinuities from the yolk-absorption check to the tenth discontinuity, including faint discontinuities in a poorly-resolved zone observed in many otoliths, were defined as delimiting daily growth increments (see Results). Following the second enumeration, increment counts were compared and those differing by one or more units for larvae up to age 15 d or by two or more units for larvae older than age 15 d were randomized and read for a third time. Increments counts were compared following the third enumeration and those not meeting the acceptance criteria just described were excluded from subsequent analysis. If increment counts from the three enumerations differed by two units, then the intermediate count was excluded from further analysis. Percent agreement and precision of increment counts were calculated. Precision was evaluated using the coefficient of variation (Chang 1982), the index of precision (Chang 1982), and the average percent error (Beamish and Fournier 1981).

Relationship between growth-increment number and true age

Ordinary least-squares (OLS) and weighted least-squares (WLS) regression was used to analyze the relationship between growth-increment number and true age. A number of possible weighting factors were evaluated for use in WLS regression. Functions of the mean, standard deviation, and variance of increment count and relationships between mean residual error and various functions of age were examined graphically for each culture group to aid in the selection of an

appropriate weighting factor. Diagnostic tests were used to determine the appropriateness of OLS and WLS regression models for evaluating the increment number-true age relationship (see below). A single regression model relating increment number to true age was selected to facilitate comparisons between the three groups.

The 1991 alewife and 1991 blueback herring groups were subdivided into two age categories, ≤age 18 d and >age 18 d, to facilitate comparisons with 1990 blueback herring larvae and to assess the increment number-true age relationship within each age category. The increment number-true age relationship within each age category for these culture groups was analyzed to determine the fit of data to the linear model and whether estimated increment formation rates differed from unit slope as a possible consequence of enumeration error. Younger ages also were excluded progressively from regression analysis to identify ages for which enumeration error resulted in nondaily increment deposition rate estimates.

The relationship between increment number and true age was analyzed for pooled 1991 alewife and 1991 blueback herring larvae to estimate increment deposition rate and age of first increment formation applicable to field-collected specimens since alewife and blueback herring preflexion larvae are indistinguishable morphologically (Chapter 2). It was assumed that otolith growth increment deposition and age at first increment deposition would have been the same had alewife and blueback herring larvae been reared under identical conditions. Pooling data confounded within the regression analysis differences attributable to conditions affecting the growth of larvae and otolith microstructure.

Regression diagnostic tests

Diagnostic tests, including the Burn-Ryan test, the pure error F test, and the Conover-Johnson-Johnson test, and examination of residual error distributions (Draper and Smith 1981; Neter et al. 1985; Fox

1991) were used to evaluate the fit of data to OLS and WLS regression models for the present research. The Burn-Ryan test (Burn and Ryan 1983; MINITAB 1989) evaluated curvature and lack of fit of data to the linear model. The significance of linear regression models for estimating the residual error mean square (σ^2) was evaluated using the standard pure error F test (Draper and Smith 1981; Neter et al. 1985). Homoscedasticity was evaluated using the Conover-Johnson-Johnson homogeneity of variances test (Conover et al. 1981; Fox 1991) in which a one-way analysis of variance is conducted on values $z_{ij} = |y_{ij} - \dot{y}_i|$, where $\dot{y}$ is the median y within the ith group. Heteroscedastic error variance increases differences between group means z_i producing a large F test statistic (Fox 1991).

Computer analysis

All statistical analyses were conducted using the statistical program package MINITAB (MINITAB 1989).

RESULTS

Effect of Preservation and Clearing on Standard Length

Larvae of the 1990 blueback herring group were manually straightened and remeasured following preservation in 95% EtOH. Smaller herring larvae often were severely contorted which made them difficult to straighten and remeasure, but clearing in 1% KOH to observe otoliths also rehydrated larvae facilitating handling and remeasurement. Consequently, preserved alewife and blueback herring larvae reared in 1991 were first cleared in 1% KOH prior to length remeasurement. Clearing usually increased standard length due to tissue swelling; therefore, it was necessary to determine and to correct for the effects of preservation and clearing on standard length and to estimate live standard length from standard length following preservation since not all larvae had been measured prior to preservation.

Larval herring standard lengths were not altered by preservation in 95% EtOH. The median difference between live and preserved standard lengths for 1990 blueback herring (not treated in 1% KOH) did not differ significantly from zero. In contrast, live standard length was significantly less than preserved standard length for 1991 alewife and 1991 blueback herring (Table 3-1). For 1990 blueback herring, the intercept and slope of the OLS regression model relating preserved standard length to live standard length did not differ from zero or from unity, respectively (Table 3-2). In comparison, intercepts of the OLS regression model for 1991 blueback herring and 1991 alewife larvae were significantly greater than zero (Table 3-2). The average increase in standard length following preservation as indicated by the regression intercept was 1.38 mm for 1991 alewife larvae and was 0.63 mm for 1991 blueback herring larvae. The slope of the OLS regression model for 1991 alewife larvae decreased slightly with increasing length but that for 1991 blueback herring did not change with increasing length indicated by 95% confidence intervals for each group (Table 3-2). Difference in the relationship between live and preserved standard length for 1991 alewife and 1991 blueback herring larvae was not significant by ANCOVA (Table 3-3) suggesting that swelling due to tissue clearing in 1% KOH was similar in these groups. Standard lengths of 5 larvae (7.2%) increased more than 1.0 mm, those of 57 larvae (82.6%) increased up to 1.0 mm, and those of 7 larvae (10.1%) either did not change or decreased.

The 1991 alewife and 1991 blueback herring groups were pooled to compute a single, functional regression model relating standard length following preservation and tissue clearing to standard length preceding preservation (Table 3-2). This model was then used to estimate pre-preservation standard length from standard length measured following preservation and clearing. Estimated pre-preservation standard length was related to observed pre-preservation standard length using linear regression (Table 3-4). The slope of the resulting linear regression

model for pooled 1991 blueback herring larvae and 1991 alewife larvae did not differ from unity and the intercept was not different from zero (Table 3-4) indicating that the functional regression model correctly predicted pre-preservation standard length from the standard length of preserved and cleared specimens. Standard lengths of preserved and cleared alewife and blueback herring larvae reared in 1991 were converted to estimated pre-preservation standard lengths using the functional regression model. These corrected standard length measurements and uncorrected standard length measurements for 1990 blueback herring larvae were used in subsequent analyses of relationships between otolith size, fish size, and true age.

Somatic Growth

Somatic growth, measured as change in standard length with age, differed markedly between the three culture groups. Standard length of 1990 blueback herring larvae increased from about 4 mm at hatching to about 17 mm at age 16 d (Fig. 3-1A). Standard length of 1991 blueback herring larvae increased from about 3 mm at hatching to about 12 mm at age 17 d and to about 13 mm by age 34 d (Fig. 3-1B). Standard length of 1991 alewife larvae increased from about 4 mm at hatching to about 8 mm at age 14 d and to about 17 mm at age 32 d (Fig. 3-1C). Standard length-at-age was greatest for 1990 blueback herring larvae compared to the other groups. Standard length-at-age was greater for 1991 blueback herring at relatively younger ages and for 1991 alewife at relatively older ages (Fig. 3-1D).

A single regression model, either linear or curvilinear, was unlikely to model adequately the growth of each group (Fig. 3-1D); therefore, standard length-at-age relationships were analyzed for larvae subdivided into two age categories, <age 18 d and ≥age 18 d, based of visual inspection of standard length-at-age plots (Fig. 3-1A to 3-1C). Regression diagnostic tests and visual inspection of studentized

residual error distributions were evaluated to determine whether linear or exponential regression models best fit the length-at-age data.

For 1990 blueback herring larvae, both linear and exponential regression models fit the data poorly; however, fit was worse for the exponential model indicated by the higher F value of the pure error F test (Table 3-5). Lack of fit to the linear model was due to higher standard lengths for age 11 d larvae followed by lower standard lengths for age 16 d larvae. Exclusion of yolk-sac larvae from the analysis did not affect significantly the fit of data to the model (Table 3-5, Fig. 3-2). Greater than expected and somewhat lower than expected standard lengths for age 11 d and age 16 d larvae, respectively, may have had offsetting influence on the estimated regression slope, but caused curvature in the data indicated by the Burn-Ryan test. Estimated somatic growth for this group, 0.82 $mm \cdot d^{-1}$, was the highest of the three groups (Table 3-6), and this group is identified subsequently as the fast-somatic growth group for 1990 blueback herring larvae.

For 1991 blueback herring larvae, the linear regression model fit the length-at-age data poorly for age 2 d to age 17 d larvae but fit the data adequately for age 5 d to age 17 d larvae as well as for age 21 d to age 34 d larvae (Table 3-5). The exponential regression model fit the data poorly for both age 2 d to age 17 d and age 5 d to age 17 d larvae, but fit the data adequately for age 21 d to age 34 d larvae (Table 3-5). The studentized residual error distribution for the linear model was improved by excluding yolk-sac larvae (age 2 d) from the regression analysis of standard length-at-age for larvae less than age 18 d (Figs. 3-3A and 3-3B). The studentized residual error distribution for larvae older than age 18 d shows that the linear model provided a good fit to the data (Fig. 3-3C). Estimated somatic growth rates were 0.52 $mm \cdot d^{-1}$ for age 2 d to age 17 d larvae, 0.58 $mm \cdot d^{-1}$ for age 5 d to age 17 d larvae, and 0.06 $mm \cdot d^{-1}$ for age 21 d to age 34 d larvae (Table 3-6). Estimated somatic growth for age 5 d to age 17 d larvae was used

in subsequent analyses as it provided a better description of growth after the onset of feeding. The age 5 d to age 17 d category for 1991 blueback herring larvae is subsequently identified as the fast-somatic growth interval, and the age 21 d to age 34 d category is identified as the slow-somatic growth interval.

For 1991 alewife larvae, linear regression models for age 1 d to age 14 d, age 4 d to age 14 d, and age 18 d to age 32 d fit the standard length-at age data adequately; whereas, the exponential model describing growth across all ages showed a significant lack of fit based on the pure error F test (Table 3-5). A single exponential model describing growth across all ages was evaluated to test the hypothesis that growth of 1991 alewife larvae was exponential since standard length-at-age was greater for older larvae. Exclusion of yolk-sac larvae from the analysis did not change significantly the fit of data to the linear model for larvae younger than age 18 d (Figs. 3-4A and 3-4B). The studentized residual error distribution for age 18 d to age 32 d showed good fit of data to the linear model (Fig. 3-4C). Estimated somatic growth rates for 1991 alewife larvae <age 18 d and ≥age 18 d were 0.25 $mm \cdot d^{-1}$ and 0.52 $mm \cdot d^{-1}$, respectively (Table 3-6). The age 1 d to age 14 d category of 1991 alewife larvae is subsequently identified as the slow-somatic growth interval and the age 18 d to age 32 d category is identified as the fast-somatic growth interval.

Relations between Otolith Size, Fish Size and True Age

Sagittal otolith size showed a curvilinear increase with standard length in each culture group and was relative larger in slow-growing larvae than in fast-growing larvae (Fig. 3-5). Natural logarithm transformation of otolith maximum diameter linearized the otolith size-fish size relationship (Fig. 3-6). Diagnostic tests for regression models relating otolith size to fish size over all lengths showed fit of the linear model to the data with slight departure from strict linearity

(Table 3-7). The Burn-Ryan test found evidence of curvature in the fit of data to the linear model for each culture group. The pure error F test, however, was not significant for either of the two blueback herring culture groups indicating that the linear model provided an adequate fit to the data despite possible slight curvature in the data. In contrast, the pure error F test indicated a poor fit of natural logarithm transformed otolith diameter to the linear model for 1991 alewife larvae.

To facilitate comparisons between the three culture groups, especially between larvae reared in 1990 and 1991 over comparable size ranges, larvae were subdivided into two length categories, <8 mm and ≥8 mm. The otolith size-fish size relationship was linear within each length category for each culture group as indicated by nonsignificant Burn-Ryan tests, and models showed good fit to data within each length category as indicated by nonsignificant pure error F tests (Table 3-7). No replicate samples at any length were available for 1990 blueback herring larvae <8 mm SL so the pure error F test could not be evaluated.

Otolith growth relative to standard length for ≥8 mm-SL blueback herring larvae reared in 1990 was significantly lower than for either length category of alewife or blueback herring larvae reared in 1991 (Table 3-8). Slopes of the otolith size-fish size relationship between comparable length groups for 1991 alewife and 1991 blueback herring larvae overlapped, but only for the 1991 alewife group were differences between the two length categories significant (Table 3-8). Confidence intervals for <8 mm-SL 1990 blueback herring larvae were wider than for any other length category of the three culture groups, probably because this group was composed of only a few specimens of a single age. The regression model for this group may not be accurately depict the otolith size-fish size relationship; therefore, this length group will not be considered further. The results suggest an inverse otolith size-fish

size relationship with relatively slower otolith growth occurring among faster growing larvae.

Sagittal otolith diameter for 1990 blueback herring and 1991 alewife larvae showed a curvilinear increase with age, while sagittal otolith diameter for 1991 blueback herring larvae showed a curvilinear increase up to age 17 d after which it increased at a much reduced rate due to reduced somatic growth (Fig. 3-7). Natural logarithm transformation of otolith diameter was used to linearize the relationship between otolith diameter and age (Fig. 3-8). Larvae were subdivided into two age categories, <age 18 d and ≥age 18 d, to facilitate comparison between the 1990 and 1991 groups over comparable age ranges. Diagnostic tests for regression models relating the natural logarithm of otolith diameter to fish age over all age classes showed that the linear model fit the data poorly (Table 3-9). The Burn-Ryan test found evidence of possible curvature and lack of fit of the data to the linear regression model for each group, and the pure error F test was statistically significant indicating inadequate fit. Data for the two age categories of 1991 blueback herring and 1991 alewife larvae showed adequate fit to the linear model indicated by nonsignificant outcomes of diagnostic tests (Table 3-9). For 1990 blueback herring larvae, exclusion of age 1 d yolk-sac larvae produced a satisfactory fit to the linear model indicated by nonsignificant outcomes for diagnostic tests (Table 3-9).

Comparison between age categories showed that increased otolith diameter (natural log) with age in each culture group equalled or exceeded 0.1 $\mu m \cdot d^{-1}$ during periods of fast-somatic growth (Table 3-10). The change in otolith size with age for 1990 blueback herring larvae was significantly greater than for 1991 alewife larvae, but was not different between these groups and 1991 blueback herring indicated by 95% confidence intervals (Table 3-10). Otolith growth with age was significantly less during slow somatic growth than fast somatic growth.

Slow-growing 1991 alewife larvae showed significantly greater otolith growth than slow-growing 1991 blueback herring larvae (Table 3-10).

Otoliths were relatively larger in slow-growing larvae than in fast-growing larvae because slow-growing larvae were older. Slopes of linear models relating otolith diameter to age or standard length during slow- and fast-somatic growth periods were regressed on estimated somatic growth rate to investigate the relationship between otolith growth and fish growth. Slopes of otolith size-fish relationships for blueback herring larvae reared in 1990 and 1991 (Table 3-11) differed somewhat from slopes estimated above (Table 3-8) because larvae were classified by age categories corresponding to fast- and slow-somatic growth periods rather than by standard length and this produced slight overlap of standard lengths between age categories. Slopes of the otolith size-fish size relationship for 1991 alewife larvae and of the otolith size-fish age relationship for all groups are the same as above (Table 3-10).

For subsequent discussion, an effect is defined the as a linear model relating otolith growth rate to somatic growth rate. Therefore, a size-effect on otolith growth is thus defined as a linear model relating slopes of the otolith size-fish size relationship to somatic growth rate per millimeter ($\mu m \cdot mm^{-1}/mm \cdot d^{-1}$), and a time-effect on otolith growth is defined as a linear model relating slopes of the otolith size-fish age relationship to somatic growth rate per day ($\mu m \cdot d^{-1}/mm \cdot d^{-1}$). The size-effect was not significant (Table 3-12) indicating that otolith growth relative to standard length was independent of somatic growth (Fig. 3-9). Otolith growth increased logarithmically with somatic growth (Fig. 3-9) so the relationship was linearized using the natural logarithm of somatic growth for linear regression analysis. The time-effect was significant (Table 3-12) with positive correlation between otolith growth relative to larval herring age and somatic growth ($R = 0.935$). At somatic growth rates from 0.3 $mm \cdot d^{-1}$ to 0.8 $mm \cdot d^{-1}$, the time- and

size-effects were approximately proportional with time-effect of otolith growth increasing less than 0.01 units per 0.1 unit increase in somatic growth (Fig. 3-9). Proportional time- and size-effects suggests a relatively constant otolith growth-somatic growth relationship. At somatic growth rates below about 0.3 $mm \cdot d^{-1}$, otolith size was no longer proportional to fish size with the time-effect approaching zero as somatic growth rate decreased. Consequently, the apparent influence of fish size on otolith growth and size increased (Fig. 3-9).

Otolith microstructure analysis

Gross morphology and identification of daily increments

Sagittae and lapilli were present at hatching in alewife and blueback herring larvae. Lapilli were larger initially, and both types were of equivalent size at the end of the yolk-sac stage. Thereafter, sagittae were larger. Sagittae were approximately spherical in yolk-sac larvae and in young larvae following yolk absorption, but became planoconvex and oval with ontogeny. Asterisci were never observed.

Otolith microstructure varied in appearance between the three culture groups with blueback herring otoliths showing generally better resolution than alewife otoliths (Fig. 3-10). Variable otolith microstructure appearance affected the accuracy and precision of increment enumeration (see below). Most otoliths exhibited a ring surrounding the central core which was of variable resolution, ranging from a distinct discontinuity to a diffuse dark band and from circular to irregular, which is suggested to be the hatch check (Fig. 3-10). The yolk-absorption check proximal to the presumed hatch check had a mean diameter of 18.3 μm (± 1.7 μm) (Fig. 3-10). The yolk-absorption check was distinct in many otoliths and was often more intense than adjacent discontinuities, but it was indistinct in other otoliths. When poorly resolved, the first discontinuity with a diameter ranging from 16 to 22 μm was defined as the yolk-absorption check. Sagittal otolith diameters

of late-stage yolk-sac larvae prior to complete yolk absorption were near to or within this size range (Fig. 3-11). Yolk-absorption check diameter did not change with increased larval herring length (Fig. 3-11). A number of increments, ranging from one to four, were sometimes observed between the hatch check and the yolk-absorption check suggesting that increments medial to the yolk-absorption check may not reliably estimate age. A poorly resolved zone, typically in otoliths from blueback herring and alewife larvae reared in 1991, occurred from the yolk-absorption check proximal to the first well-resolved and contained closely spaced, weakly resolved discontinuities (Fig. 3-10D and 3-10F, respectively).

Daily Growth Increment Identification

Daily growth increments were identified based on the appearance and relative spacing of discontinuous zones. Daily growth increments were most clearly resolved in otoliths from 1991 blueback herring larvae (Fig. 3-10D). Individual growth increments proximal to the poorly resolved zone (region I-II) displayed the characteristic bipartite structure of growth increments consisting of a translucent zone and a discontinuous zone. No other discontinuities were observed in these otoliths. Increments near the poorly resolved zone were wider than increments toward the otolith edge reflecting the greater somatic growth that occurred earlier in development of these larvae (Fig. 3-12A).

Otoliths of 1990 blueback herring and 1991 alewife larvae were characterized by a complex microstructural appearance with numerous subdaily increments (Figs. 3-10A and 3-10C, respectively) in contrast to the relatively simple otolith microstructural appearance for 1991 blueback herring larvae. Primary discontinuities delimiting otolith daily growth increments were better resolved and more pronounced than secondary discontinuities which appeared either to merge with primary discontinuities or became less distinct as the focal plane was altered.

Otolith diameter showed progressive, gradual increase with increment number when only increments delimited by primary discontinuities were enumerated, but otolith diameter increased erratically with increment number when increments delimited by both primary and secondary discontinuities were enumerated (Figs. 3-12B and 3-12C). Increment width increased abruptly in retrospective growth curves including secondary discontinuities for 1990 blueback herring and 1991 alewife larvae due to lack of observable secondary discontinuities near the otolith edge.

Verification of daily growth increments

Otolith growth increments defined as daily provided a better estimate of true age than total increment number or increment number proximal to the check. The slope of linear models relating increment number to true age were similar for total observed increment number and increment number proximal to the check not differing from one increment per day; whereas, the slope for the linear model for defined daily increments was slightly less than unity (Table 3-13). The intercept for the linear model was significantly greater than zero for total increment count and did not differ from zero for the two other models (Table 3-13). The 95% confidence interval for the daily increment count-true age relationship was narrower than for relationships between total increment number or increment number proximal to the yolk-absorption check with true age suggesting that daily growth increments provided the best estimate of true age (Table 3-13). This conclusion is supported by lower standard deviation and higher coefficient of determination for the daily growth increment regression model (Table 3-13). The results also indicate that subdaily increments may confuse the interpretation of otolith microstructure.

Comparison of left and right otoliths

Otolith diameter, nucleus diameter, and increment counts of left and right sagittae from 31 larvae did not differ significantly (Table 3-14). Consequently, sagittae from either side were randomly selected for data collection in all subsequent analyses.

Precision of Age Estimates.

Increment counts made on sagittae from a total of 143 larvae showed percent agreement between of the initial two enumerations ranging from 73.3% for 1990 blueback herring larvae to 79.6% for 1991 blueback herring larvae with an overall percent agreement of 76.9% (Table 3-15). Percent agreement increased after the third enumeration ranging from 89.7% for 1990 blueback herring larvae to 96.1% for alewife larvae with an overall percent agreement of 96.3% (Table 3-15). Ten specimens did not meet the acceptance criteria (see Methods) and two were not interpretable yielding a total of 131 specimens available for analysis of the daily increment count-true age relationship.

In comparison, the precision of increment enumeration was better for the two blueback herring groups (Tables 3-16A and 3-16B) than for the alewife group (Table 3-16C) suggesting that otolith microstructure interpretation was relatively more difficult for the latter group. Overall, precision improved with age except for age 32 d alewife larvae. Variability in the younger ages is suggested to be a consequence of poor increment resolution in smaller otoliths possibly in association with the poorly resolved zone (Figs. 3-4D and 3-4F), while variability in age 32 d alewife larvae is suggested to be due to poor resolution of otolith microstructure associated with larger otolith size.

Increment Deposition.

The increment count-true age relationship was analyzed using both ordinary least-squares (OLS) and weighted least-squares (WLS) regression

so that diagnostic tests and residual error distributions could be examined to determine the appropriateness of each model. An appropriate weighting factor for WLS regression was identified. Younger ages were progressively excluded from regression analyses to identify age groups for which increment counts caused lack of fit to the linear model. Alewife and blueback herring larvae reared in 1991 were pooled to evaluate the relationship between increment count and true age by confounding within the analysis the influence that different growth rates might have had on otolith microstructure which would effect increment interpretation. Only the 1991 groups were considered for this analysis since both encompassed the entire larval stage.

Evaluation of regression models: ordinary least-squares regression

The residual error distribution for 1990 blueback herring larvae showed increased error variance with age (Fig. 3-13A), although error variances were homoscedastic (Table 3-17). The Burn-Ryan test found evidence of curvature or lack of fit for all regression analyses except that for age 1 d to age 11 d larvae (Table 3-17). The pure error F test was marginally nonsignificant ($0.1 > p > 0.05$) for all regression analyses except for age 1 d to age 16 d larvae excluding age 11 d larvae which was not significant and for age 8 d to age 16 d larvae which was significant (Table 3-17). Correlations between increment counts or studentized residuals and the associated normal probability scores were relatively low suggesting departure of daily growth increment counts from normality. Increment counts were relatively higher for age 11 d larvae than for age 16 d larvae (Fig. 3-13A). Lack of fit of daily growth increment number for age 11 d larvae to the OLS regression model appears primarily a consequence of a single outlier (Fig. 3-13A). Imprecise daily growth increment enumeration for age 11 d and age 16 d larvae due to misidentification of secondary discontinuities as primary discontinuities is suggested to be the primary error affecting analysis

of the daily growth-increment number-true age relationship for 1990 blueback herring larvae.

The studentized residual error distribution for 1991 blueback herring showed slight differences between age groups with error variance being greater for younger and older ages than for intermediate ages (Fig. 3-13B). The Burn-Ryan test found no evidence of either curvature or lack of fit in the data to the OLS regression model, and the pure error F test was not significant in all analyses (Table 3-18). Error variances were homoscedastic for all analyses (Table 3-18). Correlations between increment counts or studentized residuals with associated normal probability scores were relatively high for most analyses suggesting that increment count data was approximately normal.

The residual error distribution for alewife larvae showed increased error variance in increment number with age (Fig. 3-13C). The Burn-Ryan test found evidence of curvature or lack of fit in the data to OLS regression models for all analyses except for age 21 d to age 32 d larvae (Table 3-19). The pure error F test was marginally non-significant for age 1 d to age 32 d larvae, but was highly significant for age 1 d to age 18 d larvae indicating lack of fit to the data, but it was not significant for the age 21 to 34 d group indicating adequate fit to the data. The pure error F test was not significant for any OLS regression model excluding younger larvae. Error variances were heteroscedastic for age 1 d to age 32 d larvae as well as for age 1 d to age 18 d larvae, but were homoscedastic for analyses of all other age ranges (Table 3-19). Correlations between increment counts or studentized residuals and associated normal probability scores were relatively lower for analyses of the increment number-true age relationship across the entire age range and for age 4 d to age 32 d larvae, but were higher for the younger and older age categories. Lack of fit to the OLS regression model appears to be associated primarily with increment counts made on sagittae from yolk-sac larvae (age 1 d).

Pooled 1991 data did not fit the OLS linear regression model adequately for any analysis. The Burn-Ryan test found evidence of curvature and possible lack of fit, and the pure error F test was highly significant also indicating lack of fit (Table 3-20). Error variances were heteroscedastic for age 1 d to age 34 d larvae, and were marginally homoscedastic ($0.1 > p > 0.05$) for both age 4 d to age 34 d and age 8 d to age 34 d larvae (Table 3-20). Relatively high correlations between increment count or studentized residuals and the associated normal probability scores indicated that increment number was approximately normally distributed (Table 3-20).

These results suggest that OLS regression was adequate for evaluating the daily growth-increment number-true age relationship for 1991 blueback herring larvae but not for alewife and 1990 blueback herring larvae. Additionally, the OLS regression model was not adequate for evaluating this relationship among the pooled 1991 groups.

Evaluation of regression models: weighted least-squares regression

Daily growth-increment number-true age relationships among the three groups of cultured river herring larvae were analyzed using WLS regression since the relationship for alewife and 1990 blueback herring larvae was not modelled adequately by OLS regression. Several functions, including age^{-1}, $(age^2)^{-1}$, and $(age^{\frac{1}{2}})^{-1}$, were evaluate as possible weighting factors. Relationships between functions of the mean ($\bar{x}$, $\bar{x}^2$, and $\bar{x}^{\frac{1}{2}}$) and standard deviation (s and s^2) of increment count as well as relationships between mean studentized residuals and functions of the independent variable (age, age^2) were examined to facilitate identification of an appropriate weighting factor. The $(s/\bar{x}^2)$ ratio became relatively stable or decreased as age increased for each culture group (Fig. 3-14). Similar results were found for the relationship of mean studentized residual with age^2 (Fig. 3-15). Therefore, the $(age^2)^{-1}$ function was selected as the weighting factor.

The WLS regression analysis for 1990 blueback herring larvae indicated that increment numbers for age-1-d yolk-sac larvae influenced the regression model, but excluding the specimens did not alter the studentized residual error distribution (Fig. 3-16). Two outliers, one each at age 5 d and at age 11 d, were identified which may have influenced the regression model since both residuals were positive (Fig. 3-16). Weighting improved the fit to the linear model indicated by the Burn-Ryan test and by lower F values for the pure error F test (Table 3-21) compared to respective OLS regression models (Table 3-17). Improved fit was gained, however, with slight reductions in correlation between studentized residuals and associated normal probability scores for all analyses except age 1 to 11 d larvae which showed increased correlation.

Weighting improved slightly the fit to the linear model for 1991 blueback herring larvae indicated by lower pure error F values for all regressions (Table 3-22), although pure error F values for respective WLS and OLS (Table 3-18) regression models were not significant. Weighting reduced the correlation between studentized residuals and the associated normal probability scores (Table 3-22) relative to respective OLS regression models. Weighting altered markedly the studentized residual error distribution showing greater error variance for younger ages that decreased rapidly and was relative constant with age (Fig. 3-17), although error variances for all WLS and OLS regression models were homoscedastic (Tables 3-22 and 3-18, respectively). Excluding age 2 d larvae had little affect on the studentized residual error distribution (Fig. 3-17). The spread of positive and negative residuals for young larvae was similar suggesting that larger residuals did not affect the WLS regression model.

The studentized residual error distribution for alewife larvae showed reduced error variance at older ages (Fig. 3-18) relative to the residual error distribution for the OLS regression model (Fig. 3-13C). However, inclusion of yolk-sac larvae in the analysis produced a trend

toward positive residuals due to a large, positive residual for one specimen (Fig. 3-18). The Burn-Ryan test found evidence of curvature and lack of fit for analyses of age 1 d to age 32 d and age 1 d to age 18 d larvae, and the pure error F test remained significant for both age groups (Table 3-23). Excluding yolk-sac larvae improved the fit to the linear model (Table 3-19) and removed the trend toward positive residuals (Fig. 3-18). Weighting increased the correlation between studentized residuals and associated normal probability scores indicating improved normality.

Weighting improved the fit of increment number-true age data to the linear model for the pooled 1991 groups as younger ages were excluded from analysis (Table 3-24). Satisfactory fit to the linear model was obtained for age 8 d to age 34 d larvae indicated by nonsignificant results for the Burn-Ryan and pure error F tests. Correlations between studentized residuals and the associated normal probability scores did not differ between the WLS model (Table 3-24) and the respective OLS model (Table 3-20).

Weighting significantly improved the fit of growth increment number with age to the linear model for 1991 alewife larvae and had a moderate effect on the fit of data for 1990 blueback herring larvae to the linear model. Although fit to the linear model for 1991 blueback herring larvae was not altered, weighting reduced normality of the data. This result is suggested to be of minor consequence relative to the improved fit to the linear model. Weighting markedly improved the fit of pooled 1991 data to the linear model. Based on these results, daily growth-increment number and true age for each culture group and the pooled 1991 group were evaluated using WLS regression.

Increment deposition rate and age of first-increment deposition

The daily growth-increment number-true age relationship for cultured river herring larvae was analyzed using increment counts made

on sagittae from 49 alewife larvae ranging from age 1 d to age 32 d, on sagittae from 26 blueback herring larvae reared in 1990 ranging from age 1 d to age 16 d, and on sagittae from 56 blueback herring larvae reared in 1991 ranging from age 2 d to age 34 d (Fig. 3-19). Weighted least-squares regression was used to analyze the daily growth-increment number-true age relationship (see above).

Estimated increment deposition for 1990 blueback herring larvae was greater than one increment per day for age 1 d to age 16 d larvae and for age 1 d to age 11 d larvae, but was daily for age 5 d to age 16 d larvae (Table 3-25). Increment deposition was estimated to begin from hatching to 2 days after hatching for age 5 d to age 16 d larvae. Estimated increment deposition for 1991 blueback herring larvae was significantly less than daily for age 2 d to age 34 d larvae and either did not differ or was only marginally less than daily for other age ranges (Table 3-25), and increment deposition was estimated to begin at hatching or shortly thereafter. Estimated increment deposition for alewife larvae was daily for age 8 d to age 32 d larvae and for age 21 d to age 32 d larvae but was marginally less than daily for age 4 d to age 32 d larvae (Table 3-25), and increment deposition was estimated to begin 1 day to 4 days after hatching. Increment deposition for pooled alewife and blueback herring reared in 1991 was marginally less than daily for age 8 d to age 34 d larvae with increment deposition estimated to begin between hatching and about 2 days after hatching. These results validate the daily growth-increment method for estimating larval river herring age after yolk-sac absorption with increment deposition beginning during the yolk-sac stage.

DISCUSSION

Effect of preservation on standard length

Larval fishes often shrink when they die (Blaxter and Ehrlich 1974; Theilacker 1980), and the amount of shrinkage may be affected by

conditions experience by larvae prior to fixation or preservation as well as by the type of fixative or preservative used. Radtke (1989) reports that preservation in 96% EtOH had no effect on the standard length of larval cod (*Gadus morhua*). Theilacker (1980) reports that preservation in 80% EtOH had no effect on the standard length of laboratory-preserved anchovy (*Engraulis mordax*) larvae, and that laboratory-preserved larvae shrank less than larvae which were subjected to simulated field collection conditions. However, Radtke and Waiwood (1980) report that cod larvae preserved in 60% EtOH shrank from 11-20% and that shrinkage was relatively constant regardless of the length of time that larvae were in the preservative. Kruse and Daily (1990) report that capelin (*Mallotus villosus*) larvae preserved in absolute ethanol shrank more than larvae preserved in 5% buffered formalin, and shrinkage was relatively greater for smaller larvae than for larger larvae. Total lengths of capelin after 22-24 weeks of preservation decreased by 14.4%, 7.2% and 2.4% for small (5-20 mm), intermediate (28-46 mm), and large (50-91 mm) larvae and juveniles, respectively.

Standardization of body length measurements is necessary to compare laboratory-reared and field-collected larvae and to compare larvae which have been fixed or preserved differently. Preservation in 95% EtOH did not alter standard lengths of alewife and blueback herring larvae examined for the present research. However, smaller larvae without skeletal elements often were difficult to measure following preservation due to moderate to severe body contortion. Theilacker (1990) also found that small anchovy larvae, which are morphologically similar to clupeid larvae, were difficult to measure following preservation in ethanol. Measurement of ethanol-preserved alewife and blueback herring larvae was facilitated by clearing specimens in 1% KOH which rehydrated soft tissues. Tissue clearing caused swelling of body lengths with smaller larvae showing the greatest relative increase (about 20% for a 5 mm specimen). Estimates of the standard length of

larvae prior to preservation as calculated from standard length of preserved and cleared specimens were not significantly different from the observed standard length of larvae while anesthetized.

Body size, otolith size and somatic growth relationships

Otoliths potentially record growth histories. The basis for using otoliths to determine previous growth history in larval fishes is predicated on correlation between otolith and somatic growth such that otolith size is scaled to body size. Increment width and otolith size in many species are correlated with somatic growth and fish size (Campana and Neilson 1985). Savoy and Crecco (1987) report that 80% of the variation in otolith size of larval American shad, *Alosa sapidissima*, was explained by total length of fast-growing larvae, while only 58% of otolith size variation was explained by total length of slower-growing larvae because these larvae did not grow beyond 14 mm total length. Others have shown that otolith size is relatively larger in slow-growing fish than in fast-growing fish at the same size (Mosegaard et al. 1988; Reznick et al. 1987; Secor and Dean 1989; Secor et al. 1989; Francis et al. 1993). The same phenomenon was observed for larval alewife and blueback herring otoliths in the present research; otolith size-at-age in alewife and blueback herring larvae was relatively larger for fast-growing larvae than for slow-growing larvae. Slow-growing larvae have larger otoliths because they require more time to attain a specific length than do fast-growing larvae.

Dissociation of otolith growth and somatic growth occurs at low somatic growth rates because otolith size increases relatively faster than fish size at low somatic growth rates as occurred in blueback herring larvae reared in 1991. Consequently, otolith growth is a time-dependent process ($\mu m \cdot d^{-1}$) rather than a size-dependent process ($\mu m \cdot mm^{-1}$) (Fig. 3-9). Time-dependent otolith growth for river herring larvae during fast-somatic growth periods did not differ and were greater than

for slow-somatic growth periods. In contrast, size-dependent otolith growth and somatic growth were unrelated. Uncoupling of the otolith size-fish size relationship at low somatic growth rates should be expected, therefore, since otolith growth is no longer scaled to body growth.

Increment deposition in otoliths

Estimated age of first-increment formation in blueback herring larvae reared in both 1990 and in 1991 was similar at about 1 day after hatching compared to about 3 days after hatching for alewife larvae. Estimated differences in the onset of first-increment deposition between the two species may reflect true species-specific differences because blueback herring typically spawn later in the season when water temperatures are higher and larvae may utilize yolk faster, but they may also result from error in the regression equations describing increment deposition rate. Savoy and Crecco (1987) showed that the estimated time of first-increment formation differed between American shad larvae reared under optimal and suboptimal conditions. The age of first-increment formation for larvae growing under suboptimal conditions estimated from linear models relating increment number to true age may be affected by ageing errors associated with older larvae and may not reflect actual differences. In the present study, alewife and blueback herring larvae were reared at similar water temperatures during the yolk-sac stage (Chapter 1) suggesting that ageing error may have influenced the estimated age at first-increment formation.

Other research suggests that the first increment may be deposited at about the same time in both alewife and blueback herring larvae. Species with smaller eggs and short incubation periods initiate increment deposition following yolk-sac absorption (Radtke and Dean 1982). Egg diameter ranges from 0.87 to 1.11 mm for blueback herring and 0.95 to 1.25 mm for alewife (Lippson and Moran 1974) with yolk

absorption occurring about 2 to 3 days after hatching. Crecco et al. (1983) suggested that first increment deposition occurs shortly after hatching in American shad otoliths. American shad have relatively large eggs from about 2.9 mm to 3.4 mm diameter (Wang and Kernehan 1979) but a relatively short yolk-sac stage from 3 to 6 days (Marcy 1976). In comparison, species with relatively large eggs and longer incubation periods initiate increment deposition prior to hatching and species with intermediate egg size and incubation period initiate increment deposition at hatching (Radtke and Dean 1982).

The daily growth increment method for age determination has been validated in larval and juvenile fishes for numerous, taxonomically diverse species (Campana and Neilson 1985; Jones 1986, 1992), including a number of clupeid species (Table 3-26). Daily incremental calcium carbonate deposition appears to be a universal mechanism for otolith growth under normal conditions (see Introduction), but non-daily increment deposition has been reported for several clupeid species. Nondaily increment deposition in otoliths of Atlantic herring larvae (Geffen 1982) and Pacific herring larvae (McGurk 1984) was suggested to occur at low somatic growth rates based light microscope evaluation of otoliths. Electron microscopic evaluation of otoliths has shown, however, that daily growth increments with widths below light microscopy resolution limits may be formed when fish larvae are reared in suboptimal conditions (Jones and Brothers 1987). Campana et al. (1987) mathematically modelled increment deposition in larval Atlantic herring otoliths and correctly predicted the number of increments in the poorly-resolved zone which was consistent with the number of days between hatching and the age of deposition of the first well-resolved daily increment.

The formation of narrow, poorly resolved increments proximal to the otolith nucleus or yolk-absorption check appears to be common in various clupeid species, and was observed in alewife and blueback

herring larvae reared in 1991. Several faint discontinuities were observed in this zone. Subtraction of the number of well-resolved increments from the true age indicates the number of "missing" increments in the poorly-resolved zone. The first well-resolved increment occurred at about one week after hatching in both alewife and blueback herring larvae reared in 1991 (Fig. 3-12). Comparing the number of "missing" increments for 1991 blueback herring larvae and 1991 alewife larvae in Fig. 3-12 with the number of faint discontinuities observed in the poorly-resolved zones of corresponding otoliths in Fig. 3-10 shows that most of the "missing" increments are accounted for by the faint discontinuities. Consequently, faint discontinuities in the poorly-resolved zone are deposited daily and should be included in growth increment enumerations when a poorly-resolved zone observed. A poorly-resolved zone may not be observed always in river herring otoliths, however, as occurred in otoliths of blueback herring larvae reared in 1990. Fast-somatic growth rates, as observed for 1990 blueback herring larvae and for 1991 alewife larvae at older ages, may introduce another potential source of error in ageing river herring larvae due to subdaily increments.

Formation of the poorly-resolved zone is probably associated with feeding behavior. Initial success of clupeid larvae at first feeding is low and larvae must learn to forage effectively (Blaxter and Hunter 1982). Low growth rates or poor physiological signals due to low daily ration during the learning period may result in poorly defined growth increments during the first days of life. Atlantic herring, for example, may not begin to deposit daily increments which are resolvable using light microscopy until about 13 to 17 days after hatching (Campana et al. 1987; Messieh et al. 1987). Atlantic herring are characterized by a larval stage of long duration and may not effectively for a relatively long time period due to low prey densities in the ocean. Feeding success of Atlantic herring larvae ranges from 2 to 6% and

reaches about 90% in about seven weeks (Blaxter and Hunter 1982). It is not unreasonable, therefore, to expect that a growth increments deposited during this time are indistinct. Feeding success increases rapidly in faster growing larvae; for example, about 70% after one week for the tropical anchovy *Anchoa lamprotaenia* (Blaxter and Hunter 1982). That the first distinct increment was laid down about one week after hatching in alewife and blueback herring larvae reared in 1991 indicates that feeding success for these larvae increases rapidly. However, absence of a poorly-resolved zone in blueback herring larvae reared in 1990 suggests that other factors influence increment formation during the first days of life.

Validation studies of the daily growth-increment method often report estimated increment deposition rates that are slightly less than one increment per day. Marginally subdaily rates of increment formation occurred for alewife and blueback herring evaluated in the present research depending upon the age groups included in regression analyses. Rice et al. (1985) identify factors which may contribute to underestimation of growth-increment deposition rates. Two of these are: 1) increased variance in the data and decreased range in the independent variable reduce the least-squares regression slope, and 2) growth increments are more likely to be missed during enumeration than to be counted more than once. Consequently, slight underestimation of the true increment deposition rate might be a more likely outcome than not.

Conclusion.

Analyses of otoliths from larval fishes have made significant contributions to the advancement of larval fish biology and ecology which were not possible prior to discovery of daily otolith growth increments. The advantage of otolith microstructure analysis for evaluation of larval fish biology and ecology lies in precise and accurate estimation of age afforded by the daily increment method. Ages

estimated by this method provide fine-scale resolution necessary to evaluate larval fish population dynamics in relation to biotic and abiotic factors which influence year-class strength. Validation of the daily increment method provides a necessary foundation for ageing wild alewife and blueback herring larvae by this technique. This study is the first to validate the otolith increment method for age determination of alewife and blueback herring larvae.

Table 3-1. Sign test of the median difference between standard lengths of cultured alewife and blueback herring larvae before (live) and after preservation in 95% ethanol and tissue clearing in 1% potassium hydroxide. Only alewife and blueback herring larvae reared in 1991 were subjected to tissue clearing before standard length remeasurement. The null hypothesis is that the median difference between live and preserved standard length measurements equals zero (no shrinkage).

Culture Group	KOH	*n*	Number of Specimens:			Median	*p*
			Below Median	Equal to Median	Above Median		
Blueback (1990)	No	32	15	2	15	0.000	1.000
Alewife (1991)	Yes	30	23	1	6	-0.500	0.002
Blueback (1991)	Yes	39	39	0	0	-0.400	<0.000

Table 3-2. Summary of regression models relating standard length after preservation and tissue clearing to live standard length.

KOH[a]	df	$t_{0.05}$	Regression Summary								SD_{regr}	r^2_{adj}
			α	SE_α	LCL	UCL	β	SE_β	LCL	UCL		
						Blueback herring, 1990						
No	33	2.036	-0.46	0.33	-1.13	0.21	1.04	0.03	0.43	1.65	0.564	0.980
						Blueback herring, 1991						
Yes	39	2.023	0.63	0.16	0.31	0.95	0.99	0.02	0.95	1.03	0.275	0.991
						Alewife, 1991						
Yes	30	2.042	1.38	0.49	0.38	2.38	0.91	0.04	0.83	0.99	0.792	0.944
						Pooled						
Yes	69	1.997	1.04	0.23	0.64	1.44	0.94	0.02	0.90	0.98	0.567	0.968

a. Preserved specimens cleared in 1% KOH before being measured.

Table 3-3. Analysis of covariance of preserved standard length as a function of live standard length for alewife and blueback herring larvae reared in 1991.

Analysis of Covariance Table						
Source	df	SS	SS_{adj}	MS_{adj}	F	p
Standard length	1	653.38	621.85	621.85	1987.23	<0.000
Group	1	0.14	0.79	0.79	2.51	0.118
Interaction	1	1.09	1.09	1.09	3.48	0.067
Error	65	20.34	20.34	0.31		
Total	68	674.94				

Table 3-4. Regression models relating estimated to observed live standard length (mm) for alewife and blueback herring larvae reared in 1991.

df	$t_{0.05}$	Regression Statistics								SD_{reg}	r^2_{adj}	F
		α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
						Blueback herring, 1991						
38	2.025	-0.44	0.167	-0.778	-0.102	1.05	0.016	1.018	1.082	0.292	0.991	4188.52
						Alewife, 1991						
29	2.045	0.36	0.522	-0.707	1.427	0.96	0.045	0.868	1.052	0.842	0.944	487.91
						Pooled, 1991						
68	1.997	0.00	0.245	-0.489	0.489	1.00	.022	0.956	1.044	0.604	0.968	2030.11

Table 3-5. Diagnostic tests of linear and exponential regression models relating standard length (mm) to age (days after hatching) for cultured alewife and blueback herring larvae.

Regression Model	Age Range	Burn-Ryan Test		Pure Error F Test		
		Symptom	p	F	p	df
		Blueback herring, 1990				
Linear	1-16	Curvature	0.007	5.05	0.009	20
	5-16	Curvature	0.007	7.51	0.004	20
Exponential	1-16	Curvature	<0.000	23.89	<0.000	20
		Lack of fit	0.009			
	5-16	Curvature	<0.000	25.40	<0.000	20
		Lack of fit	0.024			
		Blueback herring, 1991				
Linear	2-17	Curvature	0.077	6.08	0.003	28
	5-17	None	>0.1	0.09	0.917	22
	21-34	None	>0.1	0.55	0.585	18
Exponential	2-17	None	>0.1	3.54	0.025	28
	5-17	Curvature	0.044	4.55	0.022	22
	21-34	None	>0.1	0.54	0.593	18
		Alewife, 1991				
Linear	1-32	Curvature	<0.000	6.00	<0.000	40
		Lack of fit	0.030			
	1-14	None	>0.1	0.86	0.476	23
	4-14	None	>0.1	0.87	0.440	15
	18-32	None	>0.1	0.09	0.964	17
Exponential	1-32	None	>0.1	2.37	0.034	40

Table 3-6. Regression models relating standard length (mm)[a] with age (days after hatching) for cultured alewife and blueback herring larvae.

Age (days)	df	$t_{0.05}$	Regression Statistics								SD_{regr}	r^2_{adj}	F
			α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
Blueback herring, 1990													
1-16	25	2.060	3.9	0.396	3.1	4.7	0.82	0.033	0.75	0.89	0.751	0.961	597.67
5-16	23	2.069	3.8	0.462	2.9	4.8	0.82	0.038	0.74	0.90	0.767	0.952	462.10
Blueback herring, 1991													
2-34	54	2.005	4.8	0.347	4.1	5.5	0.28	0.018	0.24	0.32	1.448	0.812	234.98
2-17	34	2.034	3.0	0.194	2.6	3.3	0.52	0.020	0.48	0.56	0.590	0.954	667.67
5-17	25	2.060	2.3	0.266	1.8	2.7	0.58	0.022	0.53	0.63	0.494	0.966	713.62
21-34	22	2.074	10.5	1.199	8.0	13.0	0.06	0.043	-0.03	0.15	1.026	0.055	2.22
Alewife, 1991													
1-32	49	2.009	2.3	0.235	1.9	2.8	0.43	0.014	0.40	0.46	0.968	0.952	977.18
1-14	28	2.048	3.3	0.126	3.0	3.6	0.25	0.017	0.22	0.28	0.400	0.895	230.35
4-14	18	2.101	3.4	0.279	2.8	3.9	0.25	0.030	0.19	0.31	0.476	0.780	64.89
18-32	22	2.074	-0.1	1.089	-2.4	2.2	0.54	0.044	0.45	0.63	0.921	0.872	144.41

a. Estimated live standard length predicted from preserved standard length.

Table 3-7. Diagnostic tests of regression models relating sagittal otolith maximum diameter (μm) to standard length (mm) of cultured alewife and blueback herring larvae.

Length Category	Burn-Ryan Test		Pure Error F Test			NPS Correlation[a]
	Symptom	p	F	p	df	Residuals
		Blueback herring, 1990				
All lengths	Curvature	0.024	3.91	0.923	4	0.889
< 8 mm	None	>0.1	-	-	-	0.998
> 8 mm	None	>0.1	2.11	0.2451	4	0.980
		Blueback herring, 1991				
All lengths	Curvature	0.050	1.35	0.2649	16	0.991
< 8 mm	None	>0.1	0.95	0.5570	7	0.983
> 8 mm	None	>0.1	1.59	0.2415	9	0.975
		Alewife, 1991				
All lengths	Curvature	<0.000	3.48	0.0155	11	0.991
< 8 mm	None	>0.1	2.32	0.1000	9	0.983
> 8 mm	None	>0.1	5.68	0.1599	2	0.883

a. Correlation between studentized residuals and associated normal probability scores.

Table 3-8. Regression models relating sagittal otolith maximum diameter (μm) to standard length (mm) for cultured blueback herring and alewife larvae. The relationship was linearized by natural-logarithm transformation of otolith diameter.

Length Category	df	$t_{0.05}$	Regression Statistics[a]								SD_{reg}	r^2_{adj}	F
			α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
Blueback herring, 1990													
All lengths	24	2.064	13.5	0.083	11.3	16.0	0.16	0.006	0.143	0.167	0.116	0.963	624.17
< 8 mm	4	2.776	6.0	0.360	1.8	13.5	0.30	0.051	0.153	0.437	0.124	0.892	34.01
> 8 mm	19	2.093	15.5	0.108	12.4	19.5	0.15	0.007	0.130	0.160	0.086	0.952	381.94
Blueback herring, 1991													
All lengths	54	2.005	8.4	0.064	7.4	9.5	0.26	0.007	0.241	0.269	0.165	0.966	1529.08
< 8 mm	22	2.074	8.7	0.135	6.6	11.5	0.25	0.024	0.197	0.297	0.127	0.831	108.86
> 8 mm	31	2.040	9.8	0.299	5.3	18.0	0.24	0.025	0.192	0.294	0.186	0.952	93.82
Alewife, 1991													
All lengths	49	2.009	9.4	0.045	8.6	10.3	0.20	0.005	0.192	0.212	0.148	0.973	1787.66
< 8 mm	27	2.052	6.3	0.098	5.1	7.6	0.29	0.020	0.247	0.329	0.128	0.886	211.75
> 8 mm	21	2.080	12.0	0.129	9.1	15.6	0.18	0.010	0.162	0.204	0.117	0.941	337.21

a. Estimates of α and associated 95% confidence intervals were transformed from the natural logarithm scale to the linear scale.

Table 3-9. Diagnostic tests of regression models relating sagittal otolith maximum diameter (μm) to age (days after hatching) of cultured alewife and blueback herring larvae.

Age Range (days)	Burn-Ryan Test		Pure Error F Test			Homogeneity of variances		NPS Correlation[a]
	Symptom	p	F	p	df	F	p	Residuals
			Blueback herring, 1990					
1-16	Curvature Lack of fit	0.033 <0.000	14.43	<0.000	24	2.53	0.067	0.993
5-16	None	>0.1	2.94	0.0741	22	1.84	0.170	0.980
			Blueback herring, 1991					
2-34	Curvature Lack of fit	<0.000 0.040	15.69	<0.000	46	0.51	0.840	0.982
2-17	None	>0.1	0.95	0.6275	28	0.67	0.617	0.888
21-34	None	>0.1	0.48	0.6260	18	0.16	0.922	0.965
			Alewife, 1991					
1-32	Curvature Lack of fit	0.002 0.007	2.68	0.0184	40	1.19	0.328	0.992
1-14	None	>0.1	1.76	0.1836	23	0.80	0.537	0.992
18-32	None	>0.1	0.93	0.4491	17	1.67	0.202	0.976

a. Correlation between studentized residuals and associated normal probability scores.

Table 3-10. Regression models relating sagittal otolith maximum diameter (μm) to age (days after hatching) for cultured blueback herring and alewife larvae. The relationship was linearized using the natural logarithm of otolith diameter.

Age Range (days)	df	$t_{0.05}$	Regression Statistics[a]								SD_{regr}	r^2_{adj}	F
			α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
Blueback herring, 1990													
1-16	28	2.048	21.2	0.045	19.4	23.3	0.14	0.004	0.130	0.146	0.1108	0.976	1151.40
5-16	25	2.060	24.6	0.042	22.6	26.9	0.13	0.004	0.119	0.135	0.0790	0.980	1225.06
Blueback herring, 1991													
2-34	54	2.006	26.5	0.070	23.1	30.5	0.08	0.004	0.067	0.083	0.2928	0.888	428.39
2-17	32	2.038	18.4	0.052	16.5	20.4	0.12	0.005	0.114	0.134	0.1596	0.941	515.66
21-34	21	2.080	82.6	0.207	53.7	127.0	0.03	0.007	0.018	0.048	0.1775	0.473	19.88
Alewife, 1991													
1-32	49	2.012	14.5	0.030	13.7	15.4	0.09	0.002	0.085	0.093	0.1229	0.982	2613.20
1-14	31	2.040	15.5	0.031	14.6	16.5	0.08	0.004	0.070	0.086	0.0991	0.931	776.48
18-32	17	2.110	10.1	0.147	7.4	13.8	0.10	0.006	0.091	0.117	0.1240	0.934	193.37

a. Estimates of α and associated 95% confidence intervals were transformed from the natural logarithm scale to the linear scale.

Table 3-11. Diagnostic tests and summary of regression models relating sagittal otolith maximum diameter (μm) to standard length (mm) by somatic growth rate.

Somatic Growth Rate	Burn-Ryan Test		Pure Error F Test			df	$t_{0.05}$	Regression Statistics				SD_{regr}	r^2_{adj}
	Symptom	p	F	p	df			ß	$SE_ß$	LCL	UCL		
Blueback herring, 1990													
Fast	Curvature	0.024	3.91	0.0973	4	24	2.064	0.155	0.006	0.143	0.167	0.1161	0.963
Fast (excluding yolk-sac larvae)	None	>0.1	1.95	0.2734	4	23	2.069	0.145	0.005	0.135	0.155	0.0838	0.974
Blueback herring, 1991													
Slow	None	>0.1	1.31	0.3637	8	32	2.038	0.234	0.009	0.215	0.253	0.1393	0.955
Fast	None	>0.1	6.11	0.0278	5	21	2.080	0.182	0.027	0.126	0.238	0.1377	0.683
Alewife, 1991													
No overlap of standard lengths of larvae between fast- and slow-somatic growth intervals (see Table 8 for regression statistics).													

Table 3-12. Summary of regression models relating the slope of relationships between otolith growth with standard length ($\mu m \cdot mm^{-1}$) or age ($\mu m \cdot d^{-1}$) to somatic growth ($mm \cdot d^{-1}$) in cultured blueback herring and alewife larvae. Otolith growth rates were estimated as the slope of the natural logarithm of otolith maximum diameter regressed on standard length or age. The size-effect is the slope of otolith size with standard length regressed on somatic growth, and the time-effect is the slope of otolith size with fish age regressed on somatic growth. The time-effect was linearized using the natural logarithm of standard length for linear regression analysis.

df	$t_{0.05}$	Regression Statistics								SD_{regr}	r^2_{adj}	F	p
		α	SE_α	LCL	UCL	β	SE_β	LCL	UCL				
						Size-effect ($\mu m \cdot mm^{-1}/mm \cdot d^{-1}$)							
4	2.776	0.220	0.037	0.117	0.323	-0.053	0.071	-0.250	0.197	0.0427	0.0	0.57	0.505
						Time-effect $\mu m \cdot d^{-1}/ln(mm \cdot d^{-1})$							
4	2.776	0.139	0.005	0.125	0.153	0.037	0.003	0.029	0.045	0.0066	0.972	139.22	0.001

Table 3-13. Regression models relating the number of total increments, increments proximal to the yolk-absorption check, and defined daily increments to true age of cultured alewife and blueback herring larvae.

df	$t_{0.05}$	Regression Statistics								SD_{regr}	r^2_{adj}	F
		α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
						Total increments						
75	2.0	3.63	1.04	1.6	5.7	1.05	0.07	0.91	1.19	5.86	0.767	248.01
						Total increments from yolk-absorption check						
74	2.0	0.72	0.98	-3.3	2.7	1.06	0.06	0.94	1.18	5.49	0.796	289.23
						Estimated daily increments						
77	2.0	0.48	0.59	-0.7	1.7	0.90	0.04	0.82	0.98	3.36	0.884	590.21

Table 3-14. Comparison of otolith diameter, nucleus diameter, and number of daily growth increments between paired left and right sagittae.

Comparison	df	$t_{0.05}$	Left sagitta			Right sagitta			p
			mean	SD	SE	mean	SD	SE	
Otolith diameter	30	-0.08	86.9	73.5	13.2	88.5	75.7	13.6	0.93
Nucleus diameter	30	-0.06	19.1	11.5	2.1	19.2	11.4	2.1	0.95
Increment count	30	0.40	12.8	11.4	2.0	11.8	9.5	1.7	0.69

Table 3-15. Percent agreement between growth increment enumerations for sagittae from cultured blueback herring and alewife larvae.

Group	Percent Agreement following:											
	2nd reading						3rd reading					
	Accept		Reject		No count		Accept		Reject		No count	
	Total	Pct.	Total	Pct.	Total	Pct.	Total	Pct.	Total	Pct.	Total	Pct.
All groups	110	76.9	30	21.0	3	2.1	131	91.6	10	7.0	2	1.4
Blueback 1990	22	73.3	8	26.7	0	-	26	89.7	4	10.3	0	-
Blueback 1991	47	79.6	10	17.0	2	3.4	56	94.9	1	1.7	2	3.4
Alewife	41	75.9	12	22.2	1	1.9	49	96.1	5	3.9	0	-

Table 3-16A. Measures of precision for growth increment enumerations for sagittae from blueback herring larvae reared in 1990.

Age (days)	Average Percent Error	Coefficient of Variation	Index of Precision
1	0.333	0.500	0.354
5	0.025	0.037	0.027
8	0.048	0.072	0.051
11	0.023	0.034	0.024
16	0.023	0.042	0.030
1-16	0.063	0.097	0.068
5-16	0.028	0.044	0.031

Table 3-16B. Measures of precision for growth increment enumerations for sagittae from blueback herring larvae reared in 1991.

Age (days)	Average Percent Error	Coefficient of Variation	Index of Precision
2	0.114	0.212	0.150
5	0.054	0.082	0.058
8	0.065	0.122	0.086
13	0.027	0.041	0.029
17	0.030	0.057	0.040
21	0.038	0.067	0.048
24	0.015	0.027	0.019
29	0.015	0.022	0.016
34	0.011	0.017	0.012
2-34	0.050	0.081	0.057
5-34	0.035	0.059	0.041

Table 3-16C. Measures of precision for growth increment enumerations for sagittae from alewife larvae reared in 1991.

Age (days)	Average Percent Error	Coefficient of Variation	Index of Precision
1	0.333	0.500	0.354
4	0.722	1.083	0.766
8	0.085	0.142	0.100
12	0.043	0.065	0.046
14	0.026	0.040	0.028
18	0.015	0.022	0.015
21	0.014	0.021	0.015
24	0.034	0.064	0.045
27	0.023	0.040	0.028
32	0.146	0.223	0.158
1-32	0.175	0.266	0.188
4-32	0.139	0.213	0.151

Table 3-17. Diagnostic tests for ordinary least-squares regression models relating daily growth-increment number to true age for blueback herring larvae reared in 1990.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	p	F	p	df	F	p	Number	Residuals
1-16	26	Curvature Lack of fit	0.084 0.070	2.48	0.090	21	1.08	0.390	0.985	0.971
5-16	23	Lack of fit	0.082	3.24	0.062	19	0.94	0.441	0.978	0.975
8-16	17	Curvature Lack of fit	0.019 0.019	5.04	0.042	14	1.01	0.389	0.978	0.965
1-11	19	None	>0.1	3.14	0.073	15	0.51	0.682	0.982	0.881
1-16 (no age 11 d)	20	Lack of fit	0.040	0.15	0.859	16	1.42	0.273	0.974	0.910

a. Correlation between increment number or studentized residuals with associated normal probability scores.

Table 3-18. Diagnostic tests for ordinary least-squares regression models relating daily growth-increment number to true age for blueback herring larvae in 1991.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	p	F	p	df	F	p	Counts	Residuals
2-34	56	None	>0.1	1.47	0.202	47	0.58	0.790	0.969	0.983
5-34	48	None	>0.1	1.25	0.303	40	0.44	0.871	0.978	0.987
8-34	40	None	>0.1	1.87	0.126	33	0.17	0.984	0.980	0.990
2-17	34	None	>0.1	0.43	0.734	29	1.29	0.296	0.977	0.945
21-34	22	None	>0.1	1.51	0.248	18	0.02	0.996	0.964	0.983

a. Correlation between increment number or studentized residuals and associated normal probability scores.

Table 3-19. Diagnostic tests for ordinary least-squares regression models relating daily growth-increment number to true age for alewife larvae in 1991.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	p	F	p	df	F	p	Number	Residuals
1-32	49	Curvature Lack of fit	0.075 <0.000	1.91	0.087	39	2.9	0.010	0.970	0.949
4-32	40	Lack of fit	0.002	1.18	0.342	31	2.1	0.072	0.981	0.946
8-32	34	Lack of fit	0.066	1.15	0.363	26	1.5	0.201	0.978	0.973
1-18	31	Curvature	0.025	6.43	0.001	25	3.0	0.030	0.949	0.978
21-32	18	None	>0.1	0.25	0.785	14	0.6	0.627	0.954	0.988

a. Correlation between increment number or studentized residuals and associated normal probability scores.

Table 3-20. Diagnostic tests for ordinary least-squares regression models relating daily growth-increment number to true age for pooled alewife and blueback herring larvae reared in 1991.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	Overall p	F	p	df	F	p	Number	Residuals
1-34	105	Curvature	0.037	3.50	0.0001	89	2.45	0.005	0.976	0.988
		Lack of fit	0.090							
4-34	87	Curvature	0.002	2.78	0.303	73	0.44	0.871	0.978	0.987
		Lack of fit	0.080							
8-34	74	Curvature	0.018	2.57	0.012	62	1.70	0.095	0.982	0.981

a. Correlation between increment number or studentized residuals and associated normal probability scores.

Table 3-21. Diagnostic tests for weighted ($(age^2)^{-1}$) least-squares regression models relating daily growth-increment number to true age for blueback herring larvae reared in 1990.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	Overall p	F	p	df	F	p	Number	Residuals
1-16	26	None	>0.1	1.84	0.170	21	1.08	0.39	0.720	0.967
5-16	23	None	>0.1	2.92	0.078	19	0.94	0.441	0.938	0.944
8-16	17	Curvature Lack of fit	0.010 0.001	8.81	0.010	14	1.01	0.389	0.968	0.941
1-11	19	None	>0.1	1.82	0.196	15	0.51	0.682	0.729	0.968
1-16 (no age 11 d)	20	None	>0.1	0.47	0.636	16	1.42	0.273	0.802	0.935

a. Correlation between increment number or studentized residuals and associated normal probability scores.

Table 3-22. Diagnostic tests for weighted ($(age^2)^{-1}$) least-squares regression models relating daily growth-increment number to true age for blueback herring larvae reared in 1991.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[c]	
		Symptom	Overall p	F	p	df	F	p	Number	Residuals
2-34	56	None	>0.1	0.27	0.962	47	0.58	0.790	0.791	0.898
5-34	48	None	>0.1	0.12	0.994	40	0.44	0.871	0.875	0.838
8-34	40	None	>0.1	0.65	0.664	33	0.17	0.984	0.909	0.942
13-34	30	None	>0.1	1.88	0.144	26	0.19	0.965	0.943	0.986
2-17	34	None	>0.1	0.20	0.897	29	1.29	0.296	0.868	0.946
21-34	22	None	>0.1	1.88	0.181	18	0.02	0.996	0.965	0.992

a. Correlation between increment number or studentized residuals and associated normal probability scores.

Table 3-23. Diagnostic tests for weighted $((age^2)^{-1})$ least-squares regression models relating daily growth-increment number to true age for alewife larvae reared in 1991.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	Overall p	F	p	df	F	p	Count	Residuals
1-32	49	Curvature Lack of fit	0.009 <0.000	6.21	<0.000	39	2.9	0.01	0.659	0.988
4-32	40	None	>0.1	1.10	0.386	31	2.1	0.072	0.937	0.993
8-32	34	None	>0.1	1.22	0.327	26	1.5	0.201	0.937	0.991
1-18	31	Curvature Lack of fit	<0.000 <0.000	7.47	0.004	25	3.0	0.030	0.740	0.992
21-32	18	None	>0.1	0.26	0.771	14	0.6	0.627	0.988	0.981

a. Correlation between increment number or studentized residuals and associated normal probability scores.

Table 3-24. Diagnostic tests for weighted ($(age^2)^{-1}$) least-squares regression models relating daily growth-increment number to true age for pooled alewife and blueback herring larvae reared in 1991.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	Overall p	F	p	df	F	p	Number	Residuals
1-34	105	Lack of fit	0.001	9.65	<0.000	89	2.45	0.005	0.747	0.943
4-34	87	None	>0.1	3.59	<0.000	73	1.81	0.057	0.825	0.965
8-34	74	None	>0.1	1.56	0.139	62	1.70	0.095	0.898	0.982

a. Correlation between increment number or studentized residuals and associated normal probability scores.

Table 3-25. Weighted least-squares regression models relating daily growth-increment number to true age (days after hatching) for cultured blueback herring and alewife larvae. Estimated growth increment deposition rates are indicated as non-daily (*; UCL<0.95, 1.05<LCL), marginally non-daily (M; 0.95≤UCL<1.00, 1.00<LCL≤1.05), or daily (D; LCL≤1.00≤UCL).

Age	df	$t_{0.05}$	Regression Statistics								F	p	Rate
			α	SE_α	LCL	UCL	β	SD_β	LCL	UCL			
Blueback herring, 1990													
1-16	25	2.060	-0.34	0.164	-0.68	0.00	1.18	0.059	1.06	1.30	399.76	<0.000	*
5-16	22	2.074	-0.14	0.931	-2.08	1.80	1.16	0.120	0.91	1.41	93.88	<0.000	D
1-11	18	2.101	-0.41	0.179	-0.79	-0.03	1.23	0.075	1.07	1.39	268.83	<0.000	*
Blueback herring, 1991													
2-34	55	2.005	1.11	0.233	0.64	1.58	0.84	0.050	0.74	0.94	288.18	<0.000	*
5-34	47	2.012	0.35	0.533	-0.72	1.42	0.90	0.056	0.79	1.01	261.06	<0.000	D
8-34	39	2.022	0.22	0.486	-0.76	1.20	0.91	0.035	0.84	0.98	682.80	<0.000	M
2-18	33	2.036	1.23	0.357	0.50	1.96	0.80	0.097	0.60	1.00	68.25	<0.000	D
21-34	21	2.080	-3.67	2.058	-7.96	0.62	1.05	0.079	0.89	1.21	177.57	<0.000	D
Alewife, 1991													
1-32	48	2.013	-0.59	0.093	-0.78	-0.40	0.69	0.041	0.61	0.77	284.46	<0.000	*
4-32	39	2.025	-3.00	0.310	-3.63	-2.37	0.90	0.036	0.83	0.97	610.34	<0.000	M
8-32	33	2.038	-2.85	0.784	-4.45	-1.25	0.89	0.057	0.77	1.01	247.63	<0.000	D
1-18	30	2.042	-1.32	0.386	-2.11	-0.53	0.77	0.042	0.68	0.86	329.30	<0.000	*
21-32	17	2.120	-12.98	5.962	-25.6	-0.34	1.29	0.243	0.78	1.81	28.28	<0.000	D
Pooled 1991 groups													
8-34	72	1.996	-1.19	0.597	-2.38	0.00	0.90	0.043	0.81	0.99	438.5	<0.000	M

Table 3-26. Summary of selected otolith daily growth-increment validation studies for clupeid larvae.

Species	Source	Validation Method	Start of Increment deposition
Atlantic herring	Geffen, 1982	Laboratory-reared larvae.	Nucleus check present at complete yolk absorption.
Atlantic herring	Messieh et al., 1987	Lab-reared and field-collected larvae. Growth rates estimated from growth-increment derived age estimates.	At complete yolk absorption (age 15 to 17 d).
Atlantic herring	Lough et al., 1982	Lab-reared and field-collected larvae.	0 to 9 days after hatching.
Pacific herring	McGurk 1984	Field-collected larvae.	At complete yolk absorption (age 6 d).
Gulf menhaden	Deegan and Thompson, 1987[a]	Field-collected larvae and juveniles	At complete yolk absorption (age 5 d).
Atlantic menhaden	Simoneaux and Warlen, 1987	Laboratory- and enclosure-reared wild larvae, OTC[b] marked.	Not Determined
Gizzard shad	Davis et al., 1985	Larvae reared in outdoor tank.	At swim-up, i.e. first-feeding (age 3 days).
Sprat	Alshuth, 1988	Laboratory-reared larvae hatched from artificially-spawned and field-collected eggs.	Prior to complete yolk absorption (age 6 d).
Japanese sardine	Hayashi et al., 1989	Laboratory-reared larvae hatched from field-collected eggs.	At first feeding (age 2 - 3 d).
Herklotsichthys castelnaui	Thorrold, 1988	Wild larvae. OTC-marked larvae reared in laboratory.	Not validated. Assumed to occur at hatching.
American shad	Savoy and Crecco, 1987	Lab-reared larvae from artificially-spawned eggs, reared at two water temperatures.	Age 0 to 1 day at 18 °C, age 2 days at 15 °C.
Alewife/Blueback Herring	Sismour and Loesch (this study).	Larvae reared from artificially-spawned eggs in outdoor tanks.	For larvae ≥ 4 d: 1990 blueback: 0.1 d (95% CI: -1.6 to 1.8 d) 1991 blueback: -0.4 d (95% CI: -1.6 to 0.8 d) 1991 alewife: 3.0 d (95% CI: 2.6 to 4.0 d) Pooled 1991 groups: 1.2 d (95% CI: 0.0 to 2.6 d)

a. Based on information provided to Deegan and Thompson (1987) by S. Warlen.
b. Oxytetracycline.

Table 3-26 (continued).

Species	Nucleus	Intranuclear rings[d]	Increment deposition rate
Atlantic herring	Radius at hatching: 9.0-10.8 μm (diameter: 18.0-21.6 μm)	Not Reported	0.34 to 0.92 rings·d^{-1}
Atlantic herring	Diameter: 20.3 ± 1.3 μm	1 to 5	Similar growth rates of lab-reared and wild larvae lead to conclusion of daily increment deposition.
Atlantic herring	Average diameter: 22.5 μm.	None	Non-daily to third increment, daily thereafter.
Pacific herring	Not Reported	Present, 5.2 ± 0.8 rings at age 1 d	-0.05 to 0.96 rings·d^{-1}
Gulf menhaden	Not Reported	Not Reported	Daily (validated up to 190 days after hatching).
Atlantic menhaden	Not Determined	Present	Lab: 0.97 rings·d^{-1} Field: 0.96 rings·d^{-1}
Gizzard shad	Not Reported	Present	0.99 rings·d^{-1}. Daily deposition on average, large individual variation.
Sprat	Not Reported	Not Reported	Daily.
Japanese sardine	Radius of first ring = 6 μm	Not Reported	0.99 ring·d^{-1}.
Herklotsichthys castelnaui	Not Determined	Not Reported	Daily in OTC-marked larvae.
American shad	Not Reported	Not Reported	Daily at 18 °C, subdaily at 15 °C due to underageing of older larvae.
Alewife, Blueback Herring	Diameter: 18.3 ± 1.7 μm	0 to 4	For larvae ≥ age 4 d: Blueback herring (1990), 1.16 rings·d^{-1} Blueback herring (1991), 0.90 rings·d^{-1} Alewife (1991), 0.90 rings·d^{-1}

c. Increments medial to the nucleus edge; Geffen (1982) refers to these as yolk-sac rings.

Figure 3-1. Relationship of standard length (mm) to age (days after hatching) for younger (<age 18 d) and older (≥age 18 d) cultured blueback herring (A and B) and alewife (C) larvae. Two regression lines are shown for young 1991 blueback herring larvae, one (dashed) includes and the other (solid) excludes yolk-sac larvae. The regression model excluding yolk-sac larvae was used to estimate somatic growth of young 1991 blueback herring larvae. Standard length-age relationships for the three culture groups are compared in plate D.

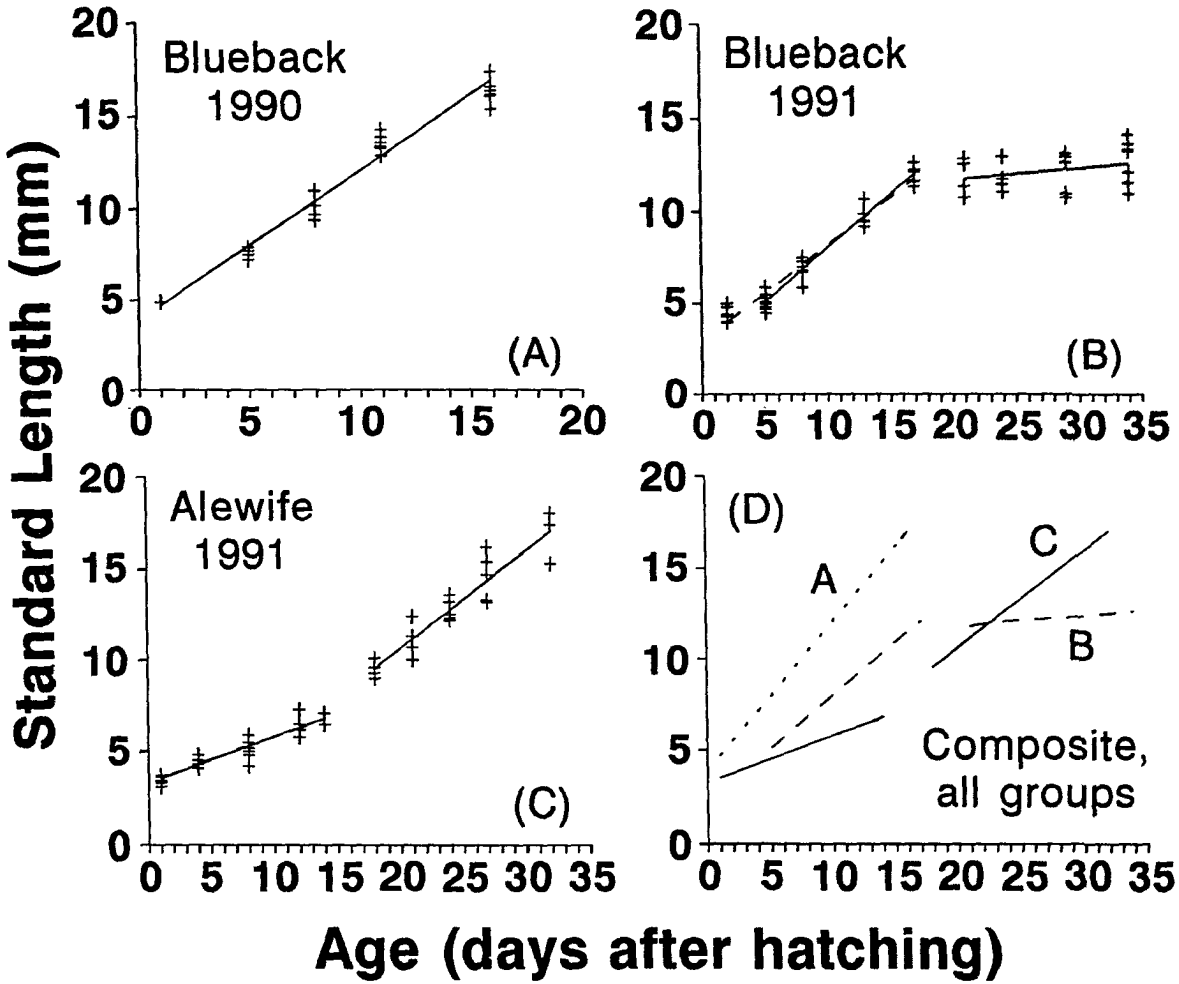


Figure 3-2. Studentized residual error distributions for linear regression models relating standard length (mm) to age (days after hatching) for blueback herring larvae reared in 1990 including (A) and excluding (B) a single age 1 d yolk-sac larva. Exclusion of the yolk-sac larva did not affect the studentized residual error distribution.

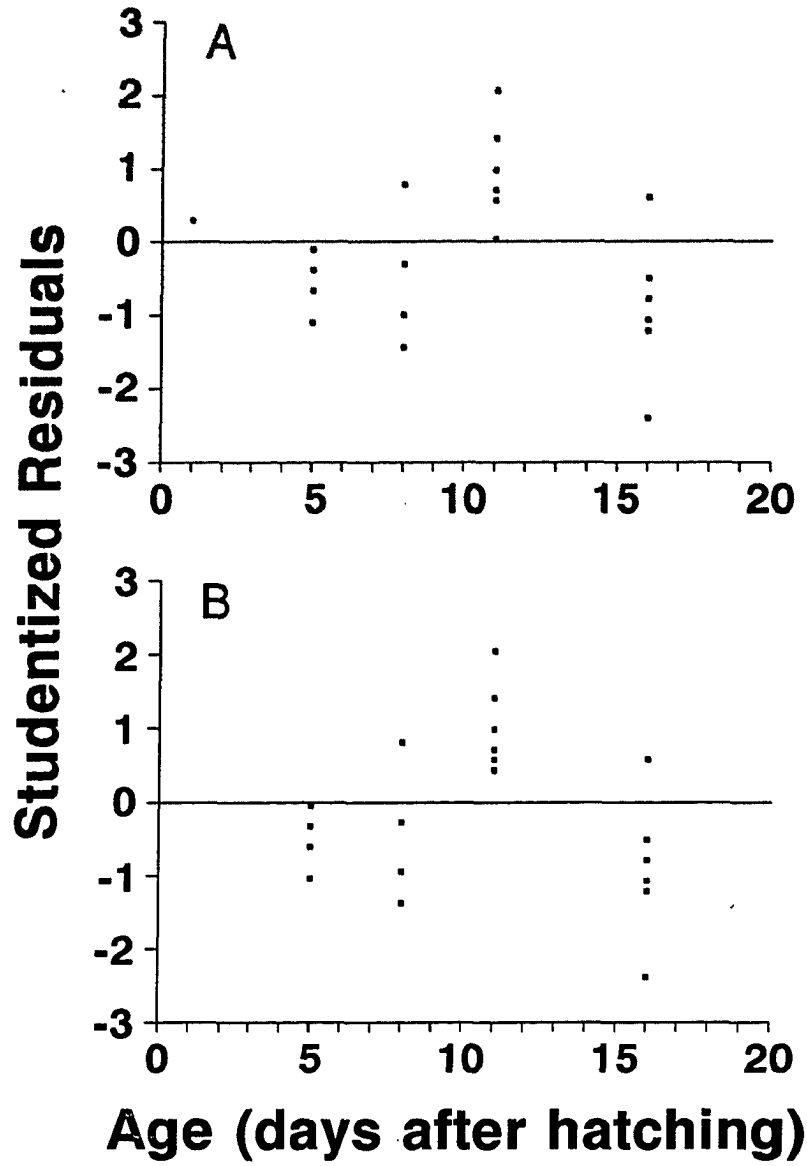


Figure 3-3. Studentized residual error distributions for linear regression models relating standard length (mm) to age (days after hatching) for blueback herring larvae reared in 1991: A) age 2 to 17 d larvae, B) age 5 to 17 d larvae, and C) age 21 to 34 d larvae. Excluding yolk-sac larvae improved the studentized residual error distribution for younger larvae.

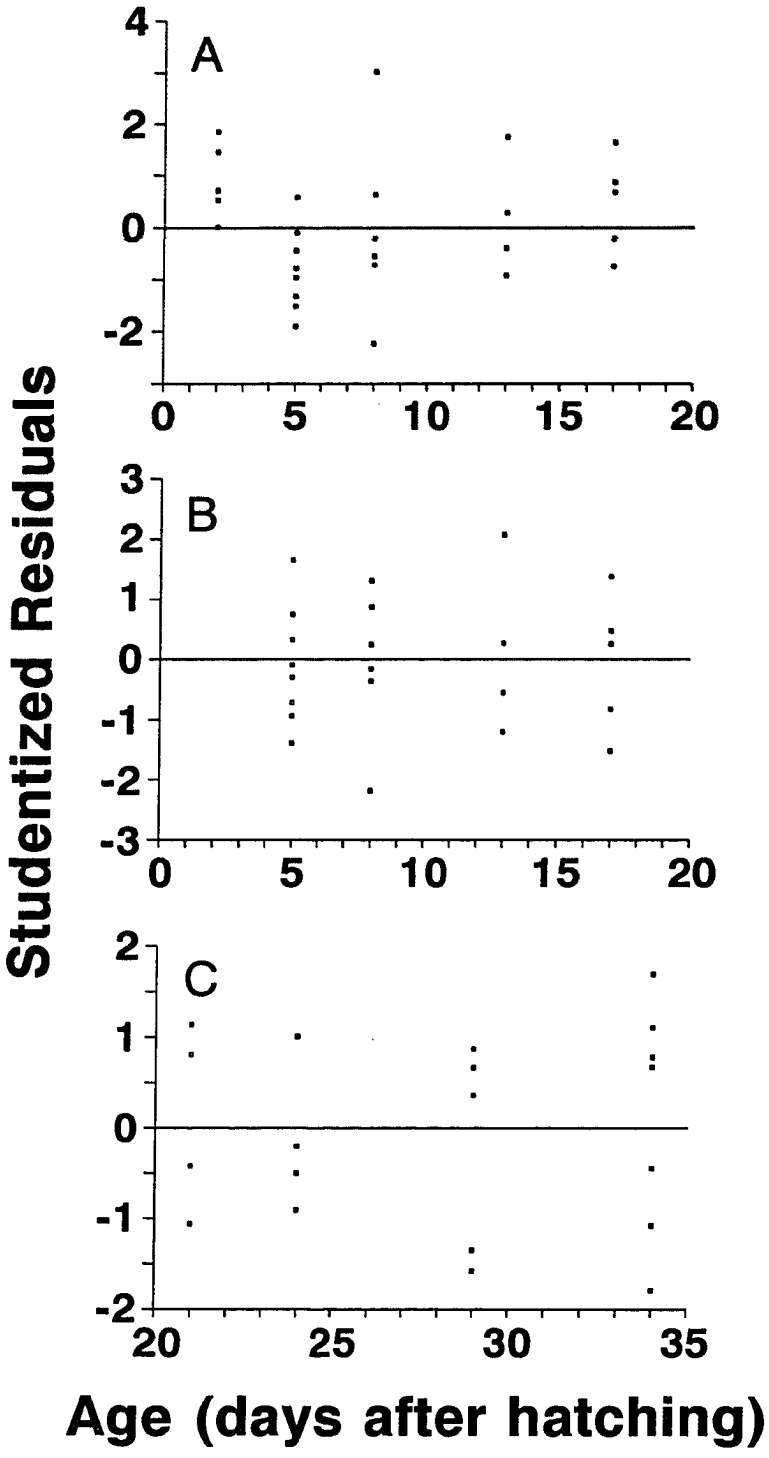


Figure 3-4. Studentized residual error distributions for linear regression models relating standard length (mm) to age (days after hatching) for alewife larvae reared in 1991: A) age 1 to 14 d larvae, B) age 4 to 14 d larvae, and C) age 18 to 32 d larvae. Excluding yolk-sac larvae did not affect the studentized residual error distribution for younger larvae.

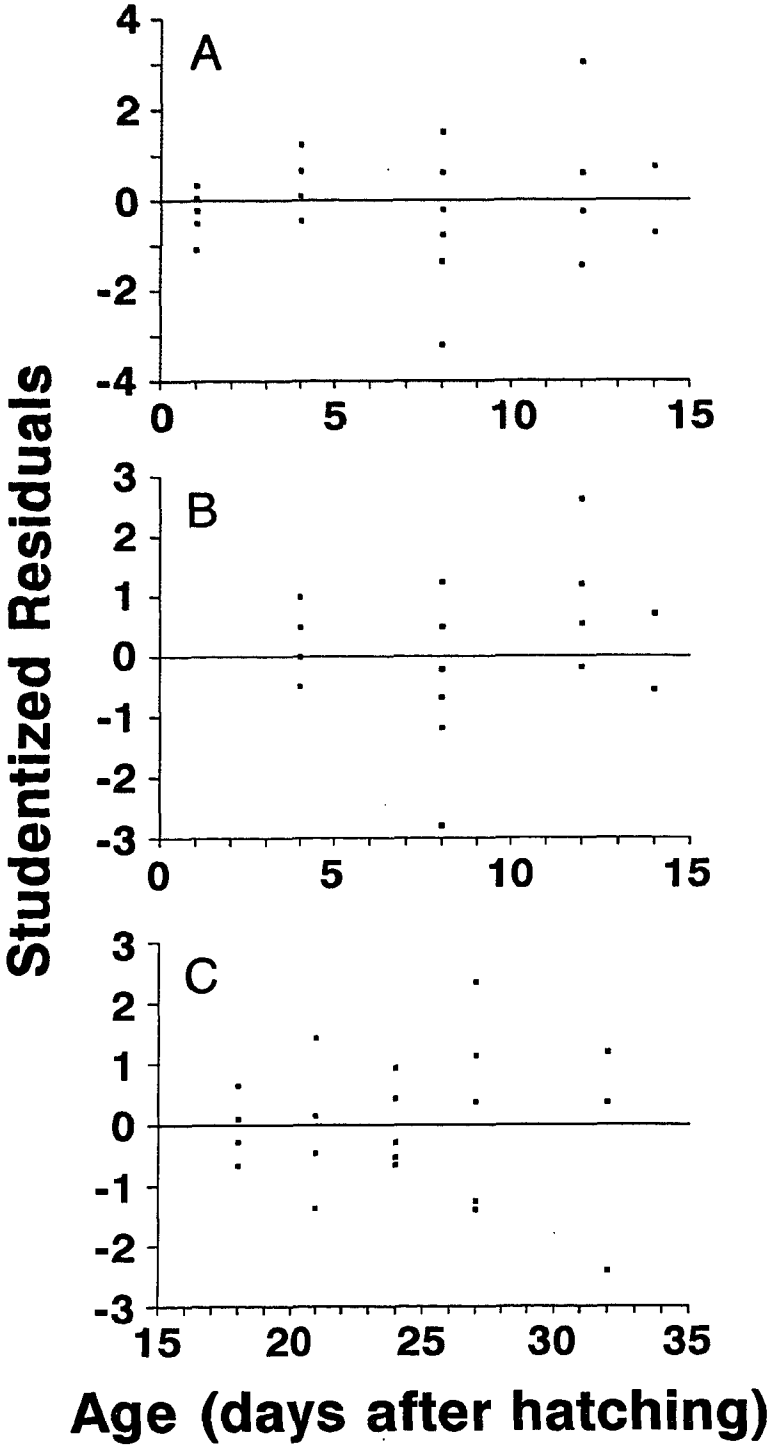


Figure 3-5. Relationship between sagittal otolith maximum diameter (μm) and standard length (mm) for cultured blueback herring (A and B) and alewife (C) larvae. The otolith diameter-standard length relationships for the three culture groups are compared in plate D.

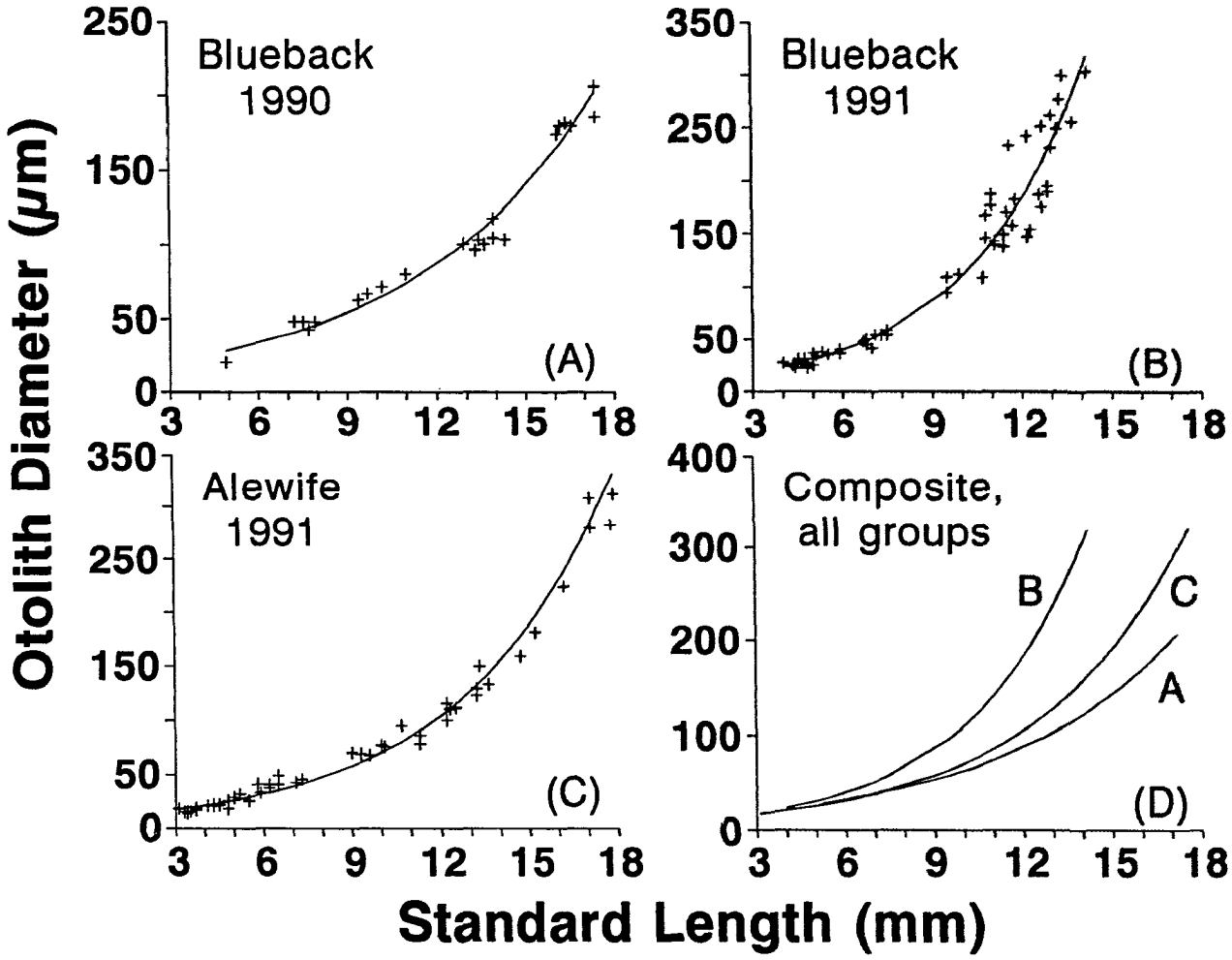


Figure 3-6. Relationship between sagittal otolith natural logarithm-transformed maximum diameter (μm) and standard length (mm) for cultured blueback herring (A and B) and alewife (C) larvae. Otolith diameter was transformed to linearize the relationship (Fig. 3-5). Linear regression models were best fit to larvae less than 8 mm SL and greater than 8 mm SL. The linearized otolith diameter-standard length relationships for the three culture groups are compared in plate D.

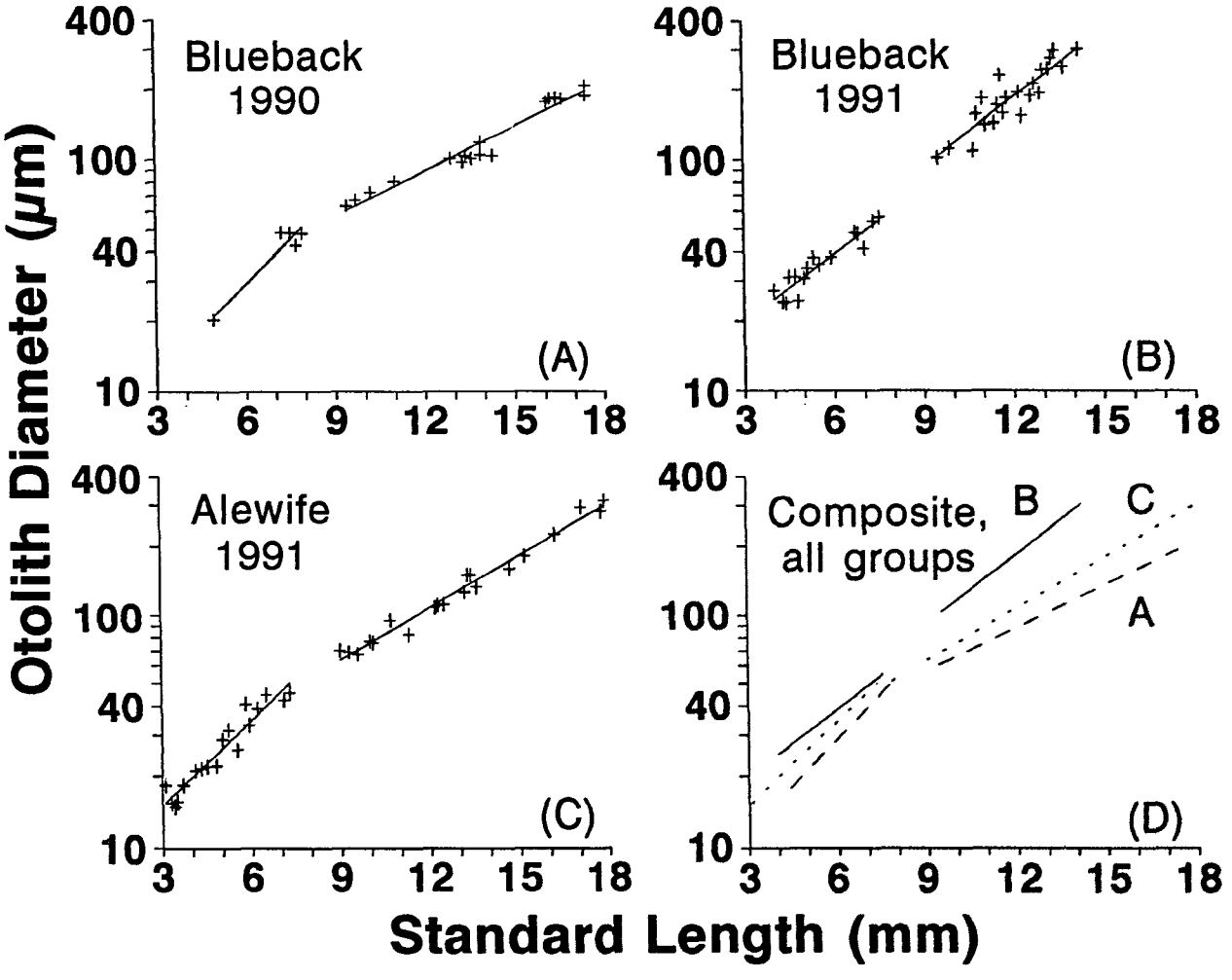


Figure 3-7. Relationship between sagittal otolith maximum diameter (μm) and age (days after hatching) for cultured blueback herring (A and B) and alewife (C) larvae. The otolith diameter-age relationships for the three culture groups are compared in plate D.

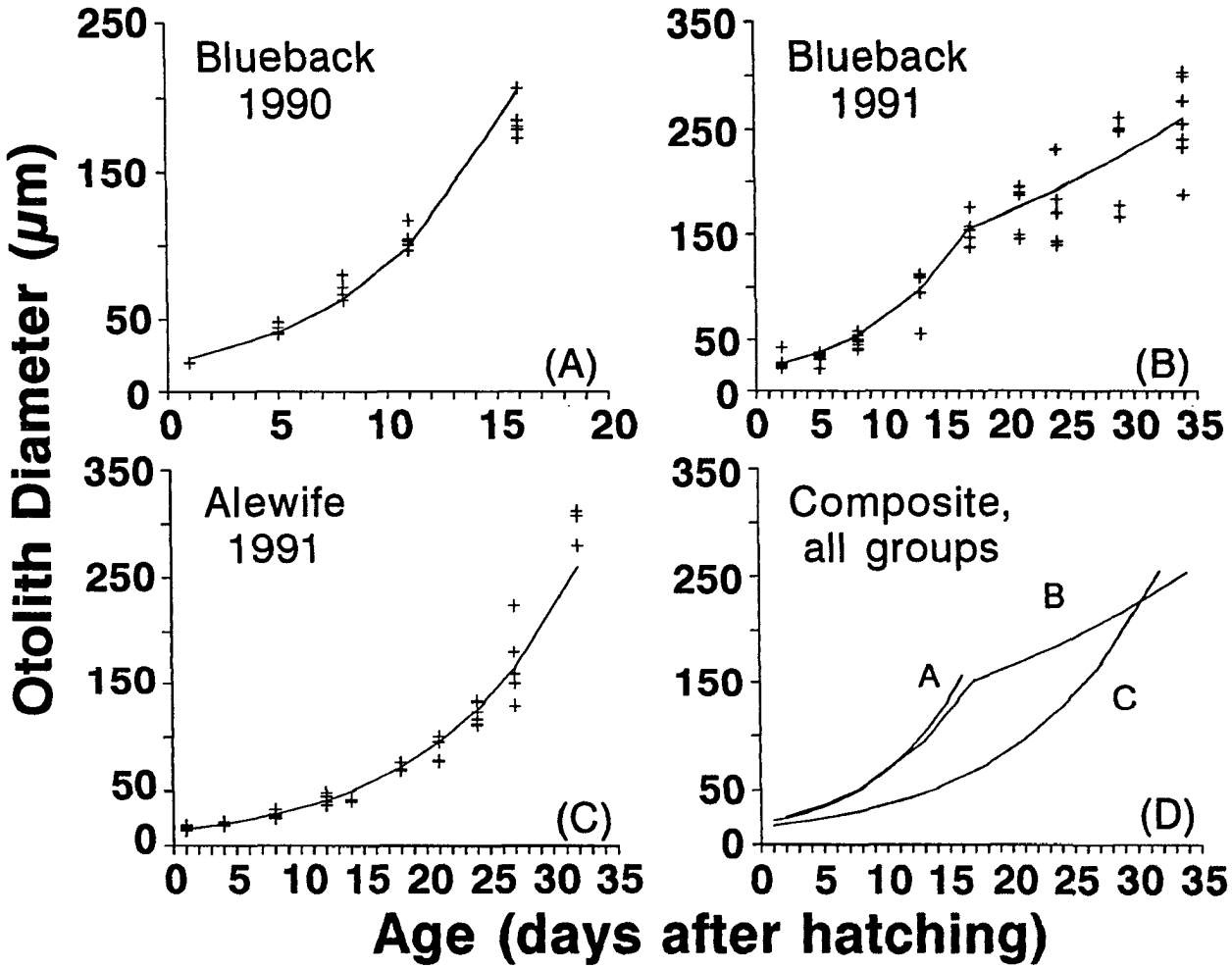


Figure 3-8. Relationship between sagittal otolith natural logarithm-transformed maximum diameter (μm) and age (days after hatching) for cultured blueback herring (A and B) and alewife (C) larvae. Otolith diameter was transformed to linearize the relationship (Fig. 3-7). Linear regression models were best fit to larvae younger than age 18 d and those age 18+ d. The linearized otolith diameter-age relationships for the three culture groups are compared in plate D.

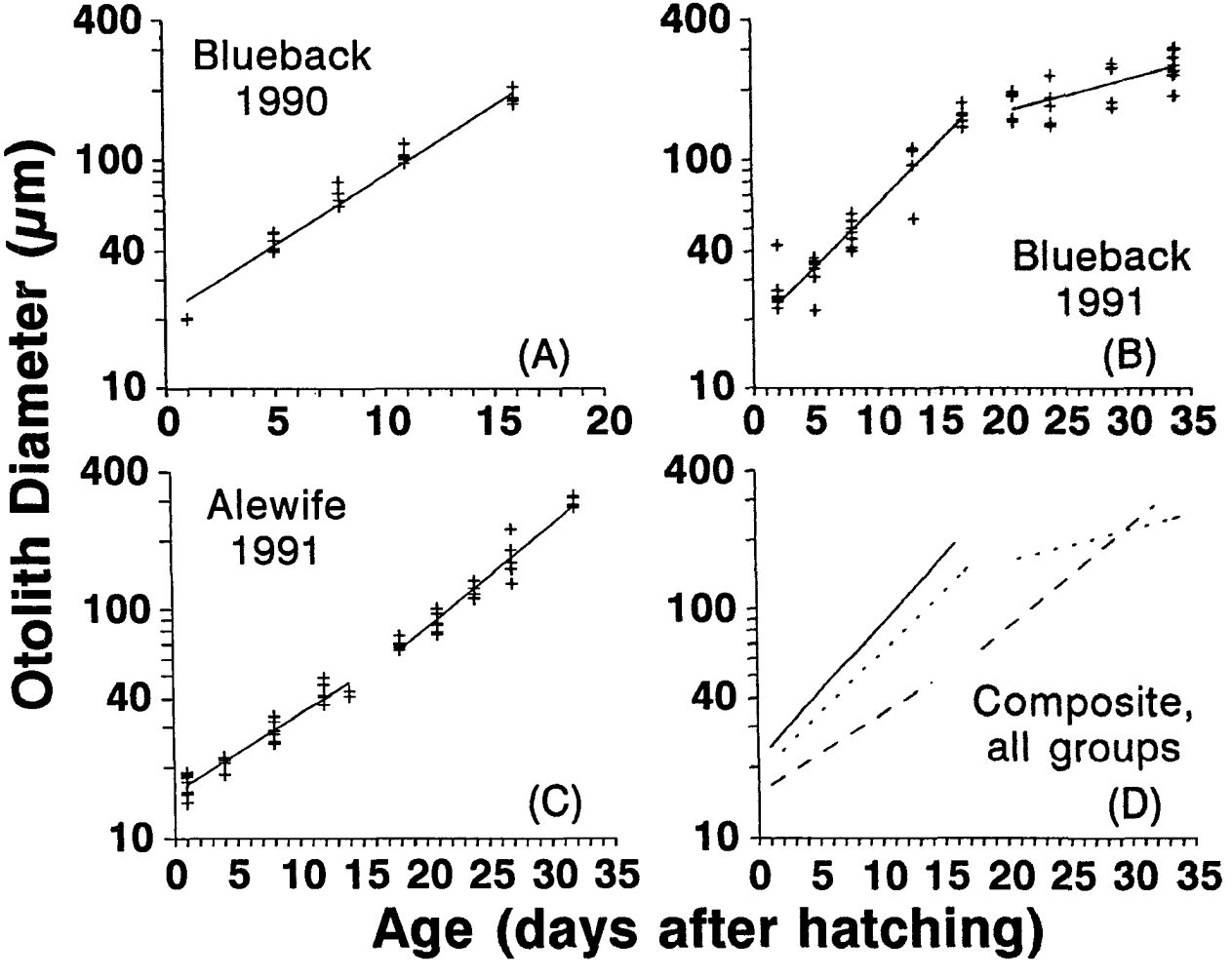


Figure 3-9. Relationship between otolith growth and somatic growth for cultured blueback herring and alewife larvae. Slopes of regression models for otolith size-standard length ($\mu m \cdot mm^{-1}$) and otolith size-age ($\mu m \cdot d^{-1}$) relationships for fast- and slow-somatic growth periods are plotted against respective somatic growth rates. Dashed lines show the increase in the slope of the otolith size-age relationship relative to somatic growth rate per 0.1 unit increase in somatic growth.

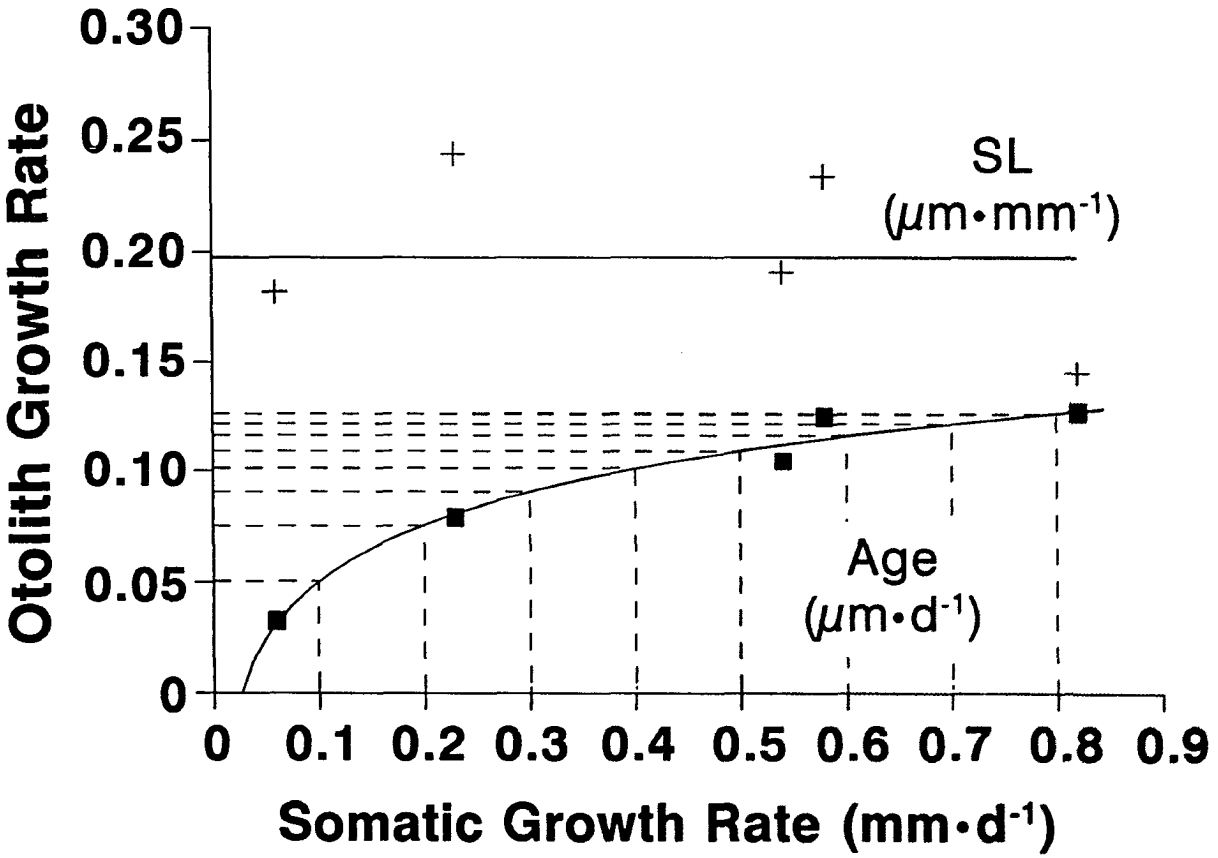


Figure 3-10. Photomicrographs of sagittae from 1990-blueback herring larvae (A and B), 1991-blueback herring larvae (C and D), and 1991-alewife larvae (E and F) showing hatch checks (H), yolk-absorption checks (Y), the first clearly-resolved discontinuity proximal to poorly-resolved zones (I), and otolith edges (II). Solid lines (B, D, and F) show discontinuous zones delimiting daily growth increments. Dotted lines (D and F) show discontinuities in the poorly-resolved zone. Dashed lines (B and F) show subdaily increments. The 1990-blueback herring otolith was dissected from an age 16 d, 17.2 mm SL larva and had a 180.4-μm maximum diameter with an 18.9 μm yolk-absorption check diameter. The 1991-blueback herring otolith was dissected from an age 29 d, 10.8 mm larva and had a 169.9-μm maximum diameter with an 18.9-μm yolk-absorption check diameter. The 1991-alewife otolith was dissected from an age 32 d, 15.2 mm SL larva and had a 149.0-μm maximum diameter with a 16.9-μm yolk-absorption check diameter.

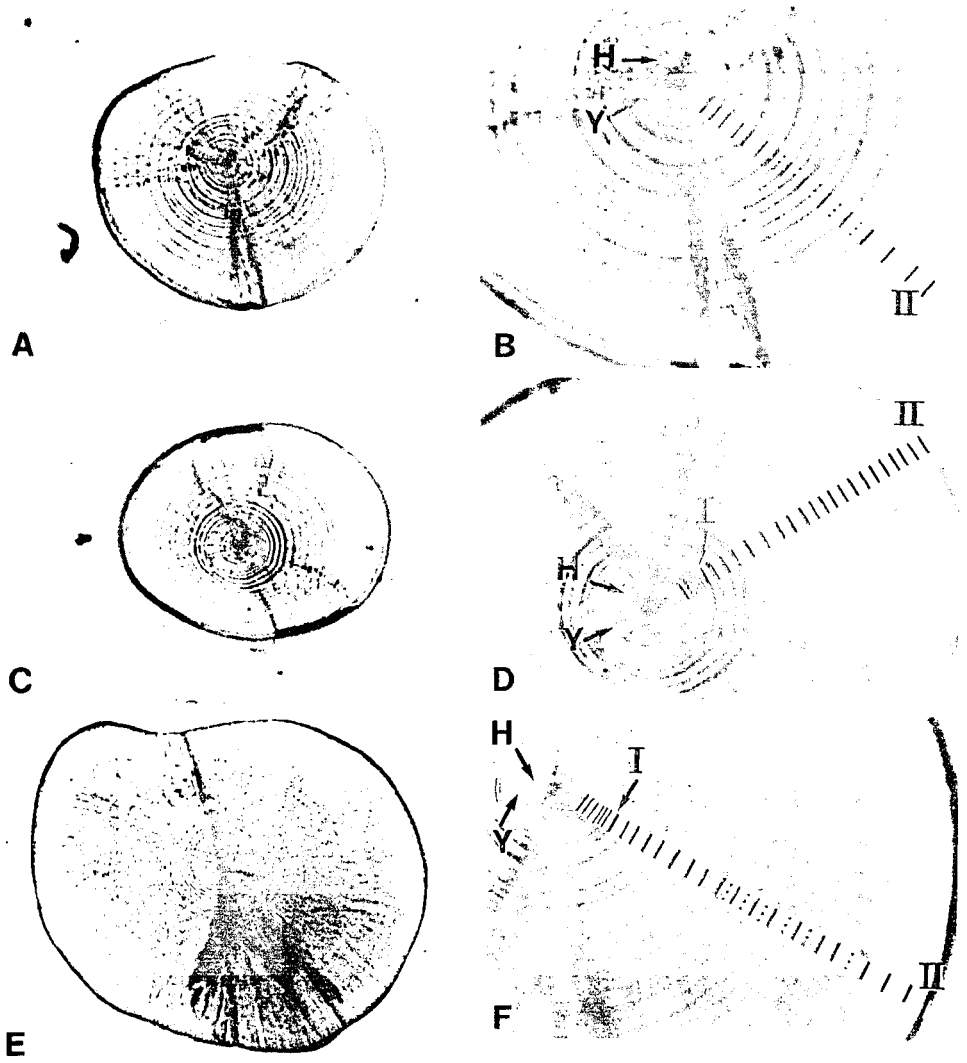


Figure 3-11. Relationship between yolk-absorption check diameter and standard length for cultured blueback herring (A and B) and alewife (C) larvae. Otolith diameters for yolk-sac larvae prior to formation of the yolk-absorption check (x) are also shown. Yolk-absorption check diameters are compared in plate D, excluding yolk-sac larvae, showing the mean yolk-absorption check diameter (center solid line) and the upper (UCL) and lower (LCL) 95% confidence limits.

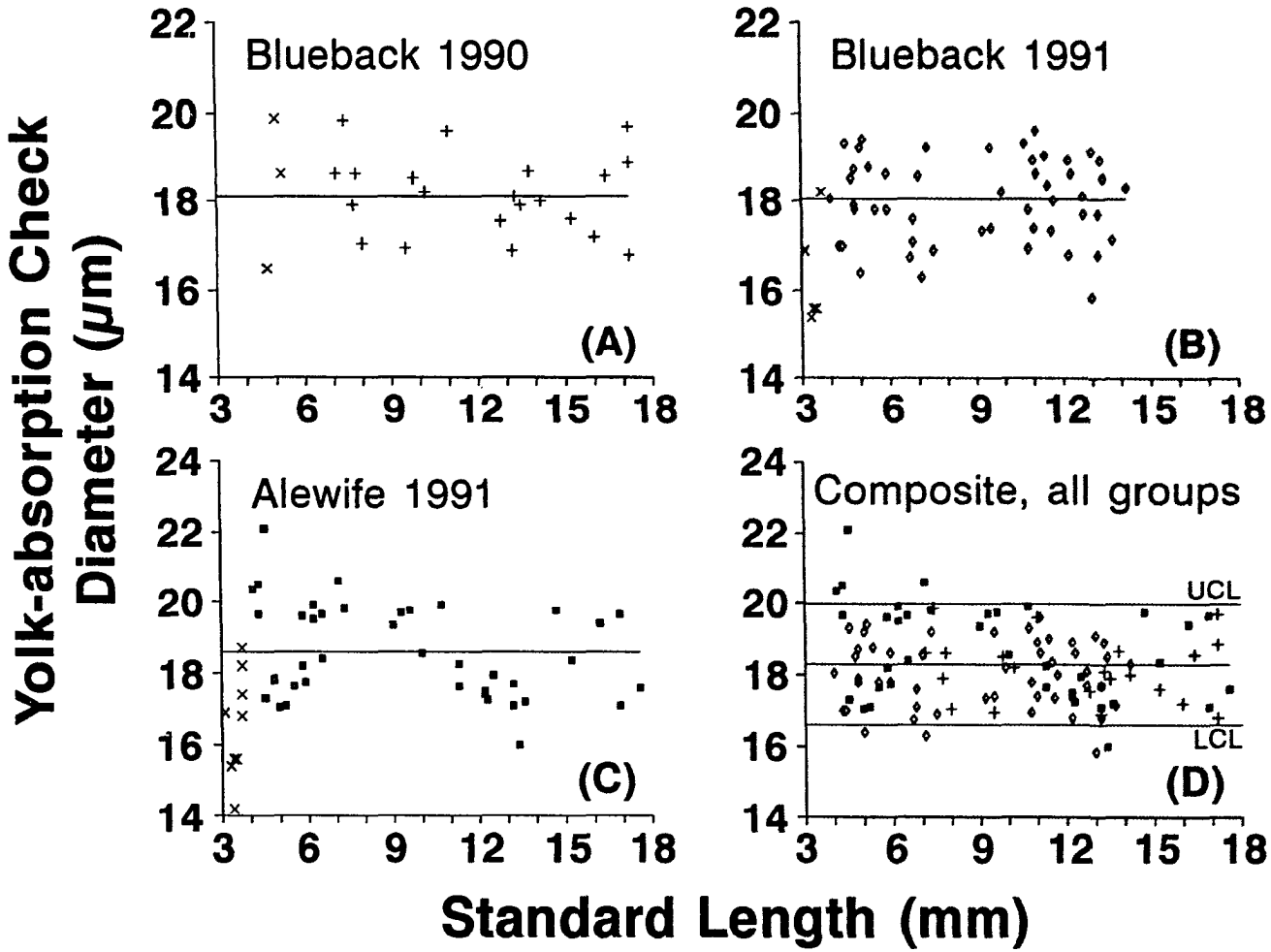


Figure 3-12. Retrospective growth curves showing the increase in radius associated with discontinuous zones delimiting daily (1°) and subdaily (2°) increments for otoliths shown in Figure 3-10: 1991 blueback herring larva (A), 1990 blueback herring larva (B), and 1991 alewife larva (C). Annotations are defined for Figure 3-10.

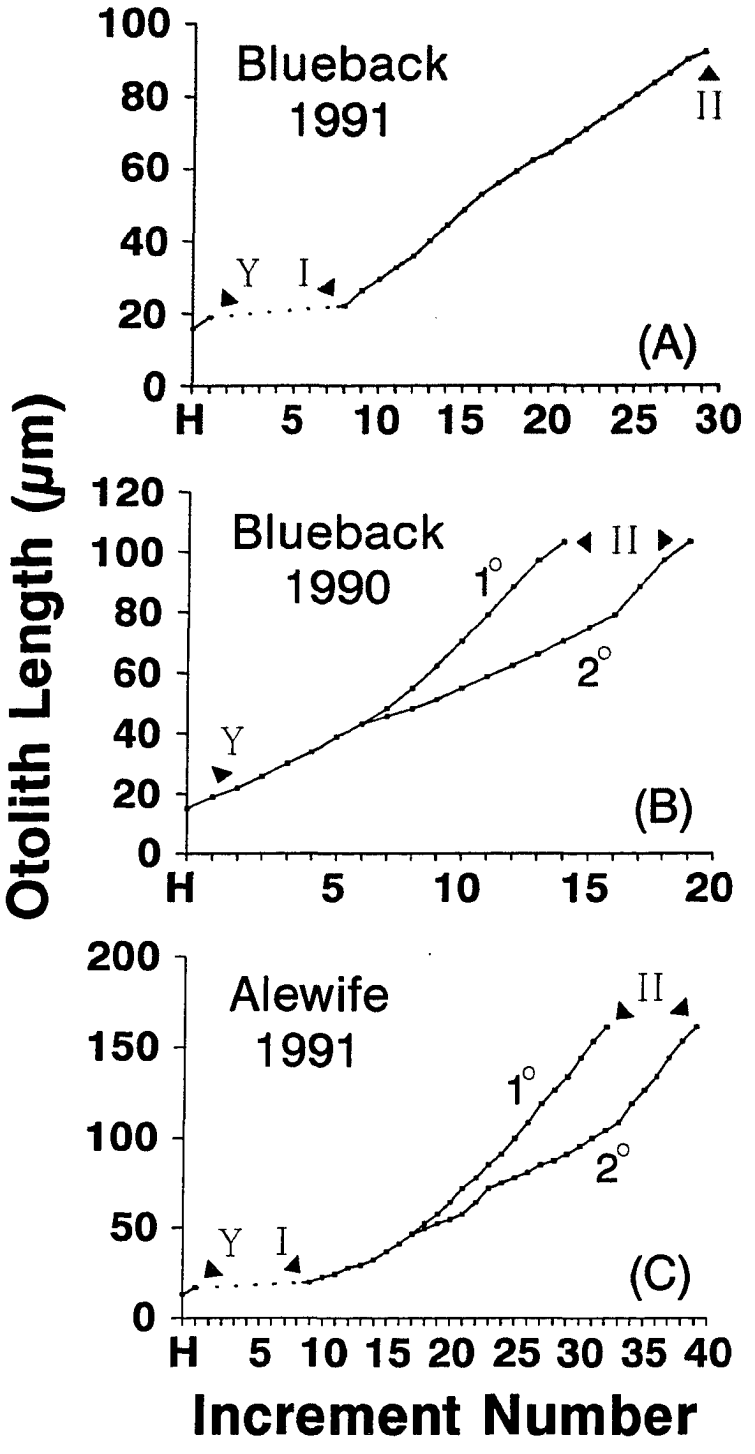


Figure 3-13. Studentized residual error distributions for ordinary least-squares regression models relating daily growth-increment number to age of cultured blueback herring (A and B) and alewife (C) larvae.

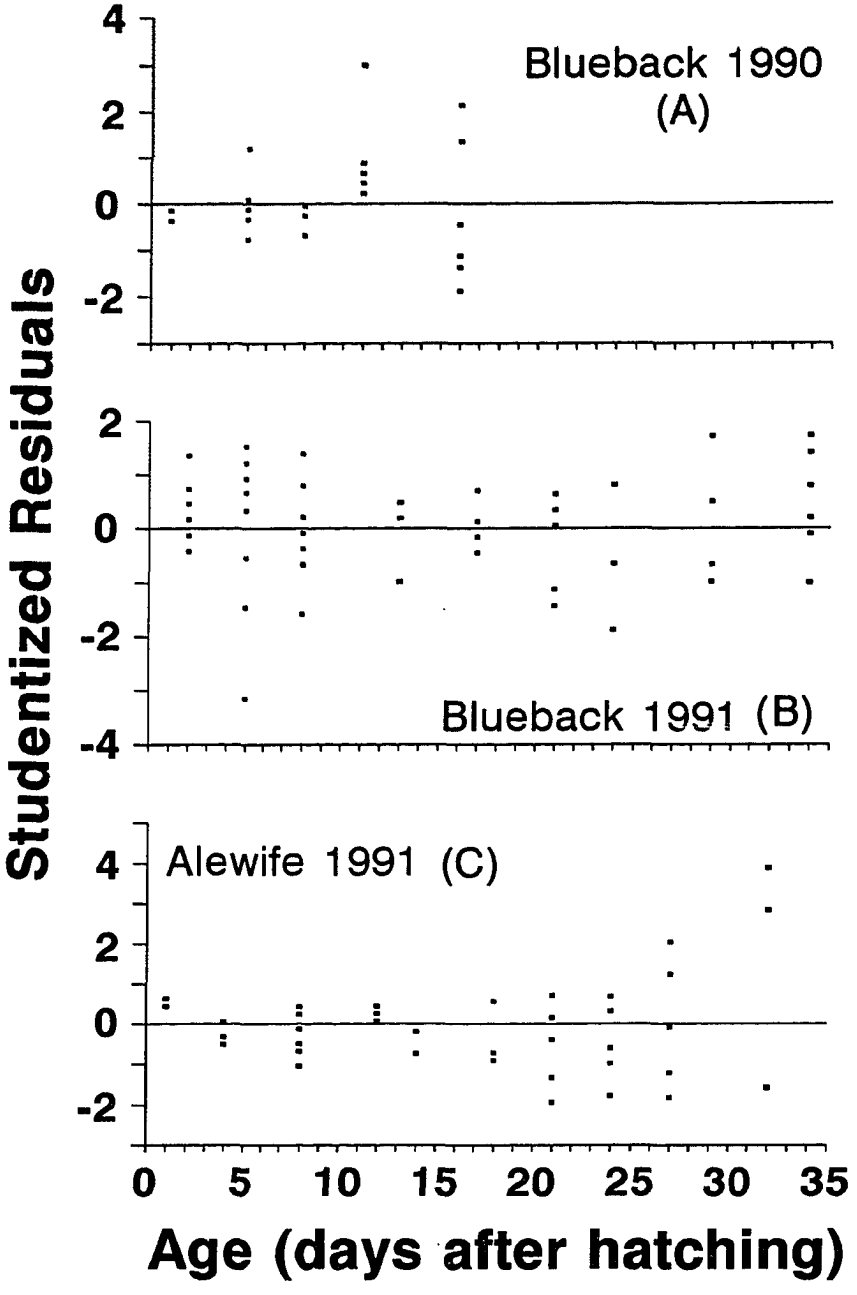


Figure 3-14. Relationships between functions of the mean and standard deviation for increment number to age of 1990-blueback herring larvae (dotted), 1991-blueback herring (dashed), and 1991-alewife (solid) larvae.

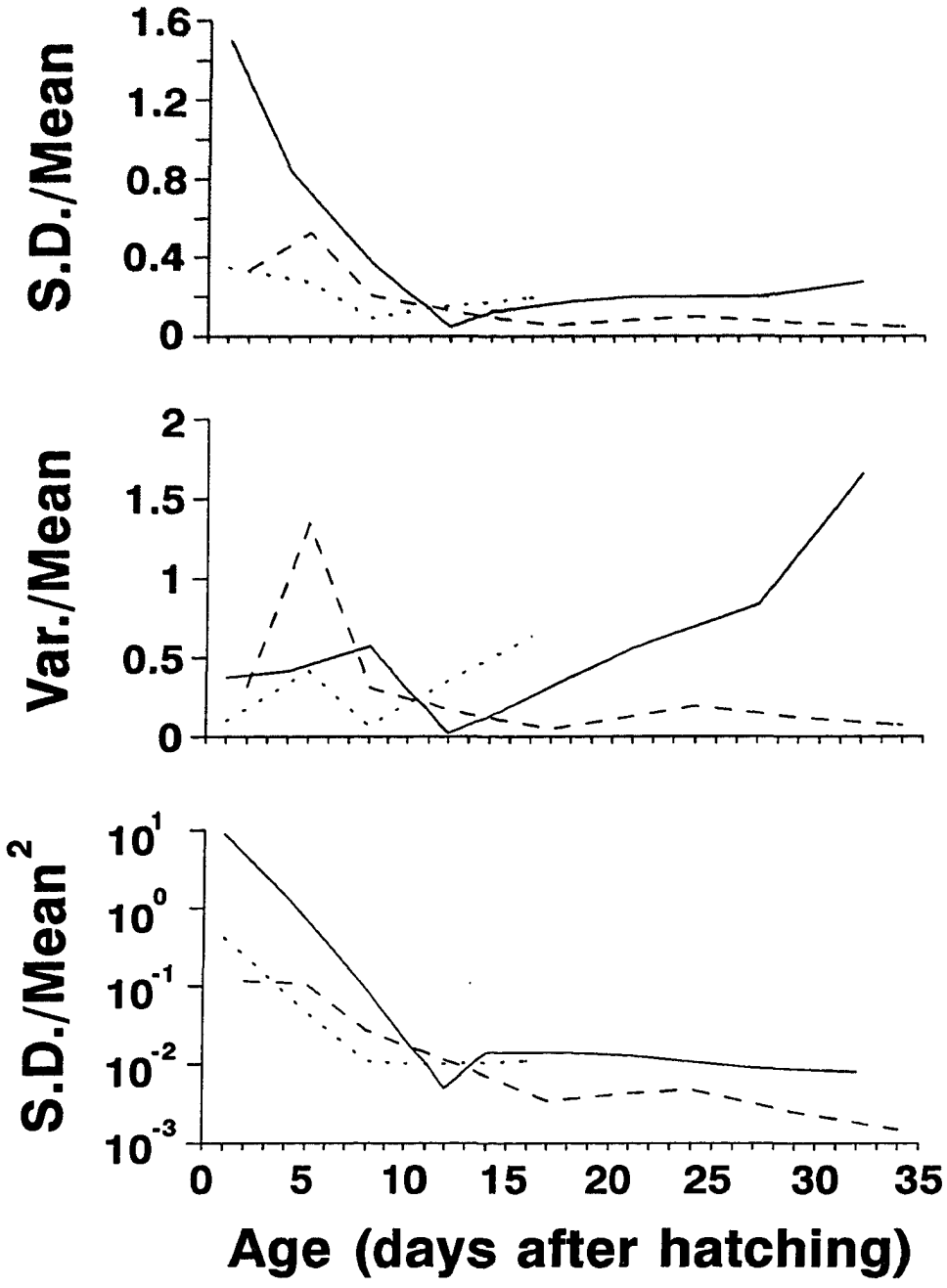


Figure 3-15. Relationships between mean studentized residual variance and functions of the independent variable (age) for 1990-blueback herring larvae (dotted), 1991-blueback herring larvae (dashed), and 1991-alewife (solid) larvae.

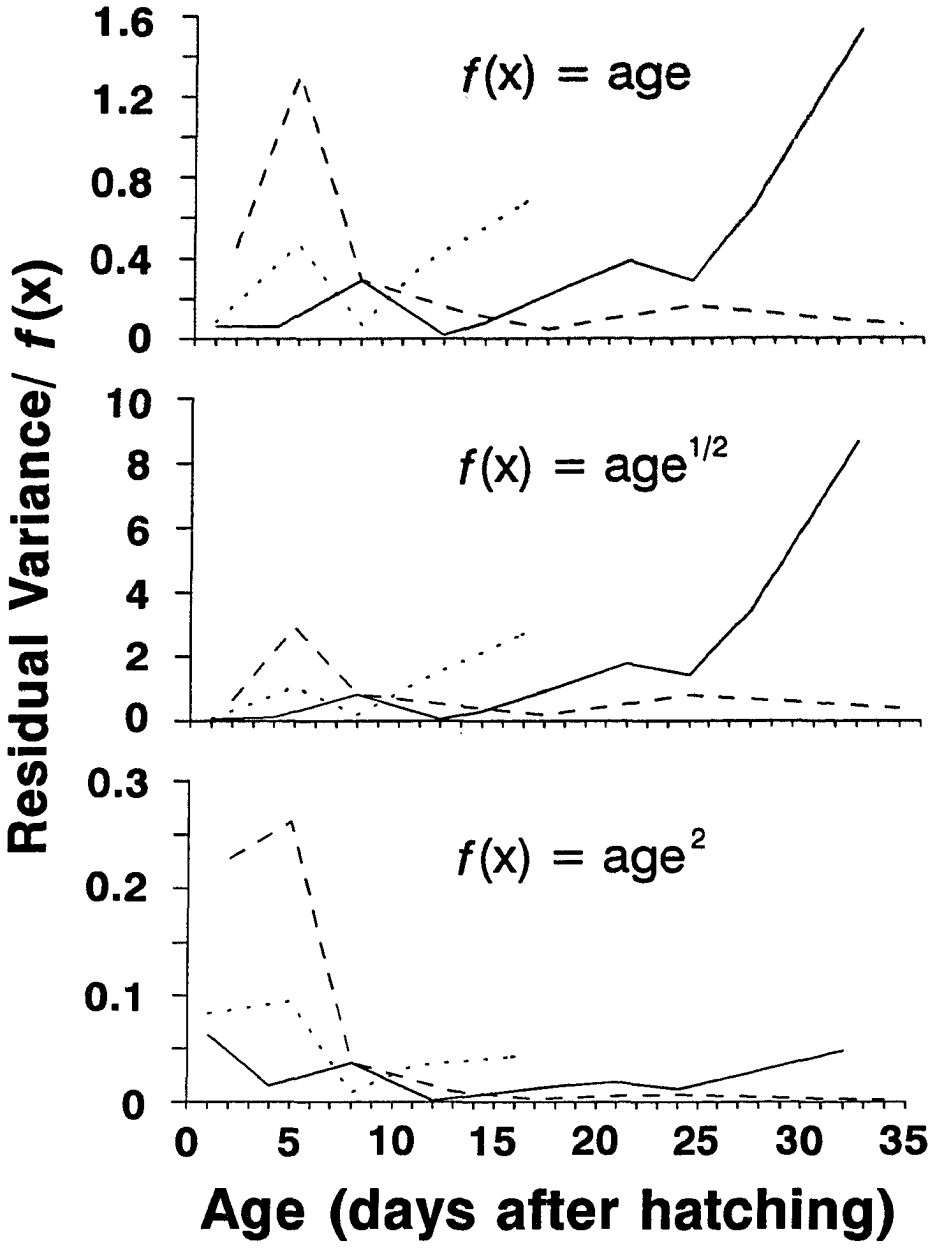


Figure 3-16. Plots of studentized residual error distributions for weighted least-squares regression models relating daily growth-increment number to age of blueback herring larvae reared in 1990: age 1 d to age 16 d larvae and age 5 d to age 16 d larvae.

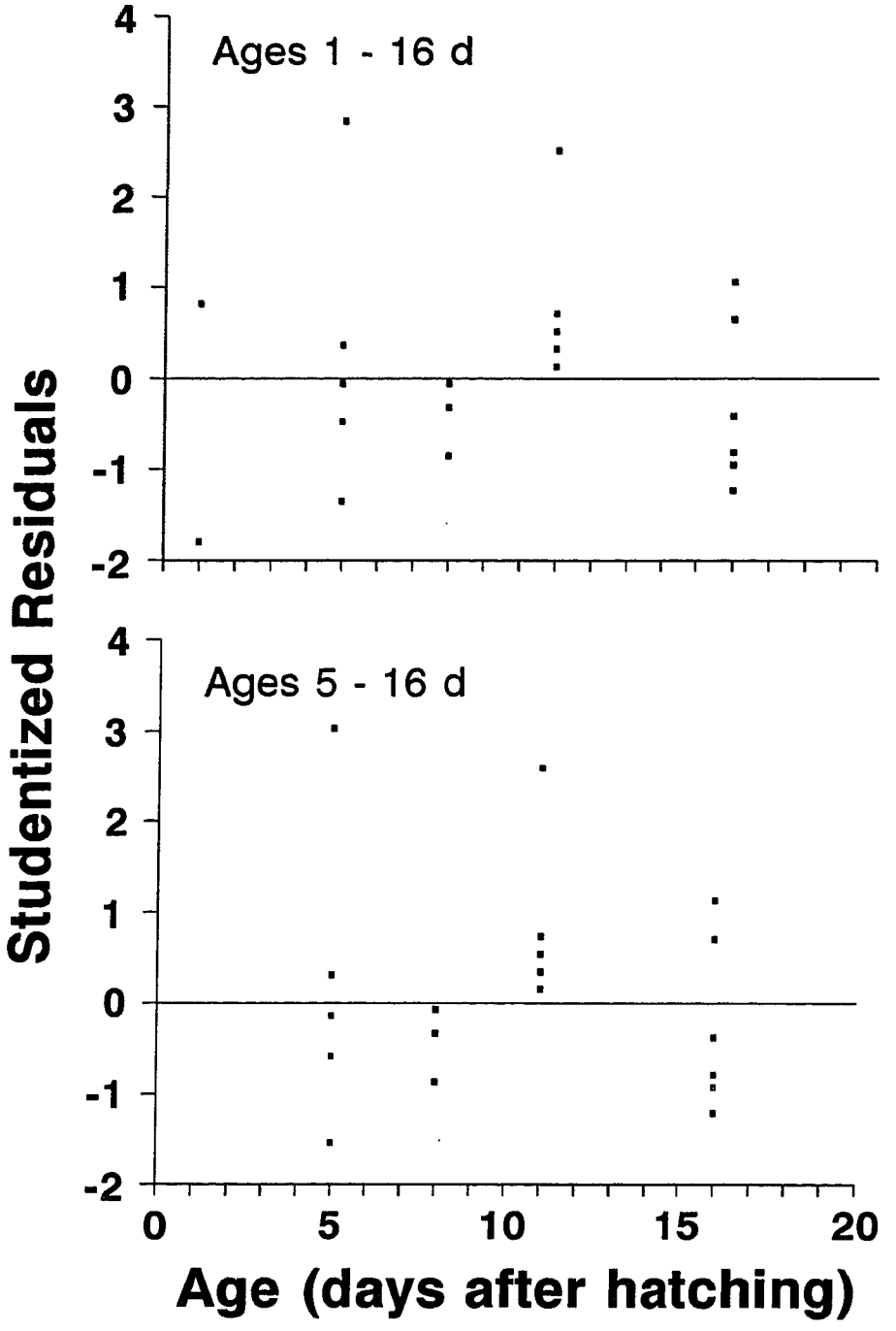


Figure 3-17. Plots of studentized residual error distributions for weighted least-squares regression models relating daily growth-increment number to age of blueback herring larvae reared in 1991: age 2 d to age 34 d larvae and age 5 d to age 34 d larvae.

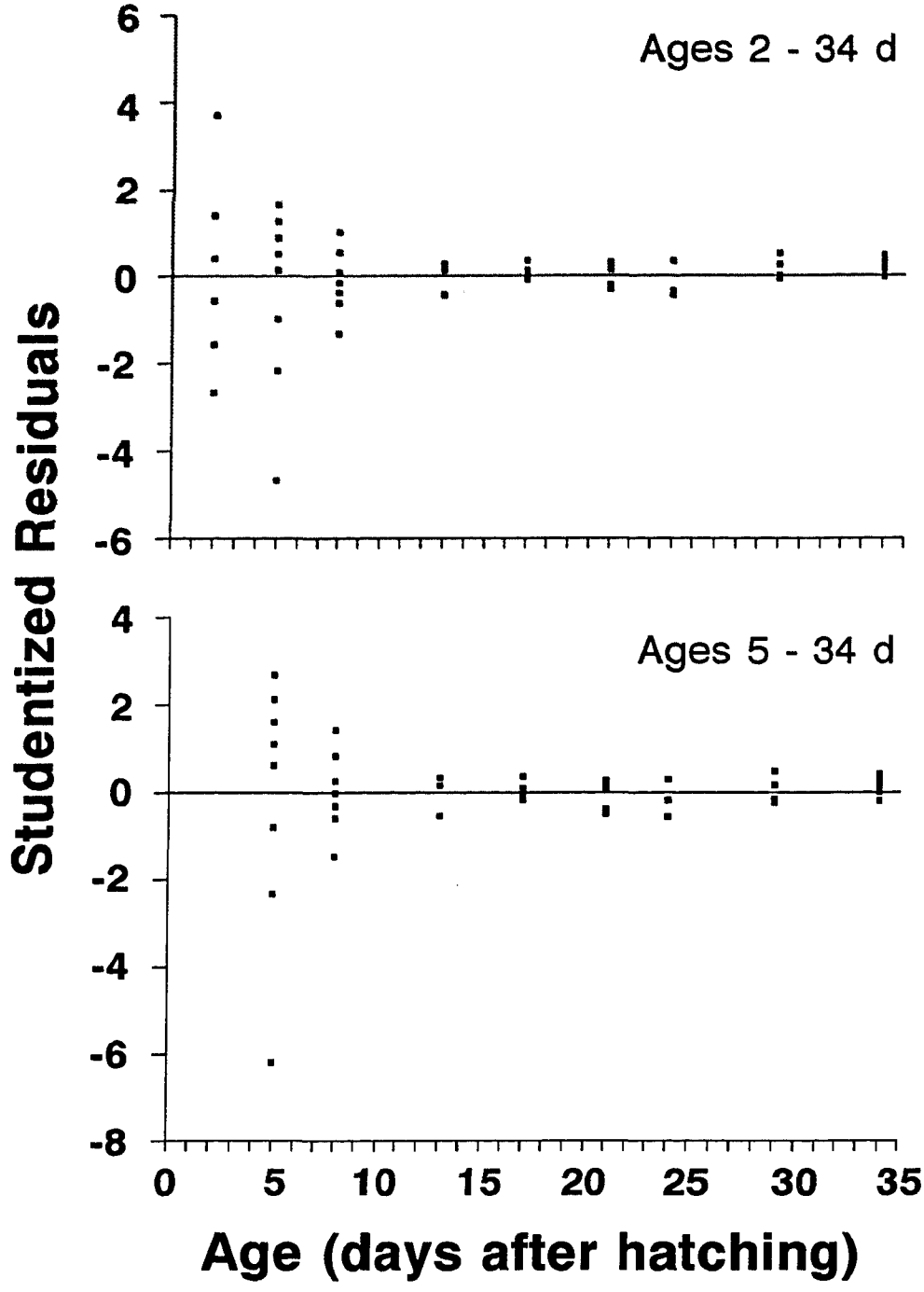


Figure 3-18. Plots of studentized residual error distributions for weighted least-squares regression models relating daily growth-increment number to age of alewife larvae reared in 1991: age 1 d to age 32 d larvae and age 4 d to age 32 d larvae.

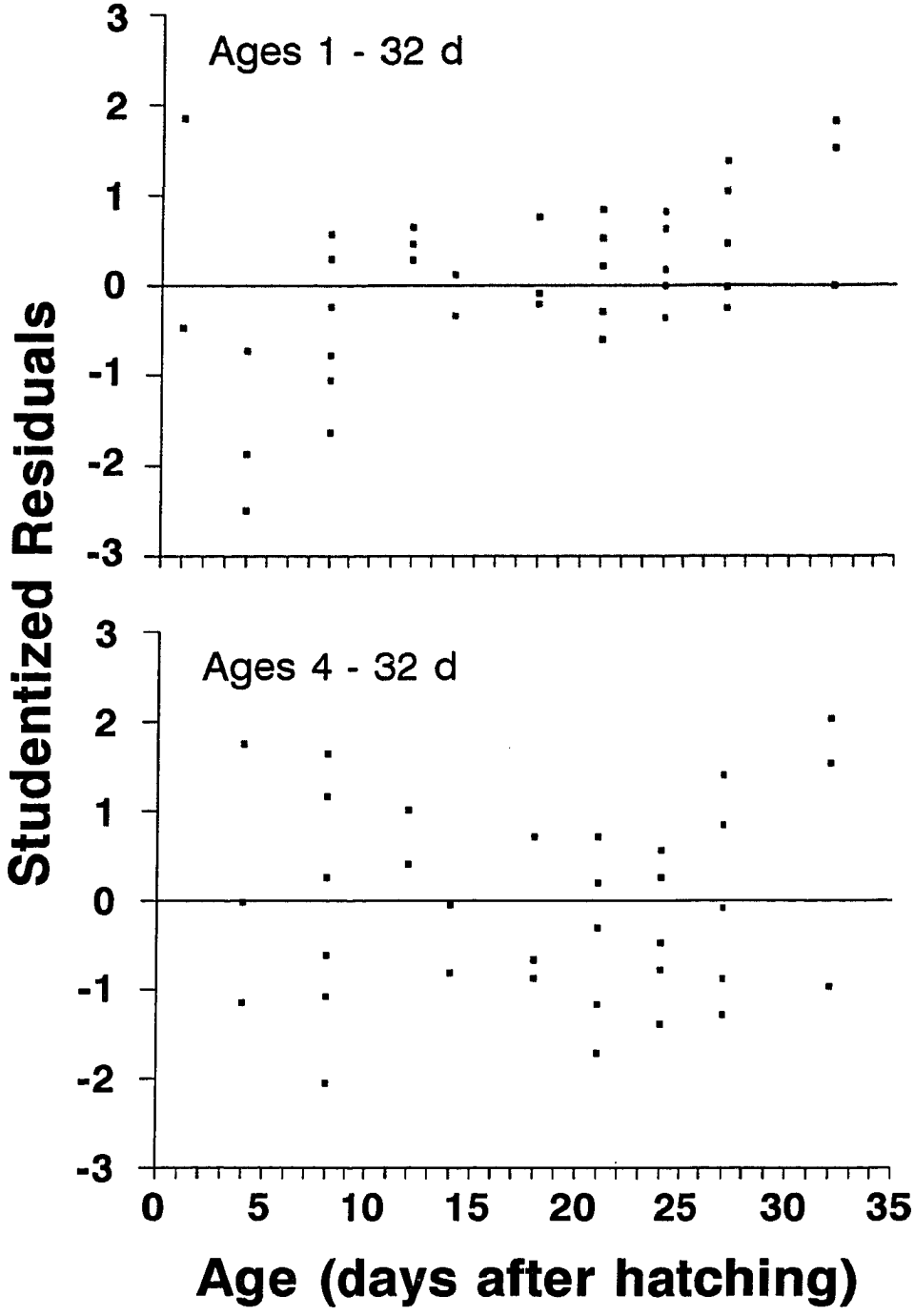
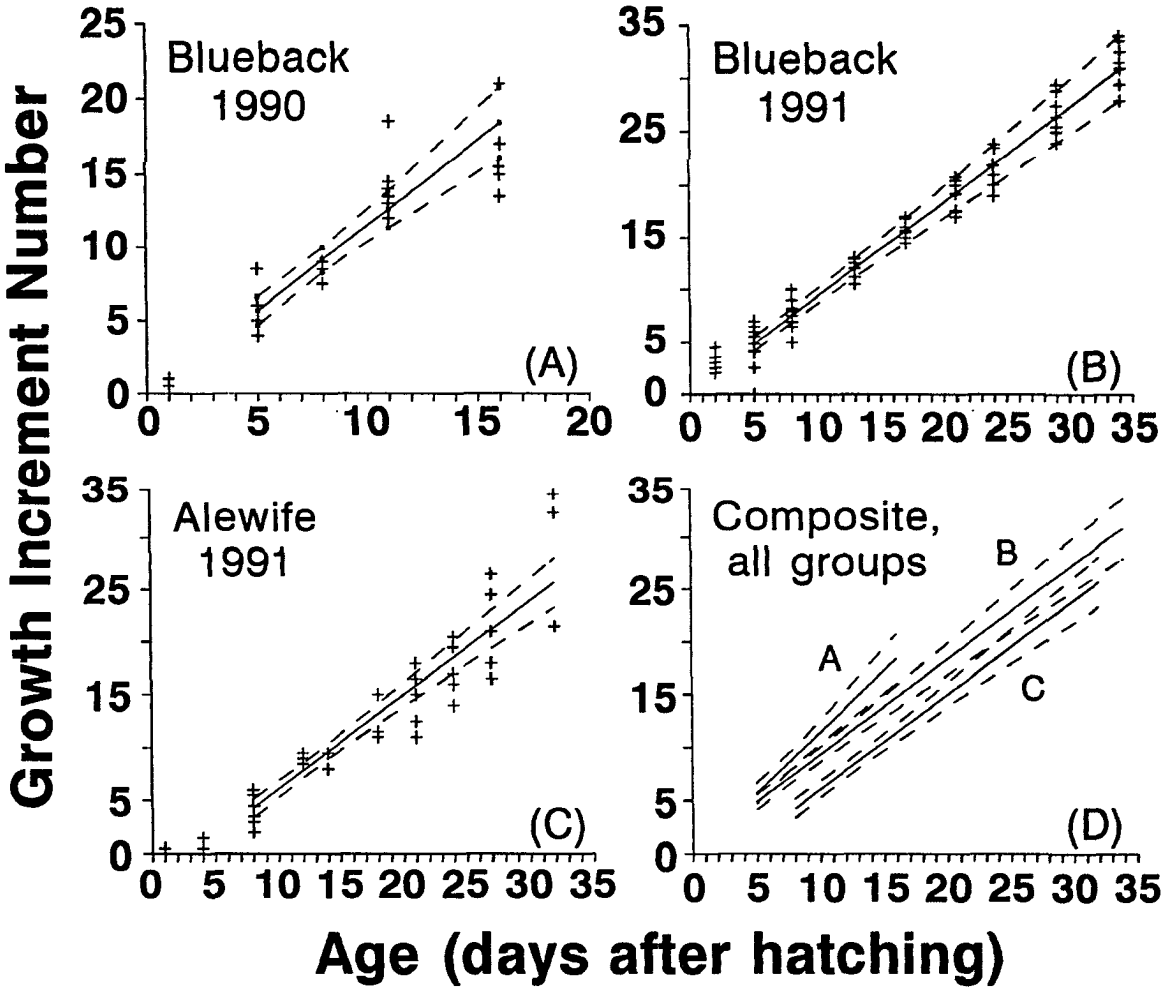


Figure 3-19. Daily growth-increment number-true age relationships for culture blueback herring (A and B) and alewife (C) larvae showing regression lines and associated 95% confidence intervals calculated from weighted least-squares regression models. Daily growth-increment number-age relationships for the three culture groups are compared in plate D.



Chapter 4.

Larval river herring distribution, abundance, growth and hatching dates in the Pamunkey River, Virginia, tidal freshwater reach.

ABSTRACT

Year-class abundance is established during the egg and larval stages of anadromous herring, yet larval river herring biology and ecology in the tidal freshwater-oligohaline reach of tributaries to Chesapeake Bay are poorly known. Improved knowledge of alewife and blueback herring early life histories will further the understanding of recruitment dynamics in anadromous herring populations, and will aid in land-, water-, and habitat-management of river herring spawning and nursery grounds. Distributions, abundances, growth and hatch date frequencies for river herring larvae and distributions and abundances of potential zooplankton prey in the Pamunkey River, Virginia, in 1989 and 1990 are analyzed in this chapter. Major findings include: 1) tidal creek utilization by river herring larvae; 2) faster larval herring growth in tidal creeks compared to the mainstem river; 3) distinct groups of larvae in the tidal freshwater reach, one associated primarily with the mainstem river and another associated primarily with tidal creeks; and, 4) rapid decline in the abundance of early preflexion larvae associated with high river flow in 1989. The results suggest that habitat quality varies in the tidal freshwater nursery zone. The distribution on river herring larvae and utilization of tidal creeks may be influenced by ontogenetically determined behavior with older larvae preferentially moving into backwater areas. Other factors which may influence utilization of tidal creeks by river herring larvae include prey abundance and quality as well as predation, and the extent to which habitat utilization differs between alewife and blueback herring larvae remains to be determined.

INTRODUCTION

Various hypotheses have been advanced accounting for fluctuations in fish population abundance. Hjort (1914, 1926) suggested that fluctuations in the abundance of fish populations arise through variable interannual mortality at the time of first-feeding (the transition from endogenous nourishment to exogenous feeding) and that larvae which do not acquire adequate nourishment die from starvation (see May 1974 for review). Other hypotheses relate larval fish survival to environmental heterogeneity as it influences the abundance and availability of prey. These include the "stable-ocean" (Lasker 1981), the "match-mismatch" (Cushing 1975), and the "member/vagrant" hypotheses (Sinclair 1988). The first two of these deal primarily with trophodynamics of larvae, especially the coincidental spatial and temporal distributions of fish larvae and their prey. The latter hypothesis emphasizes physical processes which link spawning and nursery grounds and which retain larvae in areas which promote survival. Variable mortality during the larval stage appears to be the primary determinant of year-class strength in many species of pelagic fishes (Smith 1985; Rothschild 1986; Houde 1987, 1989). Referring to the establishment of year-class strength in clupeoids, Smith (1985) stated that "significant decreases in recruitment could originate at any stage but marked increases in recruitment are only likely to arise in the embryonic and larval stages."

Growth and predation function as a "unified process" affecting larval fish mortality rates (Cushing 1975). Fast growth reduces predation risk through reduced stage duration (Shepherd and Cushing 1980; McNamara and Houston 1987). Optimal survival, therefore, is likely associated with conditions promoting growth: abundant high-

quality prey, low predation risk, and benign environmental conditions (Rothschild 1986). Sufficient prey concentrations ensuring frequent encounters between larval fish and their food promote rapid growth thereby reducing predation risk (Lasker and Zweifel 1977; Vlymen 1977; Hunter 1981), but sufficient prey concentrations may differ between larvae of taxonomically diverse groups due to different behaviors and physiologies (Houde and Schekter 1981; Govoni et al. 1986). Most perciform larvae, for example, are relatively advanced at hatching possessing a coiled gut which retains food, prolongs digestion, and increases the assimilation of nutrients. Additionally, the swimmming behavior of perciform larvae enables efficient pursuit and attack of prey. Non-perciform larvae, such as clupeiform larvae, are less developed at hatching possessing a straight, tubular gut and are characterized by swimming behavior that limits the pursuit of prey (Hunter 1972). Consequently, clupeiform larvae may require higher prey concentrations than perciform larvae for an adequate daily ration.

Intra- and interspecific differences in development, behavior, and ecological requirements of larvae may contribute to recruitment variability among and between populations and species of *Alosa*. Recruitment dynamics for most anadromous *Alosa* populations are poorly studied, although recruitment dynamics for the Connecticut River American shad population have been studied extensively (Leggett 1977; Crecco and Savoy 1987a). In contrast, the recruitment dynamics of anadromous alewife and blueback herring population are less studied (Havey 1973; Walton 1987; Jessop 1990).

Status of *Alosa* populations in Chesapeake Bay

Four anadromous herring species are common to Chesapeake Bay: American shad (*Alosa sapidissima*), hickory shad (*Alosa mediocris*), alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*). Alewife and blueback herring are referred to collectively as river

herring (Loesch 1987). Additionally, two species of freshwater herring are prevalent in fresh and brackish water reaches of Chesapeake Bay tributaries. Gizzard shad (*Dorosoma cepedianum*) is common to most tributaries of Chesapeake Bay and threadfin shad (*Dorosoma petenense*) is an introduced species limited to a few tributaries, primarily the James and Rappahannock Rivers (Wass 1972), and both species utilize tidal and nontidal freshwater habitats for spawning and nursery habitat.

Anadromous alewife and blueback herring spawning populations in Chesapeake Bay are at historically low abundance levels. The status of these populations in major tributaries of the Chesapeake Bay was reviewed by Klauda et al. (1991a) (Tables 4-1 and 4-2, respectively). Similar numbers of alewife and blueback herring populations were either established or remnant populations, but twice as many alewife populations compared to blueback herring populations were extinct (Table 4-3). More alewife populations than blueback herring populations were at low or very low abundance levels (89 percent and 67 percent, respectively) (Table 4-3). Similar numbers of alewife and blueback herring populations showed increasing, stable, or declining trends in abundance, although only a few populations of either species appear to be recovering from reduced abundance (Table 4-3). These data suggest that declines in abundance may be more severe for alewife populations than blueback herring populations in Chesapeake Bay. Has some aspect of the biology or ecology of these species been overlooked which might aid the understanding of recruitment variability and help to account for lack of recovery of these spawning populations?

Alewife and blueback herring early life histories in Chesapeake Bay are poorly known. All major southern tributaries of Chesapeake Bay (the James, Mattaponi, Pamunkey, and Rappahannock rivers) support alewife and blueback herring spawning populations (Klauda et al. 1991a). Van Engel and Joseph (1968) found river herring larvae in the upstream reach of the York-Pamunkey River estuary. Birdsong et al. (1987)

documented the occurrence of river herring eggs and larvae in Crump Creek, a nontidal tributary of the Pamunkey River. Juvenile *Alosa* abundance is high throughout the tidal freshwater reach of all southern tributaries of the Chesapeake Bay (Loesch et al. 1979). Biological and ecological studies of river herring larvae are needed to provide greater understanding of recruitment for these species in Chesapeake Bay and throughout their respective ranges. Such studies will contribute also to land-use, water-use, and habitat management policies which affect spawning and nursery habitats utilized by river herring.

Purpose, goals, and objectives

The purpose of the present research was to describe and evaluate, qualitatively and quantitatively, selected aspects of anadromous river herring biology and ecology in the tidal freshwater nursery zone of the Pamunkey River, a southern Chesapeake Bay tributary. To accomplish this research, the distribution, abundance, growth and hatch dates of river herring larvae during 1989 and 1990 within the Pamunkey River tidal freshwater reach were evaluated and analyzed. Specific objectives were to: 1) characterize the temporal and spatial distributions of river herring larvae and zooplankton both along the mainstem river channel and between areas hypothesized to be distinct nursery habitats, 2) estimate larval river herring growth rates in areas potentially differing in habitat quality (e.g. zooplankton abundance, larval herring abundance), and 3) determine whether larval herring survival, as indicated by the frequency of hatch dates of larvae, may be associated with zooplankton or larval herring abundance. Rationale in support of these objectives is summarized below. This is the first detailed study of larval river herring ecology in a southern Chesapeake Bay tributary.

Distribution of organisms in space and time is a fundamental element of ecology. The first objective for this research, therefore, was to determine the spatial and temporal distributions of river herring

larvae in the Pamunkey River tidal freshwater nursery zone. Several questions were addressed: 1) are river herring larvae distributed randomly throughout the tidal freshwater reach and when are larvae most abundant, 2) do river herring larvae occur in tidal creek habitats and when are they abundant, 3) do river herring larvae tend occur in areas of relatively high zooplankton abundance, and 4) are distinct groups of river herring larvae identifiable within the study area and are these groups identifiable as alewife and blueback herring larvae?

Another question concerns the affect of river flow and rainfall on larval herring survival. Establishing a causal relationship between river flow, rainfall and larval herring survival requires a time series of annual abundance estimates for larvae (Crecco and Savoy 1984). Although the design and limited duration of the present research did not provide larval herring abundance estimates necessary for such analysis, the distribution of larvae along the mainstem river channel was evaluated qualitatively relative to river flow and rainfall since these factors were higher in 1989 than in 1990. The correlation between river flow and dissolved oxygen was evaluated since elevated river flow reduces residence time of water in the tidal freshwater zone and may depress primary production thereby potentially affecting zooplankton and larval herring survival.

Differential distribution of larvae between areas within a nursery zone may yield variable intra- and interannual survival rates of larvae if habitat quality varies within or between seasons. The second objective, therefore, was to test the hypotheses that growth of river herring larvae differs between habitats or between seasons. The hypothesis of differential growth between habitats was tested by analyzing standard length-at-age relationships for larvae captured in tidal creek and mainstem river habitats. The hypothesis of differential growth between seasons was tested by analyzing standard length-at-age relationships for larvae captured during a comparable time interval in

each season. Mortality rates could not be estimated for this study due to the openness of the system and limitations in specimen collection. However, the number of individuals surviving to the juvenile stage at arbitrary instantaneous daily mortality rates was estimated based on the larval stage duration calculated from larval river herring growth rates in the mainstem river and in tidal creeks.

The final objective was to evaluate the hatch date frequency distributions for larvae captured in the tidal creeks and mainstem river relative to zooplankton abundance and larval herring abundance to characterize the association between larval herring production, zooplankton abundance, and larval herring survival.

METHODS

Study area

The Pamunkey River, located in east-central Virginia (Fig. 4-1), originates at the confluence of the North Anna and South Anna rivers and ends approximately 157.5 km downstream at its confluence with the Mattaponi River at West Point, Virginia, creating the York River. The Mattaponi River-Pamunkey River confluence occurs about P54, i.e. 54 km upstream from York River mouth in Chesapeake Bay (all locations along the mainstem Pamunkey River channel are reported as kilometers from the York River mouth). The Pamunkey River is a flood-plain river varying from relatively narrow and shallow upstream to relatively wide and deep downstream with broad meanders. It drains approximately 3,781 km^2 of agricultural land, marshes, swamps, and forested wetlands (Brooks 1983). Wetlands along the Pamunkey River undergo a transition from freshwater marsh to swamp at about P83 (Doumlele et al. 1985). Extensive wetlands occur on the interior of meanders in the lower reach of the river, and a few are transected by channels referred to as thoroughfares. Cumberland Thoroughfare, the largest thoroughfare in the Pamunkey River, connects P91 and P100. Little industrial development occurs upstream of West

Point (Brooks 1983). The approximate upper limit of the York-Pamunkey estuary occurs at P93 (Van Engel and Joseph 1968), and tidal influence extends upstream to about P137. The Pamunkey River at P93 is characterized by a mean annual salinity of 0.2‰ (range: 0.0 to 1.8‰) with lowest salinities in winter and spring associated with higher freshwater runoff (Van Engel and Joseph 1968). By definition, the tidal freshwater environment is characterized by an average annual salinity less than 0.5‰; although, salinity may rise above this concentration during periods of low water flow or drought (Odum 1988).

Lilly Point marsh is a tidal freshwater wetland located from about P100 to about P102 along the mainstem river with its downstream margin adjacent to Cumberland Thoroughfare (Fig. 4-2). The vegetational community of this area as that of a swamp with soil ranging from inundated and mucky to almost upland in character (Doumlele et al. 1985). Emergent vegetation consists primarily of arrow-arum (*Peltandra virginica*) and yellow pond lily (*Nuphar luteum*). Lilly Point marsh is drained by Holts Creek along the southeast margin, by Big Creek at the center, and by White House Creek at the northwest margin. Holts Creek is bordered by a forested and shrub-lined ridge with farmland occurring inland. Holts Creek and Big Creek are separated by about 0.3 to 0.8 km and neither exhibits extensive subdivision into smaller tributaries. Topographic maps suggest that temporary rills may provide direct connection between the two creeks, most likely at high tide. The direction and magnitude of water flow through the swamp and the extent of water exchange between Holts Creek and Big Creek are not known.

Ichthyoplankton and zooplankton collections were made in the tidal freshwater reach of the Pamunkey River to evaluate and analyze the distributions and abundances of river herring larvae and their potential zooplankton prey both along the mainstem river channel and between selected areas hypothesized to represent distinct nursery habitats. The Pamunkey River tidal freshwater reach from P83.4 to P116.8 was selected

as the study area along the mainstem river channel (Fig. 4-3). One-third of the study area was within the upper estuary, as defined by Van Engel and Joseph (1968) and collections were made in the mainstem river channel both upstream and downstream of the Cumberland Thoroughfare. The vicinity of Lilly Point marsh was selected as the study area for evaluating potential nursery habitats because of the diversity of habitats present in this region and especially due to the location of Cumberland Thoroughfare. Potential nursery habitats sampled for this study included Holts Creek, Big Creek, Cumberland Thoroughfare, over the river shoulder and over the mainstem river channel (Fig. 4-4). Of the creeks draining Lilly Point marsh, only Holts Creek and Big Creek were accessible for sampling by boat; shoaling at the mouth made White House Creek inaccessible.

Study design and sampling techniques

Ichthyoplankton collections along the mainstem river channel

The early life stages of river herring are of relatively short duration (Lippson and Moran 1974; Wang and Kernehan 1979); therefore, sampling in 1989 along the mainstem Pamunkey River channel was conducted at high frequency to facilitate comparisons between the distributions and abundances of river herring larvae and potential zooplankton prey and abiotic factors which might influence larval herring or zooplankton distributions and abundances. Sixteen collection events were made in 1989 during a 10-week period from mid-March to late May with the greatest sampling frequency occurring from early April to early May when greatest spawning intensity was expected (Appendix 4-A). Collections events were made at lower frequency in 1990, four events from mid-March to mid-May, due to increased sampling of potential nursery habitats (see below). Collection events were classified in four time intervals for statistical analysis: 21 March to 6 April, 10 April to 22 April, 25 April to 5 May, and 9 May to 25 May.

Ichthyoplankton collections along the mainstem channel followed a randomized block design to ensure that collections were made throughout the study area for each collection event. The study area was divided into six 5.6-km strata (blocks): P83.4 to P87.1 (stratum 1), P89.0 to P92.7 (stratum 2), P94.5 to P98.2 (stratum 3), P100.1 to P103.8 (stratum 4), P105.6 to 109.3 (stratum 5), and P112.2 to 114.9 (stratum 6). Each stratum was comprised of three 1.9 km substrata. One substratum from each block was selected randomly for sampling ichthyoplankton and zooplankton during each collection event. Additional collections were made in Cumberland Thoroughfare for comparison with collections from the mainstem river channel. Samples were collected near the center of selected substrata and the thoroughfare. Cumberland Thoroughfare was sampled routinely after mid-April 1989.

Ichthyoplankton collections from the mainstem river channel were made using towed, paired 333 μm-mesh plankton nets with a 5-to-1 aspect ratio (net length to mouth diameter). The nets were attached to an aluminum frame consisting of two 60-cm diameter (0.36 m^2) rings weighted additionally with about 18 kg. The filtered water volume was measured using calibrated flow meters positioned approximately half the distance between the center and rim in the mouth of each net (Tranter and Smith, 1968). The aluminum frame with attached nets was deployed using a winch and boom from a 21 ft Privateer powered by a 155 hp outboard engine. The boat was maneuvered in a slight arc while nets were deployed to position the nets outside of the propeller wash. The boat speed was not measured, but engine power during net deployment was maintained at minimum throttle (750 RPM to 800 RPM). The water column was sampled in a stepped-oblique manner from the surface proceeding at two-meter depth intervals to within one to two meters of the substrate. Each depth interval, including the surface, was sampled for 30 seconds and the nets were retrieved without stopping. Water depth was monitored electronically using an LCD (liquid-crystal display) depth finder which

aided the identification of underwater topography and obstructions. A tow was repeated if the nets appeared to touch bottom or hit a snag.

Ichthyoplankton collections within potential habitats

Initial ichthyoplankton collections in the five potential nursery habitats made in 1989 were to determine when river herring larvae occurred in Holts and Big creeks. Four collection events were made from early April to late May, but the first event was not completed successfully and could not be repeated prior to the next event. River herring larvae were captured in the tidal creeks during the remaining three events indicating that further sampling was warranted. Seven collection events were made in 1990 from mid-March to mid-May were made with greater frequency to characterize the distributions and relative abundances of river herring early life stages between nursery habitats (Appendix 4-B).

Ichthyoplankton collections in the nursery habitats followed stratified random sampling with each location treated as a stratum. Study sites (strata) in Holts Creek and Big Creek were 1.9 km long and were subdivided into two equivalent length substrata (Fig. 4-4). The downstream limit of the study site in each creek occurred 1.9 km from the creek mouth. Cumberland Thoroughfare was divided into two substrata on either side of the mouth of Holts Creek (Fig. 4-4). Study sites for the mainstem river channel and the river shoulder habitats were located in the region from P98 to P100. For considerations of river bottom topography and accessibility during low-tide, substrata of the river shoulder were defined as the eastern side of the channel in P98 and the northern side of the river channel across from the mouth of Big Creek in P100. Substrata of the river channel were adjacent to river shoulder substrata just described (Fig. 4-4). One substratum from study sites in each potential nursery habitat was selected randomly for each collection event.

Ichthyoplankton collections were made using plankton nets attached to a pushnet frame on a 4.3 m jon boat (Fig. 4-5). The pushnet assembly consisted of two parts, an aluminum frame and a polyvinyl-chloride (PVC) frame with attached plankton nets (see below). The aluminum frame was made using 50.8 mm-diameter aluminum pipe with a guide for the PVC frame located at the distal end of the frame made using 31.8 mm-channel aluminum. The proximal end of the frame consisted of an outer aluminum casing, attached to the jon boat, with an inner aluminum pipe of slightly smaller diameter and slightly greater length. The side supports of the aluminum frame were attached to the inner pipe allowing the pushnet assembly to pivot vertically to facilitate deployment and retrieval of plankton nets and sample recovery from cod-end jars.

The PVC frame was made using 25.4 mm-diameter PVC pipe with two PVC vertical center supports adjusted to make two 42 cm by 35 cm (0.15 m^2) openings. Two 60-cm 335 μm-mesh (5:1 aspect ratio) plankton nets were lashed to the PVC frame. During deployment, the plankton nets were positioned vertically in the water with the top of the PVC frame slightly beneath the surface. Flow meters were positioned in the mouth of each net along the vertical mid-line slightly below the horizontal mid-line. A nylon rope was used to raise the aluminum frame after sampling, and a knotted loop in this rope was placed over the bow cleat to maintain the nets in a constant position during sampling.

Two ichthyoplankton collections, one with and one against the tide, were made in each habitat during each collection event. Replicate collections were obtained to reduce the influence of tidal effects on estimated relative density (catch-per-unit-effort). The direction of the first 'push' was randomized. Each 'push' was conducted for 5 minutes at minimum engine throttle of a 25 hp outboard motor.

Field preparation of ichthyoplankton collections

Ichthyoplankton collections were made using two identical plankton nets during each tow both along the mainstem river channel and in potential nursery habitats. Collections from one net were always fixed in 5% phosphate buffered formalin (5% PBF) (Markle 1984). In 1989, collections from the second net were fixed, alternately, either in 95% ethanol (EtOH) to preserve otoliths or in Bouins' solution for the histological analysis. However, in 1990, collections from the second net were fixed solely in ethanol. Ethanol-fixed samples were changed twice at approximately 24 hour intervals to ensure preservation of otoliths. Bouins-fixed larvae were transferred to 70 percent ethanol after 24 hours and stored for later analysis.

Zooplankton collections

Zooplankton collections were made after ichthyoplankton collections were made at each sampling location. A 20-ℓ river water sample was pumped from a standard depth of one meter below the surface using a 2000-GPH Rule pump powered by a 12-volt marine battery. The sample was concentrated on a 50-μm nylon-screen sieve, rinsed into a 110-mℓ sample jar, and 5% PBF was added to the threads of the jar. The final formalin concentration was about 3.8% formalin (3 parts 5% PBF, 1 part water). A sample was reconcentrated when the water volume exceeded about one-quarter volume of the sample jar prior to adding 5% PBF.

Measurement of environmental variables

Water transparency was measured using a 10-inch secchi disk lowered in a shaded location. Dissolved oxygen and water temperature were measured at a standard depth of 1 m below the surface using a portable YSI dissolved oxygen-temperature meter.

Laboratory methods and data analysis

Distribution and abundance of river herring larvae

Identification of river herring larvae

Ichthyoplankton samples were sorted in the laboratory using dissecting microscopes to remove fish eggs and larvae. Eggs and larvae from all samples were identified to species, except for clupeids. Clupeid larvae from samples preserved in 5% PBF were enumerated for the analysis of distribution and abundance, but larvae in samples preserved in 95% EtOH were not enumerated. Samples of clupeid eggs and larvae were further processed to separate American shad eggs and larvae from other herring eggs and larvae. Hickory shad eggs and larvae were assumed not to occur in the collections or to occur in insignificant numbers.

Clupeid early life stages were identified as herring eggs, river herring or *Dorosoma* yolk-sac larvae, and herring larvae. River herring yolk-sac larvae and *Dorosoma* spp. yolk-sac larvae were identified based on yolk sac morphology (Lippson and Moran 1974; Wang and Kernehan 1979). The snout-to-vent length (SVL) and standard length (SL) of post yolk-sac clupeid larvae were measured following Lippson and Moran (1974) and the SVL-SL ratio was used to delimit river herring and *Dorosoma* spp. larvae (Lam and Roff 1976). Lengths were measured using a Wild M3Z stereo-zoom dissection microscope fitted with a 120-unit reticle micrometer to the nearest 0.5 reticle unit at one of three magnifications (6.5x, 10x, or 16x). Lengths in reticle units were converted to millimeters using calibration factors for each magnification. All larvae in samples containing 30 or fewer specimens were measured, otherwise 30 larvae were selected randomly. Measurements of formalin-preserved larvae were not corrected for fixation-induced shrinkage. Post yolk-sac herring larvae were further classified into three developmental stages: early preflexion (no medial fins present), late preflexion (dorsal-fin anlagen or dorsal fin present), and postflexion (notochord flexion initiated).

Larvae greater than 11 mm SL were identified as alewife or blueback herring based on pigmentation (Chapter 2).

Data acquisition, evaluation, and statistical methods

Relative densities of larval herring were computed as catch-per-unit-effort standardized to 100 m^3:

$$CPUE = (\text{number of larvae/filtered volume}) \cdot 100 \qquad \text{Eq. 4-1.}$$

Standardized relative densities of herring eggs, yolk-sac larvae, and larvae are referred to subsequently as abundances.

Zooplankton relative densities were estimated using the following procedure. Zooplankton collections were adjusted to 110 mℓ with 5% PBF. The sample was resuspended, then a 1-mℓ sample was removed using a Hensen-Stempel pipet and transferred to a Sedgewick-Rafter counting chamber for the enumeration of zooplankton using a binocular compound microscope at 40x magnification. Zooplankton, including rotifers, copepod nauplii and copepodites, and cladocerans, were enumerated in three subsamples from each collection. The estimated relative density of each zooplankton group was computed as:

$$\text{number} \cdot \ell^{-1} = (((\text{mean count} \cdot m\ell^{-1}) \cdot 110\ m\ell) \,/\, 20\ \ell) \qquad \text{Eq. 4-2.}$$

The estimated relative density of total zooplankton was computed as the sum of the estimated relative densities for each zooplankton group. Zooplankton relative densities are referred to as abundances.

Larval river herring and zooplankton distributions along the Pamunkey River mainstem was visualized by graphing abundance on two-dimensional plots using location of capture (strata) along the vertical axis and time of capture (date) along the horizontal axis. The spatio-temporal pattern of distribution was then graphed by manually plotting

abundance isopleths based on visual inspection. No assumptions regarding linear changes in abundances are implied by the position of the abundance isopleths. The abundance isopleths are simply delineations between collections with relatively higher and relatively lower abundances. These 'space-time' distribution plots are used as a visual method to facilitate interpretation of abundance data.

Full factorial, unbalanced Model I analysis of variance (ANOVA) with interaction was used to test hypotheses that larval herring or zooplankton abundances differed between strata or habitats, time intervals, sampling seasons, or groups (larval herring developmental groups or zooplankton taxonomic groups). All abundances were transformed using natural logarithms to improve the fit of data to the normal distribution. Abundances of river herring early life stages in Cumberland Thoroughfare in relation to abundances in strata along the mainstem river channel were evaluated qualitatively because Cumberland Thoroughfare was not sampled randomly and inclusion of Cumberland Thoroughfare data in ANOVA tests for the mainstem river channel data was not appropriate. Statistical analysis of river herring and zooplankton abundances in the five habitats was conducted between mid- to late April and early to mid-May time periods when larval river herring were in highest abundance and occurred in all habitats. Herring eggs were captured infrequently usually at low abundance and, therefore, were evaluated qualitatively.

ANOVA assumptions were evaluated using Cochran's C homogeneity of variance test, normal probability plots and stem-and-leaf plots. Relative densities of river herring larvae and zooplankton potential prey groups were transformed using common logarithms to better fit the assumption of normality. Cochran's C homogeneity of variances test was used due to unequal replication between sampling seasons. ANOVA was used to identify significant statistical interactions between factors.

Analysis of environmental factors

Meteorological data were obtained from published records of the U.S. National Weather Service. Mean daily air temperature and daily rainfall measurements made at three monitoring stations in eastern Virginia in the vicinity of the Pamunkey River (Ashland, Walkerton, and West Point) were averaged to estimate the regional mean daily air temperature and rainfall. Mean daily water flow measurements for the Pamunkey River were obtained from published records for the National Stream-Quality Accounting Network, Station No. 01673000, located near Hanover, Virginia (latitude 37° 46' 57", longitude 77° 19' 57").

Water temperature measurements were available only for dates on which collection events were made, therefore daily air temperature was used to examine intra- and interannual differences in temperature. Linear regression analysis was used to relate water temperature to air temperature. Daily air temperature was regressed on day number to estimate the rate of increase in temperature for each year.

Higher river flow reduces residence time in the tidal freshwater reach, rapidly flushes phytoplankton downstream, and increases turbidity. Consequently, dissolved oxygen concentration may be depressed at higher water flow. Pearson's correlation coefficient was used to determine the significance of the association between dissolved oxygen concentration and river flow. Dissolved oxygen concentrations and water transparencies were evaluated visually using 'space-time' distribution plots as described above.

Growth of river herring larvae

Otolith preparation

Detailed methods for dissection, preparation, and data acquisition from otoliths of river herring larvae are presented in Chapter 3. The procedure is summarized here to show differences in the handling of larvae and in the preparation and evaluation of otoliths which were made

to improve the methodology and increase the efficiency of specimen preparation.

Otolith daily growth increments were used to age field-collected larvae for analysis of standard length-at-age relationships from which average growth rates were estimated. Field-collected clupeid larvae preserved in 95% EtOH were sorted to remove specimens which showed evidence of growth: visibly larger sagittal otolith diameter compared to lapillar otolith diameter. Sagittal and lapillar otoliths are of equivalent size at the end of yolk-sac absorption in river herring (Chapter 3). Up to 30 clupeid larvae with relatively larger sagittae were selected randomly from each collection for the enumeration of growth increments.

Larvae were soaked in 1% potassium hydroxide (Brothers 1987) prior to otolith dissection to facilitate measurement of vent and standard lengths as well as the dissection of otoliths. Each larva was treated for about 60 seconds to standardize the effect of tissue swelling on length (Chapter 3), although some larvae were soaked for longer periods. Larvae were identified as river herring, *Dorosoma* spp., or 'unidentified' based on the SVL/SL ratio (Lam and Roff 1976). River herring and 'unidentified' larvae greater than 11 mm were identified as alewife or blueback herring based on pigmentation (Chapter 2). The development and distribution of pigment in alewife and blueback herring was assumed to differ from that in *Dorosoma* spp. larvae so that positive identification of older larvae of these groups was possible.

Otoliths were dissected from a treated larva following measurement of standard and vent lengths, and were washed and cleaned of adherent tissue in water. Otoliths were air dried and mounted on a glass slide using histologic-grade mounting fluid. Non-spherical otoliths were mounted medial side down. Otoliths were not ground or polished.

Measurements of otoliths and counts of growth increments were made using the image-analysis system described in Chapter 3. Measurements

made on otoliths included the maximum diameter, the maximum radius, the diameter of the yolk-absorption check, and the number of daily growth increments. Measurements of otolith dimensions and counts of growth increments were made at 625x, except for large otoliths which required lower magnification. Because otoliths were not ground and polished, higher magnification resulted in poor resolution of growth increments in larger otoliths. In these few cases, the enumeration of growth increments was accomplished at 350x to 500x. Increments were enumerated in the posterior region of non-spherical otoliths. All observed discontinuous zones in the poorly resolved zone adjacent to the yolk-absorption check (Chapter 3) were defined as daily. Following the enumeration of growth increments, otoliths from larvae identified as gizzard shad were excluded from statistical analyses of age and growth and were not replaced.

Data acquisition and statistical methods

Standard length measurements

Standard length measurements of ethanol-preserved river herring larvae were corrected for tissue swelling caused by clearing in 1% KOH using the regression equation developed in Chapter 3 relating live standard length to the standard length of preserved and cleared larvae. Corrected standard length estimates were used in all statistical analyses of standard length-at-age relationships.

Age estimation

Growth increments of all otolith preparations were enumerated twice, non-sequentially, without knowledge of specimen identity. The sequential order of otoliths and the specimen type (left or right sagitta) were selected randomly for each reading. If only one sagitta was available for analysis then it was always read. Increment counts were compared following the second reading and counts differing by one

or more units for specimens with up to 15 daily growth increments and by two or more units for larvae with greater than 15 growth increments were randomized and read for a third time. Increment counts were compared after the third reading, and data for specimens not meeting the acceptance criteria just described were excluded from subsequent analysis. If the three increment counts differed by 2 units, the intermediate count was excluded.

The percentage agreement between enumerations meeting the acceptance criteria was calculated, and the precision of otolith increment counts was evaluated using the coefficient of variation (CV) and the index of precision (Chang 1982), as well as the average percentage error (Beamish and Fournier 1981). The precision of increment enumeration was evaluated for all specimens with otolith increment counts meeting the acceptance criteria without regard to larval herring identity. The precision of increment enumeration was evaluated for larvae collected during each sampling season and between the river channel mainstem and tidal creek habitats. The difference in precision between sampling seasons and habitat types was evaluated by comparing 95% confidence intervals of the CV values (Sokal and Rohlf 1969).

The number of days elapsed since complete yolk absorption was estimated as the mean otolith increment count rounded to the nearest integer. The age of larvae was estimated as the number of days following yolk absorption increased by 2 units to account approximately for the duration of the yolk-sac stage. Hatching dates of larvae were computed as the date of capture minus the estimated age.

Evaluation of larval river herring growth

Larval river herring growth was estimated as the slope of the standard length-at-age relationship. Larval river herring standard length-at-age relationships were analyzed to determine the significance

of differences in growth in 1989 and 1990 (pooled across habitats) and between the mainstem river and tidal creeks (pooled across spawning seasons). To compare growth between years, river herring larvae were divided into an early-spawned cohort, from 9 April to 2 May, and a late-spawned cohort, from 11 May to 26 May, based on visual inspection of hatch date frequency distributions. Larvae with hatch dates falling in an 8-day interval intermediate to the two defined cohorts, from 3 May to 10 May, were excluded to reduce misclassification of larvae between cohorts. Analysis of larval river herring growth between in 1898 and 1990 was restricted to the early-spawned cohort due to limited length and age of late-spawned larvae in 1989 and no late spawned larvae were captured in 1990. Comparison of larval river herring growth between the mainstem river and tidal creeks was limited to larvae with estimated ages ranging from age 3 d to age 14 d due to limited data for 1989.

Standard length-at-age relationships were evaluated using ordinary least-squares (OLS) and weighted least-squares (WLS) linear regression. The weighting factor was the inverse of the squared estimated age ($(age^2)^{-1}$) (Chapter 3). The appropriateness of OLS and WLS regression models for evaluating standard length-at-age relationships was determined using diagnostics tests and by visual examination of residual error distributions (Draper and Smith 1981; Neter et al. 1985; Fox 1991). Diagnostic tests evaluating the fit of length-at-age data to the linear model included the Burn-Ryan test (Burn and Ryan 1983), the pure error F test, and the Conover-Johnson-Johnson homogeneity of variances test (Conover et al. 1981; Fox 1991). The Burn-Ryan test is a lack of fit test used to evaluated curvature and lack of fit in data to the linear regression model. The significance of linear regression models for estimating the residual error mean square ($\sigma^2_{N\cdot y}$) was evaluated using the standard pure error F test (Draper and Smith 1981; Neter et al. 1985). The Conover-Johnson-Johnson homogeneity of variances test is a one-way analysis of variance of the $z_{ij} = |y_{ij} - \hat{y}_i|$, where $\hat{y}$ is the

median y of the ith group. Heteroscedasticity inflates the difference between group means producing a large F test statistic (Fox 1991). Normality of observed values and of the residual error values was assessed using normal probability plots and correlations between observed values or residual values and the associated normal probability scores. Extreme observations were tested for statistical significance as possible outliers using the maximum normed residual criterion (Snedecor and Cochran 1980).

Average increment width was evaluated to identify specimens for which increment counts were severely over- or undercounted to determine whether such specimens should be considered as statistical outliers. The average increment width was computed as:

$$[RADIUS - (YSA / 2)] / COUNT \qquad \text{Eq. 4-3,}$$

where $RADIUS$ = maximum radius along maximum otolith diameter,

YSA = yolk sac absorption check, and

$COUNT$ = number of otolith daily-growth increments.

The average increment width was regressed against age to determine if increment width changed with age.

Differences in larval river herring growth between early-spawn cohorts of 1989 and 1990 and between mainstem river and tidal creeks pooled across seasons were analyzed using weighted analysis of covariance (ANCOVA). Weighted ANCOVA was conducted using $((age^2)^{-1})$ as the weighting factor. If the difference between groups was not significant then the average rate of change in standard length with age for the pooled groups was used to estimate growth.

Potential larval river herring survival based on growth rate

The potential number of larvae surviving from initiation of exogenous feeding to transformation to the juvenile stage was estimated

for the river mainstem and the tidal creeks based on the estimated larval stage duration in each habitat. Larval river herring standard length at the initiation of exogenous feeding was estimated as 5 mm and final standard length at transition was estimated as 20 mm. The difference, 15 mm, was the length that larvae must increase prior to transformation. The time required to achieve this growth is the larval stage duration and was estimated as

$$t = 15 \text{ mm} / g \ (\text{mm} \cdot \text{d}^{-1}) \qquad \text{Eq. 4-4,}$$

where t = the larval stage duration, and

g = the estimated growth rate.

This analysis assumes constant growth throughout the larval stage at rates estimated for each habitat and no migration of larvae between the mainstem river and tidal creeks. The number of larvae surviving to the juvenile stage was then calculated over a range of instantaneous mortality rates using the exponential decay equation:

$$N_t = N_o \cdot e^{(-zt)} \qquad \text{Eq. 4-5,}$$

where N_t = the number of larvae surviving to the juvenile stage,

$N_o = 10^6$ larvae at the initiation of exogenous feeding,

z = instantaneous mortality, and

t = larval stage duration.

Evaluation of hatch date frequency distribution

The chi-square tests for independence were used to test whether hatch date frequency distributions for river herring larvae captured in the mainstem river and in the tidal creeks were independent of river flow and time of hatching (early-hatch and late-hatch groups) in 1989 and 1990. Division of early-hatch and late-hatch groups differed

between seasons; the 1989 early-hatch group was defined as hatch dates occurring prior to 1 May, and the 1990 early-hatch group was defined as hatch dates occurring prior to 24 April. River flow was arbitrarily divided into low (<1200 cfs) and high (≥ 1200 cfs) flow levels so that both flow levels were present for chi-square analyses for each season.

Computer Analyses

Analysis of variance used for evaluating the distributions and abundances of river herring larvae and potential zooplankton prey and chi-square analyses of hatch date frequency distributions were computed using the SPSS-PC microcomputer statistical package. Linear regression analyses and associated diagnostic tests and the analysis of covariance were conducted using the MINITAB microcomputer statistical package.

RESULTS

Environmental conditions

Temperature

Mean daily water temperature in 1989 and 1990 ranged from 11.0 °C to 24.3 °C and from 11.8 °C to 21.6 °C, respectively. Mean monthly water temperature for March was higher in 1990 but did not differ for April or May between years (Table 4-4). Average daily air temperature was used to compare seasonal trends between 1989 and 1990 since a continuous record of water temperature was not available. Regression analyses relating average daily water temperature to average daily air temperature were significant for the mainstem river ($T\ °C_{water} = 10.9 + 0.365\ T\ °C_{air}$, $F = 9.91$, $p = 0.006$) and the five habitats ($T\ °C_{water} = 10.2 + 0.546\ T\ °C_{air}$, $F = 11.46$, $p < 0.000$). Average daily water temperature showed relatively close correspondence to average air temperature for both 1989 and 1990 (Figs. 4-6A and 4-6B, respectively).

Within-season difference in air temperature was less in 1990. Mean monthly air temperature was about 2.5 °C higher in March 1990 than

in March 1989 while mean monthly air temperatures were similar for both April and May in both years, about 1 °C difference (Table 4-4). Air temperature increase relative to calendar day number was T $°C_{air}$ = 22.3 + 0.317 day number ($F = 86.59$, $p < 0.000$) for 1989 and T $°C_{air}$ = 34.9 + 0.222 day number ($F = 36.71$, $p < 0.000$) for 1990. Air temperature in March 1989 during a single day and over a four-day period exceeded 20 °C with the latter occurring in late March (Fig. 4-6A). In contrast, air temperature in mid-March 1990 during one six-day period exceeded 20 °C (Fig. 4-6B). Differences in air temperature between the two seasons was greater prior to mid-April than after mid-April (Fig. 4-6C). Seasonal variation in the timing and magnitude of the late-winter/early-spring warming trend may affect adult river herring spawning and, consequently, may influence the production river herring larvae relative to the onset of the spring plankton bloom.

Rainfall and river flow

Rainfall was heavier in 1989 than in 1990 although the number of rainfall events were similar. Rainfall in both years was most prevalent primarily from about mid-March to mid-April and from late April to late May (Figs. 4-7A and 4-8A, respectively). From late March to mid-April, four rainfall events in 1989 and only one event in 1990 exceeded 1.0 cm. From late April to late May, four rainfall events in 1989 and three in 1990 exceeded 1.0 cm. Three major rainfall events during early May 1989 exceeded 2 cm, but no event prior to late May 1990 exceeded this amount.

Mean monthly river flow was higher in March and May and lower in April in 1989 (Table 4-4). High river flows showed close correspondence with rainfall events in both years (Figs. 4-7 and 4-8, respectively). The frequency of higher river flows was similar during both seasons (Figs. 4-7B and 4-8B). River flows exceeding 2000 cfs occurred from about early to mid-March through mid-April and after about 1 May in both years, while river flow from about 20 April to about 1 May was

relatively low. River flow regimes in 1989 and 1990 differed primarily in magnitude. River flow during three events from 1 May to 15 May, 1989, exceeded 5000 cfs with maximal flow of about 8400 cfs. River flow was less intense in 1990, two high river flow events occurred from 1 May to 15 May but maximal flows were lower than 3000 cfs.

Dissolved oxygen and water transparency

Mean dissolved oxygen concentration did not differed between the 1989 and 1990, although it was lower for May 1989 and for April 1990 than for remaining months (Table 4-4). Dissolved oxygen often was lower upstream in the study area in both seasons but this pattern was not always observed (Fig. 4-9). Dissolved oxygen was not markedly different between the five habitats during any sampling event (Table 4-5). Water transparency, by comparison, was often greater upstream than downstream in both years (Fig. 4-10), and was often greater in the river channel than in the other habitats (Table 4-6).

Factors affecting primary production in the tidal freshwater zone may affect zooplankton productivity and influence prey availability for herring larvae. Dissolved oxygen concentrations were relatively lower from about early to mid-May 1989 in association with high rainfall and elevated river flow. River flow explained a significant amount of variation in dissolved oxygen concentration ($F = 14.94$; $p = 0.006$; $df = 8$; $r^2 = 0.635$) when data associated with the high-flow event (week 1 to week 3 of May 1989) were excluded from the analysis, but no relationship was found when these data were included in the analysis ($F = 0.1$; $p = 0.917$; $df = 10$; $r^2 = 0.0$) (Fig. 4-11). Dissolved oxygen increased with increased river flow up to about 3000 cf suggesting that short-duration water-flow events of low to moderate intensity may not adversely affect primary production in the tidal freshwater reach. Extreme flow events, however, adversely affect dissolved oxygen concentration and primary

production, possibly in association with short residence time, increased turbidity and increased oxygen demand.

Composition of clupeid ichthyofauna

The composition of river herring and gizzard shad yolk-sac larvae and larvae in ichthyoplankton collections was consistent between 1989 and 1990 (Figs. 4-12 and 4-13) and between habitats (mainstem river and tidal creeks) (Figs. 4-14 and 4-15). River herring yolk-sac larvae were predominant earlier in the season than gizzard shad yolk-sac larvae. The percent composition of gizzard shad yolk-sac larvae did not exceed about 90% until late May 1989 but it was about 100% by early May 1990. The greater percentage of gizzard shad larvae in 1990 was likely a consequence of warmer water temperature which may have prompted earlier spawning. In contrast to the marked shift in the percent composition of yolk-sac larvae, river herring larvae always predominated. A number of possible explanations may account for this observation: 1) gizzard shad larvae experienced excessive mortality during the transition to exogenous nourishment, 2) gizzard shad larvae became unavailable to the sampling gear following yolk absorption, or 3) the SVL/SL ratio was not a unique character for delimiting river herring and gizzard shad larvae.

Length frequencies of river herring and gizzard shad larvae

Larvae captured using towed plankton nets in the mainstem river in 1989 ranged from 4 to 12 mm SL for river herring and from 4 to 8 mm SL for gizzard shad with predominant size classes of 5 mm SL and 6 mm SL (Fig. 4-16). Larvae captured in the mainstem river and thoroughfare using pushed nets showed a similar, narrow size distribution ranging from 4 to 6 mm SL in 1989 and from 4 to 7 mm SL in 1990 (Figs. 4-17 and 4-18, respectively). In contrast, lengths of larvae captured in the two tidal creeks using pushed nets ranged from 4 to 15 mm SL in 1989 and from 4 to 11 mm SL in 1990. The smaller upper size limit for specimens

collected in 1990 may have been due to the shorter sampling season. Early preflexion larvae ranged from 4 to about 8 mm SL, although a few larger larvae (9 to 10 mm SL) were classified as early preflexion larvae possibly due to late development of the dorsal fin or misclassification of the larval stage. Late preflexion larvae ranged from 7 to 10 mm SL, and postflexion larvae were ≥9 mm SL. Abundances of river herring and gizzard shad larvae along the mainstem river and in the potential nursery habitats in 1989 and 1990 are summarized by date, location of capture and developmental stage (habitats only) in Appendix 4-C.

River herring early life stages and zooplankton

Distribution along the mainstem Pamunkey River channel

Herring eggs

River herring and gizzard shad eggs are morphologically indistinguishable and are semi-demersal and adhesive so that their abundance in the water column relative to the river bottom or adhered to detritus or other substrates might be quite variable. Nevertheless, the present research provides an indication of herring egg distribution within the study area. Herring egg occurrence within and between strata was highly variable (Fig. 4-19). Herring eggs were captured primarily in lower and upper strata of the study area in both years. Maximal herring egg relative density in the mainstem channel exceeded 1300 eggs·100 m^{-3} in stratum 1 on 6 April 1989 and was about 300 eggs·100 m^{-3} in stratum 5 on 10 April 1990. Herring egg abundances in 1989 and 1990 were similar at comparable time periods. Maximal herring egg abundance in Cumberland Thoroughfare exceeded 1500 eggs·100 m^{-3} on 18 April 1989 and exceeded 900 eggs·100 m^{-3} on 27 April 1990 (Fig. 4-20A).

One possible explanation for reduced herring egg abundance in the middle reach of the study area may be selection of out-of-channel areas for spawning. Herring egg abundance in Cumberland Thoroughfare, for example, was always higher than herring egg abundance in stratum 1 to

stratum 4, and it was often higher than herring egg abundance in strata 5 and 6 (Table 4-7). Herring eggs occurred consistently in Cumberland Thoroughfare in March and April compared to May suggesting that this area may be utilized preferentially by river herring spawning early in the season. Only for two of 11 sampling events in 1989 were herring eggs found in the mainstem river channel but not in the thoroughfare, both occurring in May (Table 4-7). Higher herring egg abundance in Cumberland Thoroughfare may result from a lower dispersal of eggs than occurs in the mainstem river, and might occur also if advection into Cumberland Thoroughfare exceeds exportation.

River herring larvae

River herring yolk-sac larvae were captured from 28 March to 25 May 1989. Abundances exceeding 100 yolk-sac larvae·100 m^{-3} were common from mid- to late April, and peak abundances exceeding 1000 yolk-sac larvae·100 m^{-3} occurred on 22 April and 3 May in stratum 6 (Fig. 4-21A). River herring early preflexion larvae were captured from 4 April to 25 May 1989. Abundances exceeding 100 larvae·100 m^{-3} occurred in the lower half of the study area from about 6 April to about 18 April and occurred throughout most of the study area from about 25 April to about 3 May (Fig. 4-22A). Abundances exceeding 1000 larvae·100 m^{-3} occurred in strata 2 and 4 on 3 May and in stratum 4 on 5 May; these strata were located to either side of Cumberland Thoroughfare. Maximal abundance of yolk-sac larvae in Cumberland Thoroughfare was about 450 yolk-sac larvae·100 m^{-3} on 22 April 1989, four days after the observed maximal abundance of herring eggs (Fig. 4-20B). Maximal abundance of early preflexion larvae in the thoroughfare was about 550 larvae·100 m^{-3} on 3 May, about nine days after the observed maximal abundance of yolk-sac larvae (Fig. 4-20C).

River herring yolk-sac larvae were captured during all sampling events from mid-March to early May 1990. Abundances in 1990 were

usually below 100 yolk-sac larvae·100 m^{-3} which were less than in 1989 at comparable time periods, except in March (Fig. 4-21B). Abundance in Cumberland Thoroughfare showed a slight increase over time, from 25 yolk-sac larvae·100 m^{-3} on 21 March to about 50 yolk-sac larvae·100 m^{-3} on 27 April (Fig. 4-20B). Yolk-sac larvae were captured on 21 March 1990 indicating that spawning occurred in conjunction with higher temperatures in mid-March.

Abundances of early preflexion river herring larvae in 1990 were below about 100 larvae·100 m^{-3}, except in the upper reach of the study area in late April when observed maximal abundance exceeded 1000 larvae·100 m^{-3} in stratum 5 (Fig. 4-22B). Abundances in strata along the mainstem river channel were similar in 1989 and 1990 for collections made from mid-March to mid-April. Abundances were higher in early May 1990 than in early May 1989, but were similar to relative densities observed in late May 1989 following the passage of the high-flow event.

Full factorial analyses of variance (ANOVA) were used to determine the statistical significance of differences in the abundance of river herring yolk-sac larvae and early preflexion larvae between strata along the mainstem river, between time intervals of the sampling season, between sampling seasons, and of all interaction terms. ANOVA results were similar for both yolk-sac larvae (Table 4-8) and early preflexion larvae (Table 4-9). Interactions between factors were not significant for either group. Differences in the abundance of yolk-sac larvae and in the abundance of early preflexion larvae between strata were not significant because of high within-stratum variability. However, yolk-sac larvae were slightly more abundant upstream while the abundance of early preflexion larvae was similar between strata (Fig. 4-23A).

Differences in the abundances of yolk-sac larvae and early preflexion larvae between time intervals and sampling seasons were significant (Tables 4-8 and 4-9, respectively). The highest mean abundance of yolk-sac larvae occurred during interval 2 (10 April to 22

April), and the highest mean abundance of early preflexion larvae occurred during interval 3 (25 April to 5 May) (Fig. 4-23B). The mean abundance of yolk-sac larvae was higher than that of early preflexion larvae in 1989 but was lower than that of early preflexion larvae in 1990 (Fig. 4-23C). Mean abundances of both yolk-sac larvae and early preflexion larvae were lower in 1990 than in 1989 (Fig. 4-23C).

River flow affects larval river herring distribution along the river mainstem as shown by the marked decline in early preflexion larvae in association with the high-flow event of early May 1989. However, yolk-sac larvae did not exhibit a similar decrease in abundance suggesting that high river flow may not affect these life stages equally. Lower river flow reduces the advective transport of river herring larvae as indicated by similar distributions of yolk-sac larvae and early preflexion larvae in late May 1989, following the high-flow event, and in early May 1990. Yolk-sac larvae were absent from a large number of collections for 1990 (Fig. 4-21), primarily in the lower reach of the study area suggesting that yolk-sac larvae were not advected downstream in 1990 to the same extent as in 1989. Other factors, however, may also affect the distribution of yolk-sac larvae between seasons, such as spawning site selectivity by adults as influenced by water temperature or river flow.

Zooplankton

Zooplankton abundance along the mainstem river channel in 1989 was characterized by three periods when total abundance exceeded 100 zooplankters$\cdot \ell^{-1}$ in the lower half of the study area: 22 March to 6 April, 22 April to 5 May, and 20 May to 25 May (Fig. 4-24A). Zooplankton abundance in late March and early April 1990 was below 100 zooplankters$\cdot \ell^{-1}$, but exceeded 100 zooplankters$\cdot \ell^{-1}$ in late April as occurred in 1989 (Fig. 4-24B). In contrast to 1989, zooplankton abundance exceeded 100 zooplankters$\cdot \ell^{-1}$ in mid-May 1990 and was higher

farther upstream during late April and mid-May in association with reduced river flow.

Rotifers, copepodites and nauplii, and cladocerans are prey for river herring larvae. Variable composition and abundance of these groups in the potential prey field available to river herring at first-feeding and throughout the larval stage may influence growth and survival. Abundances of these groups differed spatially and temporally during and between the 1989 and 1990 seasons. Variable abundances of these groups shows that the potential prey field for river herring larvae hatching at different times during the spawning season may differ markedly.

Zooplankton from 22 March to 6 April 1989 was dominated by copepod nauplii and copepodites at abundances exceeding 100 individuals$\cdot \ell^{-1}$ (Fig. 4-25A). Rotifers and cladocerans were dominant during 22 April to 5 May (Figs. 4-26A and 4-27A, respectively); rotifer abundances exceeded 100 individuals$\cdot \ell^{-1}$ from about 3 May to about 5 May and cladoceran abundances exceeded 100 individuals$\cdot \ell^{-1}$ from about 28 April to about 3 May. Rotifers and copepod nauplii and copepodites were dominant during 20 May to 25 May; rotifer abundances exceeded 100 individuals$\cdot \ell^{-1}$ throughout the lower half of study area but copepod nauplii and copepodite abundance exceeded 100 individuals$\cdot \ell^{-1}$ only in stratum 3 (Fig. 4-25A).

The spatial and temporal distributions of copepod nauplii and copepodites in 1990 differed from 1989 (Fig. 4-25B). Copepod nauplii and copepodite abundances exceeded 100 individuals$\cdot \ell^{-1}$ on 27 April from stratum 3 to stratum 5; whereas, abundances at this time in 1989 were usually below 50 individuals$\cdot \ell^{-1}$. Nauplii and copepodite abundances were lower from mid-March to early April in 1990 compared to the same time in 1989. Distributions of rotifers, by comparison, were similar between seasons (Fig. 4-26B). Rotifer abundances in 1990 were usually below 50 individuals$\cdot \ell^{-1}$ from mid-March through April and exceeded 100

individuals·ℓ^{-1} in mid-May from stratum 1 to stratum 4, slightly farther upstream compared to 1989. Higher rotifer abundances on 9 May 1990 compared to early to mid-May 1989 are suggested to result from lower river flow and increased residence time enabling rotifer populations to expand. Cladoceran abundance in 1990 was highest in late April at about the same period when abundance was maximal in 1989. Observed abundances in 1990, however, were less than about 30 individuals·ℓ^{-1} (Fig. 4-27B). Limited temporal duration of higher cladoceran abundance in 1989 suggests that higher abundances of cladocerans may not have been observed in 1990 because of the low frequency of sampling.

Analysis of variance of total zooplankton abundance showed that differences associated with each main effect (stratum, time of season, and sampling season) were statistically significant (Table 4-10). All interactions were not significant (Table 4-10). Mean zooplankton abundance decreased progressively upstream from about 161 zooplankters·ℓ^{-1} in stratum 1 to about 21 zooplankters·ℓ^{-1} in stratum 6 (Fig. 4-28A), was highest for time interval 3, 141 zooplankters·ℓ^{-1} (Fig. 4-28B), and was higher for 1989 as compared to 1990, 74 zooplankters·ℓ^{-1} and 65 zooplankters·ℓ^{-1}, respectively.

Distributions between potential nursery habitats

Herring eggs

Few herring eggs were captured in surface waters of the five potential habitats in either year, except for 30 May 1989 (Table 4-11). Eggs captured on 30 May 1989 probably were gizzard shad, but positive confirmation of species identity was not possible. Herring eggs often were more abundant in Cumberland Thoroughfare than in the remaining habitats, and were captured more often in April than in early or mid-May. Low herring egg abundance in pushnet collections was likely a consequence of the semi-demersal and adhesive nature of these eggs.

River herring larvae

Ichthyoplankton collections made in the five potential nursery habitats in 1989 showed that river herring larvae were abundant in the tidal creeks; therefore, sampling was conducted with greater frequency in 1990 to characterize further the distribution of larvae between these areas. Similarities were evident between 1989 and 1990 despite the lower frequency of sampling in 1989. First, the abundance of yolk-sac larvae was greater in collections made in April than in May (Figs. 4-29 and 4-30). Second, yolk-sac larvae were captured in May from Holts Creek in both years, albeit at low relative density, but only in 1990 were they captured in the channel and over the shoulder at this time (Figs. 4-29 and 4-30). Last, late preflexion and postflexion larvae were captured primarily in the tidal creeks, especially Holts Creek, in May (Figs. 4-29 and 4-32). A few older larvae were captured in 1990 in the mainstem river and thoroughfare.

The spatial and temporal distributions of river herring larvae differed markedly between the five potential nursery habitats in each season. In 1989, maximal abundance of river herring yolk-sac occurred in Big Creek in mid-April with lower abundance occurring over the river channel and river shoulder (Fig. 4-29). Early preflexion larvae were captured from all habitats in mid-April compared to mid- or late May. The abundance of river herring early preflexion larvae was highest in the tidal creeks, intermediate in the thoroughfare, and lowest in the mainstem river in mid-April, and had decreased in all habitats by mid-May, except in Holts Creek where abundance increased over 2-fold, from 70 larvae·100 m^{-3} to 150 larvae·100 m^{-3}. Abundances of river herring early preflexion larvae declined to about 10 larvae·100 m^{-3} in all habitats by 30 May, except over the shoulder where no larvae were captured. River herring late preflexion and postflexion larvae were captured in Big Creek at relatively low abundance, 3 larvae·100 m^{-3} in mid-April and 14 larvae·100 m^{-3} in mid-May, respectively. Late

preflexion and postflexion larvae were captured in Holts Creek in mid-May at abundances of 78 larvae·100 m^{-3} and 27 larvae·100 m^{-3}, respectively. No late preflexion or postflexion larvae were captured in any potential nursery habitat in late May.

In 1990, river herring yolk-sac and early preflexion larvae (Figs. 4-30 and 4-31, respectively) were collected as early as 18 March with yolk-sac larvae occurring in all habitats and early preflexion larvae occurring in all habitats except Holts Creek. By 8 April, river herring early preflexion larvae were captured only in Cumberland Thoroughfare and Holts Creek. The timing of maximal abundances of river herring yolk-sac larvae between habitats differed: 16 April over the river shoulder, 22 April in Cumberland Thoroughfare and in Holts Creek, and 29 April over the river channel and in Big Creek (Fig. 4-30). In contrast, maximal abundance of river herring early preflexion larvae occurred on 22 April in Cumberland Thoroughfare, over the river channel, and in Big Creek and on 29 April over the river shoulder (Fig. 4-31). In Holts Creek, the abundance of river herring early preflexion larvae was highest from 29 April to 8 May (Fig. 4-31). By 12 May, the abundance of early preflexion larvae fell to zero over the channel and shoulder, did not change in Big Creek, and increased in Cumberland Thoroughfare as it decreased in Holts Creek (Fig. 4-31).

Late preflexion larvae were captured initially on 29 April from Big Creek, Cumberland Thoroughfare and the river channel (Fig. 4-32). Postflexion larvae were initially captured on 8 May from Big Creek, Holts Creek, and the river shoulder (Fig. 4-32). The low incidence of late preflexion and postflexion larvae in Cumberland Thoroughfare and the mainstem river suggests either that these older larvae were absent from these habitats, that most of these larvae in these habitats were able to escape capture, or that most of these larvae were not accessible to the sampling gear. In contrast, large numbers of late preflexion and postflexion larvae were captured in the tidal creeks, especially Holts

Creek. River herring late preflexion larvae abundance in Holts Creek decreased from 1623 larvae·100 m^{-3} on 8 May to 345 larvae·100 m^{-3} on 12 May, but river herring postflexion larvae abundance increased from 67 larvae·100 m^{-3} on 8 May to 178 larvae·100 m^{-3} on 12 May. In Big Creek, by comparison, abundances of both late preflexion and postflexion larvae were highest on 8 May, 503 larvae·100 m^{-3} and 28 larvae·100 m^{-3}, respectively, and declined to about 5 larvae·100 m^{-3} by 12 May.

Analysis of variance river herring yolk-sac larvae abundance between late April (20 April to 29 April) and early May (8 May to 18 May) found significant interaction between time interval and sample season, but nonsignificant interactions between these factors and habitat (Table 4-12). Nonsignificant difference between habitats was likely due to high intra-site variability. Mean abundance of river herring yolk-sac larvae was greater in all habitats in April with highest relative abundance in Big Creek and lowest relative abundance in Holts Creek, although it was higher in Holts Creek in May (Fig. 4-33A). Mean abundance was higher in Big Creek in 1989 and was higher in Cumberland Thoroughfare and Holts Creek in 1990 than in the other habitats, and it was greater in all habitats in 1990 than in 1989 (Fig. 4-33B).

Analysis of variance for river herring early preflexion larvae, late preflexion larvae, and postflexion larvae abundances (Table 4-13) found nonsignificant interactions between developmental stage and habitat, habitat and sample season, and time interval and sample season suggesting that larvae were distributed similarly in both seasons. Significant interaction was found between habitat and time interval indicating change in distributions and abundances of the three developmental groups in the study area (Fig. 4-34A). Mean river herring early preflexion larvae abundance was higher in April while that for late preflexion and postflexion larvae was higher in May resulting in a significant interaction between developmental stage and time interval

(Fig. 4-34B). Mean abundance was higher in 1990 possibly because higher densities were encountered due the greater frequency of sampling which may have produced the significant interaction between developmental stage and sample season (Fig. 4-34C). However, environmental factors, especially rainfall and river flow, might have contributed to differences between the two years.

River herring early preflexion larvae abundance was highest in Big Creek in April while abundances of all developmental stages were highest in Holts Creek in May (Fig. 4-35). Mean abundances of river herring early preflexion, late preflexion and postflexion larvae were usually higher in 1990 than in 1989 for all habitats, except for early preflexion larvae in Holts Creek and postflexion larvae in Big Creek (Fig. 4-36).

Zooplankton

Total zooplankton (rotifers, copepod nauplii and copepodites, and cladocerans) abundance was consistently higher in the tidal creeks than in the thoroughfare and mainstem river in both 1989 and 1990. Differences in zooplankton abundance between habitats were greater in 1990 than in 1989 possibly due to differences in residence time in each year (Fig. 4-37). Total zooplankton abundance was greater in Big Creek than in Holts Creek for most sampling events made in either year from mid-March (18 March) to mid-April (22 April), but was greater in Holts Creek from late April (29 April) to late May (30 May). Total zooplankton abundance in Cumberland Thoroughfare, over the channel, and over the shoulder fluctuated, but in early to mid-May it was lowest over the channel, intermediate over the shoulder, and highest in Cumberland Thoroughfare.

Differences in zooplankton composition were evident between habitats and sampling seasons. Copepodites and nauplii were predominant in all habitats in mid-April 1989, but rotifers were predominant in the

thoroughfare and both tidal creeks by mid-May and in all habitats by late May (Fig. 4-38). In 1990, copepodites and nauplii were numerically dominant over the channel and the shoulder throughout April and in the thoroughfare during most of April (through 22 April), but were replaced thereafter by rotifers as the numerically dominant group (Fig. 4-39). Rotifers were numerically dominant in both tidal creeks throughout the 1990 season (Fig. 4-39). Cladocerans were usually the least abundant group in these collections in both years (Figs. 4-38 and 4-39).

Analysis of variance found significant interaction between main effects for zooplankton group, habitat, time of season, and sample season (Table 4-14). Mean rotifer abundance was higher in all habitats in May (Fig. 4-40A), while mean abundance of copepod nauplii and copepodites was higher or about equal in all habitats in April (Fig. 4-40B). Mean cladoceran abundance was also higher in all habitats in April, except in Holts Creek where abundance was higher in May (Fig. 4-40C). Mean total zooplankton abundance in Holts Creek was higher in May (Fig. 4-40D), primarily due to high rotifer abundance. Mean rotifer abundance was higher in all habitats in 1990 (Fig. 4-41A). Similarly, mean abundance of copepod nauplii and copepodites was also higher in all habitats in 1990, except Holts Creek (Fig. 4-41B). Mean cladoceran abundance was higher in all habitats in 1989 (Fig. 4-41C). Mean total zooplankton abundance was higher in all habitats in 1990, and the difference between seasons was greater in the tidal creeks than in other habitats (Fig. 4-41D). Differences in mean zooplankton abundances between 1989 and 1990 may have been caused by different sampling protocols, but higher rainfall and river flow in 1989 were also likely to affect zooplankton abundance.

Analyses of otolith daily growth increments

Precision of otolith daily growth-increment enumeration

Sagittal otoliths were dissected from 306 field-collected river herring larvae for otolith growth-increment enumeration. Following the second enumeration, 271 (88.6%) specimens had increment counts which met the acceptance criteria for further evaluation. Those which did not meet the acceptance criteria were read again. Otoliths from 298 (97.4%) specimens met the acceptance criteria following the third enumeration. Otoliths from six specimens were not interpretable, and increment counts for otoliths from two specimens did not meet the acceptance criteria and were rejected from further analyses. Precision of daily growth-increment enumeration was greater for larvae sampled in 1990 than in 1989 and for larvae sampled from tidal creeks than from the mainstem channel (Table 4-15), since the majority of tidal creek specimens were sampled in 1990. The results suggest that otoliths from larvae sampled in the mainstem river channel were relatively more difficult to interpret than otoliths from larvae sampled in tidal creeks.

Growth of river herring larvae between seasons

Preliminary evaluation of length-at-age data

Numbers of larvae with available age data are summarized by taxonomic group, sampling season, and habitat type in Table 4-16. The number of river herring larvae sampled from the mainstem river channel was low, probably as a consequence of gear avoidance during sampling. Low sample sizes, especially for larger larvae from the mainstem channel, necessitated pooling data between spawning seasons across habitat type and between habitat type across spawning seasons to analyze growth of larvae over comparable standard lengths and estimated age ranges. Several constraints, addressed below, reduced the sample size and range of standard length-at-age data available for statistical tests

of differences in larval river herring growth either between sampling season or habitat types.

Estimated ages for two specimens were suspected statistical outliers. One specimen, sampled in 1990 from the mainstem river, had an estimated age of 11 d and a standard length of 12.0 mm. Standard length ranged from 6.2 mm to 9.1 mm for other age 11 d specimens sampled in 1990 and from 6.2 mm to 6.5 mm for other age 11 d specimens sampled in the mainstem river channel. The greater length of the suspected outlier suggested that the age of this specimen was underestimated. Analysis showed that the age 11 d datum was a significant statistical outlier for both the 1990 and the mainstem river collections (Tables 4-17 and 4-18, respectively), therefore it was excluded from subsequent statistical analyses of larval river herring length-age relationships.

The second specimen, captured in 1990 from the mainstem river, had an estimated age of 18 d and a standard length of 15.4 mm, and was the only representative of its age class so direct comparison of standard lengths between larvae of similar estimated age was not possible. However, evaluation of maximum otolith diameter for larvae from age 16 d to age 24 d was used as an alternative approach to determine the significance of this datum as a statistical outlier. Maximum otolith diameter for the age 18 d specimen was 163 μm. Only two specimens with older estimated ages had larger maximum otolith diameters: age 21 d (179 μm) and age 24 d (247 μm). Maximum otolith diameters for other river herring larvae with estimated ages from 19 to 24 days ranged from 110 μm to 150 μm. Maximum otolith diameters for age 16 d and age 17 d specimens ranged from 72 μm to 109 μm. These data suggest that otolith diameter relative to standard length was much larger for the age 18 d specimen than for other larvae of similar estimated age. Analysis of otolith diameters for age 17 d to age 19 d specimens showed that otolith diameter for the age 18 d specimen was a significant statistical outlier

(Table 4-19), therefore it was excluded from further analyses of larval river herring length-age relationships.

Growth of river herring larvae in 1989 and 1990.

In this section, standard length-at-age relationships for river herring larvae captured in 1989 and 1990 are evaluated using ordinary and weighted linear regression analyses. A brief summary of this section is provided to aid the reader. The standard length-at-age relationship is evaluated first for 1989 specimens and then for 1990 specimens. The results show that ordinary and weighted least-squares linear regression models do not describe adequately the standard length-at-age relationship for these groups. Next, each group is divided into two age classes (<11 d and ≥11 d) and the standard length-at-age relationship for each age class is evaluated. The results show that a weighted least-squares linear regression model describes adequately the standard length-at-age relationship of each age group. Analysis of covariance is then used to test the statistical significance of differences in the standard length-at-age relationship between age groups within and between seasons. The slope of the standard length-at-age relationship provides a measure of average somatic growth of larvae.

Standard length-at-age relationship within seasons

Analysis of the growth of river herring larvae between spawning seasons was constrained to larvae which had hatched during similar time intervals. River herring larvae sampled in 1989 and 1990 were subdivided into two cohorts based on hatch date frequency distributions (Fig. 4-42). The 'early-spawn' cohort was defined as larvae hatching from 9 April to 2 May, while the 'late-spawn cohort' was defined as larvae hatching from 11 May to 26 May. Larvae hatching from 3 May to 10 May were excluded to minimize misclassification of larvae between the 'early-spawn' and 'late-spawn' cohorts. However, absence of the 'late-

spawned' cohort in 1990 limited the analysis to larvae of the 'early-spawn' cohort.

Larval river herring standard lengths and estimated ages for the 1989 'early-spawn' cohort ranged from 4.5 mm to 15.9 mm and from age 3 d to age 24 d, respectively (Fig. 4-43A). The standard length-at-age relationship for this cohort was not fit adequately by ordinary least-squares (OLS) linear regression (Table 4-20). The Burn-Ryan test found significant curvature and lack of fit of data to the OLS linear model, but the pure error F-test was marginally nonsignificant. Variances between age groups were heteroscedastic. Visual examination of the studentized residual error distribution showed that residual variance increased among younger larvae (<age 11 d) without trend, but residuals for older larvae (≥age 11 d) showed a slight increase in variance and a positive trend (Fig. 4-43B). Weighted least-squares (WLS) linear regression showed slight improvement in the fit of data to the linear model as indicated by the Burn-Ryan test and the pure error F-test as well as improved homoscedasticity (Table 4-20). However, the studentized residuals plot showed that error variance was greater for younger larvae than for older larvae with a trend toward positive residuals within the older ages (Fig. 4-43C).

Larval river herring standard lengths and estimated ages for the 1990 'early-spawn' cohort ranged from 5.3 mm to 12.5 mm and from age 4 d to age 19 d, respectively (Fig. 4-44A). The standard length-at-age relationship was not fit adequately by either OLS or WLS regression as indicated by the Burn-Ryan test and the pure error F-test, although weighting improved homoscedasticity (Table 4-21). Studentized residuals for the OLS regression model were nonrandomly distributed showing increased variance with a negative trend among younger larvae and relatively constant variance with a positive trend among older larvae (Fig. 4-44B). Similar trends were observed in the plot of studentized

residuals for the WLS regression model, except that error variance decreased with age among older larvae (Fig. 4-44C).

Standard length-at-age relationship within age classes

The deviation from linearity for the standard length-at-age relationship of the 1989 and 1990 'early-spawn' cohorts appeared to be associated with a transition in growth trajectory at about age 11 d. The standard length-at-age relationship, therefore, was evaluated for larvae of both cohorts subdivided into younger (<age 11 d) and older (≥age 11 d) age classes. Standard length-at-age for younger larvae of the 1989 cohort was not adequately fit by the OLS model (Table 4-20). The Burn-Ryan test found evidence of significant lack of fit, and the error variances were heteroscedastic. The studentized residuals plot showed a trend of increasing variance with age (Fig. 4-45A); although, residual variance for the age 6 d and age 7 d specimens was relatively low as compared to other ages. Weighting improved the fit of the standard length-at-age data to the linear model for this class so that there was no indication of curvature or lack of fit and also resulted in homoscedastic residual variances (Table 4-20). Weighting improved the scatter of studentized residuals, but a slight trend toward increased variance remained (Fig. 4-45B). Increased correlation between observed standard lengths and studentized residuals with associated normal probability scores for the WLS regression model reflects improved fit of data to the linear model over the OLS regression model (Table 4-20).

Standard length-at-age data for older larvae of the 1989 cohort was adequately fit by the OLS regression model (Table 4-20), and no trend was evident in the studentized residual error distribution (Fig. 4-46A). However, it was necessary to evaluate the fit of the WLS regression model to these data to compare the younger and older age classes. Diagnostic tests showed that these data were adequately fit by the WLS regression model, but the correlation for observed standard

length and studentized residuals with the associated normal probability scores decreased indicating a relatively poorer fit compared to the OLS regression model (Table 4-20). No trend was evident in the studentized residual error distribution (Fig. 4-46B). Differences in parameter estimates between OLS and WLS regression models evaluating standard length-at-age relationships across all ages and in each age class were nonsignificant as indicated by 95% confidence intervals (Table 4-21).

The standard length-at-age relationship for the younger age class of the 1990 'early-spawn' cohort was fit adequately by OLS regression (Table 4-22), although studentized residuals showed a trend toward increased variance with age (Fig. 4-47A). Weighting did not alter the fit of the standard length-at-age data to the linear model nor did it change the correlation between the studentized residuals and the associated normal probability scores, but correlation between observed standard lengths and the associated normal probability scores was reduced (Table 4-22). Weighting also detrended the scatter of studentized residuals (Fig. 4-47B).

The standard length-at-age relationship for the older age class of the 1990 cohort was poorly fit by OLS regression. Diagnostic tests showed significant lack of fit, especially the pure error F-test, but error variances were homoscedastic (Table 4-22). The studentized residual error distribution showed slight reduction in variance with age (Fig. 4-48). The standard length-at-age relationship was fit adequately by WLS regression as indicated by the Burn-Ryan test and the pure error F-test, but error variances were heteroscedastic (Table 4-22). Heteroscedasticity was due to marked reduction in studentized residual error variance with age, but studentized residuals were equitably distributed to either side of the predicted value, except for age 16 d larvae, without trend toward either positive or negative residuals (Fig. 4-48). Correlation between observed standard lengths and associated normal probability scores was lower for WLS regression than for OLS

regression, but correlation of studentized residuals and associated normal probability scores did not differ between the two models. Weighting increased slightly the estimated intercepts and decreased the estimated slopes for regression models relating standard length to age (Table 4-23).

The difference in standard length-at-age relationship for river herring larvae between cohorts and age classes was analyzed using weighted analysis of covariance (WANCOVA) since the diagnostic tests showed that weighting tended to improve the fit of standard length-at-age data to the linear model. The estimated growth of larvae within each age class between the two cohorts did not differ significantly (Table 4-24), but older larvae grew significantly faster than younger larvae (Table 4-25). The pooled growth rate estimates for younger and older larvae were 0.35 $mm \cdot d^{-1}$ and 0.59 $mm \cdot d^{-1}$, respectively.

Growth of river herring larvae between habitat types

Standard length-at-age relationships

Standard lengths and estimated ages of river herring larvae sampled from the mainstem river ranged from 4.2 mm to 15.4 mm and from age 3 d to age 18 d, respectively (Fig. 4-49A). The age 18 d specimen was excluded from statistical analysis (see above), therefore the maximum standard length and estimated age available for this group was 9.6 mm and 14 d, respectively. Diagnostic tests found poor fit of the standard length-at-age relationship to the OLS linear regression model. Error variances were heteroscedastic (Table 4-26) and increased with age (Fig. 4-49B). Weighting improved the fit of data to the linear model, resulting in only marginally significant heteroscedasticity (Table 4-26), and detrended the studentized residual error distribution (Fig. 4-49C). Correlation between standard length or studentized residuals and associated normal probability scores was higher for the WLS regression model than for OLS regression model (Table 4-26).

Standard lengths and estimated ages of river herring larvae sampled from the tidal creeks ranged from 4.1 mm to 15.9 mm and from age 4 d to age 24 d, respectively (Fig. 4-50A). Analysis of standard length-at-age relationship for these larvae was constrained to estimated ages ranging from age 4 d to age 14 d, inclusive, to evaluate larval river herring growth in the tidal creeks and mainstem river. The maximum standard length of age 14 d larvae was 10.5 mm. Diagnostic tests for OLS linear regression found no evidence of deviation from the linear model (Table 4-26). Error variances were homoscedastic (Table 4-26) and the studentized residuals randomly distributed (Fig. 4-50B). Diagnostic tests for WLS regression showed that the standard length-at-age data adequately fit the linear model, but error variance was heteroscedastic (Table 4-26). The studentized residual error distribution was characterized by large variance associated with the age 3 d to age 6 d classes, but studentized residuals for specimens older than age 6 d were relatively uniform (Fig. 4-50C). The distribution of studentized residuals showed no trend or pattern other than the decrease that occurred between the age 6 d to age 7 d specimens. Consequently, the WLS regression model was interpreted as describing adequately the standard length-at-age relationship.

The difference in standard length-at-age relationships for river herring larvae from the tidal creeks and mainstem river was analyzed using weighted ANCOVA since the diagnostic tests showed that weighting tended to improve the fit of standard length-at-age data to the linear model. ANCOVA results showed that the difference in standard length-at-age was significant (Table 4-27). Larval river herring growth was significantly faster in the tidal creeks, 0.46 $mm \cdot d^{-1}$, than the mainstem river, 0.34 $mm \cdot d^{-1}$ (Table 4-28). This small, significant difference in growth yields different stage durations for river herring larvae in these locations. Stage duration in the tidal creeks and in the mainstem river were estimated at 32 days and 44 days, respectively. Differences

in larval stage duration may affect the relative survival of larvae in the tidal creeks and mainstem river from the onset of exogenous feeding to the juvenile stage (Fig. 4-51). An initial abundance of $1x10^6$ river herring larvae at the onset of feeding subjected to an instantaneous mortality rate of 0.2, for example, potentially yields over ten times more larvae surviving to the juvenile stage in the tidal creeks than in the mainstem river, about 1,662 fish and about 151 fish, respectively, assuming that the difference in growth persists throughout the larval stage and that larvae do not migrate between locations.

Average increment width.

The change in average daily growth-increment width with age in otoliths from larvae captured in the tidal creeks was significant, about 0.1 $\mu m \cdot d^{-1}$, while it was not significant in otoliths from larvae captured in the mainstem river (Table 4-29). Increasing increment width with age for larvae from the tidal creeks indicates accelerated somatic growth while constant increment width for larvae from the mainstem river indicates constant somatic growth. This result supports the previous finding that growth of larvae in the tidal creeks was faster than that in the mainstem river. While average increment width differed between larvae from the two locations, variability (indicated by 95% prediction intervals for the respective regression models) appeared to preclude increment width as a potential indicator of the location in which larvae reside (Fig. 4-52).

Hatch dates in relation to the abundance of river herring larvae and zooplankton potential prey

Hatch dates for the 1989 sampling season

Hatch dates in 1989 ranged from 9 April to 17 May with a median hatch date of 28 April for river herring larvae captured from the mainstem river, and from 15 April to 27 May with a median hatch date of

10 May for river herring larvae captured in the tidal creeks (Fig. 4-53A and B, respectively). About 82 percent of hatch dates for larvae from the mainstem river ranged from 9 April to 30 April, while about 88 percent of hatch dates for larvae from the tidal creeks ranged from 1 May to 27 May. Median hatch dates differed by about two weeks. Ranges of the hatch date distributions were similar, 39 days for larvae from the mainstem river and 42 days for larvae from the tidal creeks.

Hatch date frequency distributions were compared to the mean abundances of river herring larvae and their potential zooplankton prey (Fig. 4-53). Yolk-sac larvae in the mainstem river showed two periods of higher abundance: 22-25 April and 3 May (Fig. 4-53C). Yolk-sac larvae in Cumberland Thoroughfare also showed two periods of high abundance, 22 April and 11 May, but only the first coincided partially with the earlier peak in abundance in the mainstem river (Fig. 4-53D). In comparison, abundances of early preflexion larvae in the mainstem river and thoroughfare were maximal on 3 May (Fig. 53C and D, respectively). The greatest frequency of larval herring hatch dates from the mainstem river occurred prior to the maximal abundances of early preflexion larvae.

Larval river herring hatch dates from the mainstem river were associated with higher cladoceran abundance, while larval river herring hatch dates from the tidal creeks occurred primarily during the subsequent period of low prey abundance in the mainstem river (Fig. 4-53E). Differences in zooplankton abundances in the mainstem river and tidal creeks potentially affect the survival of first-feeding larvae. Hatch dates of larvae in the mainstem river and in the tidal creeks appear to be associated with higher zooplankton abundances in each locality. For example, between 20 April and 18 May, 1989, average rotifer abundance increased about 8-fold in the tidal creeks compared to about 2-fold in the mainstem river (Fig. 4-54). In contrast, nauplii and copepodite abundance decreased by about 46 percent in the tidal

creeks compared to about 29 percent in the mainstem river. Average cladoceran abundance changed the least in the tidal creeks decreasing by only about 9 percent compared to about 59 percent in the mainstem river.

Hatch dates for the 1990 sampling season

Two groups of larvae were captured in the study area in 1990: an early-hatch group associated primarily with the river mainstem and the thoroughfare (Figs. 4-55B, C, and D) and a late-hatch group associated primarily with the tidal creeks (Fig. 4-55A and E). Hatch dates ranged from 15 April to 7 May for the early-hatch group with about 67 percent of hatch dates from 15 April to 23 April and about 33 percent from 27 April to 7 May. Hatch dates for late-hatch larvae ranged from 21 April to 5 May with about 91 percent of hatch dates from 24 April to 5 May. Median hatch dates, 22 April for larvae from the mainstem river and 27 April for larvae from the tidal creeks, differed by about one week.

Hatch dates for larvae from the mainstem river corresponded primarily to the period of maximal abundance of early preflexion larvae in the river channel and thoroughfare (Fig. 4-55B and C, respectively). Late-hatching larvae were not as abundant as early-hatching larvae in these areas. Early preflexion larvae abundance over the river shoulder increased along with that in the channel, the thoroughfare and in Big Creek, but abundance over the shoulder continued to increase until 29 April while it decreased in these other locations. Larval river herring hatch date frequency distributions from the mainstem river suggests that collections made over the shoulder consisted of early-hatching larvae on 22 April and of late-hatching larvae on 29 April (Fig. 4-55D).

Preflexion larvae captured in Holts Creek were primarily from the late-hatch group (Fig. 4-55E). The hatch date frequency distribution for river herring from Big Creek was similar to that for larvae captured in Holts Creek, and there was little apparent association between hatch dates and early preflexion larvae abundance in this creek (Fig. 4-55A).

Relatively few larvae were captured in Big Creek with hatch dates corresponding to the early-hatch group.

Larvae captured in the tidal creeks which had developed pigment characters useful for determining species identity were identified as alewife. No larvae captured in the tidal creeks or in the mainstem river were identified as blueback herring. This does not imply, however, that only alewife larvae occurred in the tidal creeks. Identifiable blueback herring larvae may not have been captured because they may not have develop sufficiently to exhibit diagnostic pigment patterns prior to the end of the sampling season, especially in 1990.

Evaluation of hatch dates relative to river flow

Larval river herring hatch date frequency distributions in 1989 suggest that hatch dates for larvae in the tidal creeks might have been associated with higher river flow. River flow was lower in 1990 and no obvious association was observed. Chi-square tests of independence evaluating hatch date frequencies for larvae from the mainstem river and tidal creeks with river flow and time of season (early-hatch and late-hatch groups) were significant indicating that hatch dates were not independent of the factors in question. However, only the association between location of capture and relative time of hatching was consistent in both 1989 and 1990 (Tables 4-30 and 4-31, respectively). Hatch dates were earlier for larvae from the mainstem river than from the tidal creeks. The association between river flow and location of capture of larvae in 1989 showed that hatch dates for larvae from the tidal creeks were more prevalent during periods of high water flow and were more prevalent for larvae capture in the river during periods of low water flow. In contrast, hatch dates for larvae from the tidal creeks in 1990 were more prevalent during periods of low flow, and equal numbers of larvae from both locations had hatch dates associated with periods of high flow. A similar association was found between time of capture and

river flow. Hatching was not, therefore, more frequent in the tidal creeks during higher river flow in 1989 or 1990.

DISCUSSION

Results of the present research are discussed in relation to factors which may influence the ecology and vital rates of river herring larvae, including habitat utilization, the zooplankton prey field and potential predation. Components of habitat utilization by river herring larvae which are discussed include distribution, abundance, growth, and hatch date frequencies. The zooplankton potential prey field is then examined, including prey species composition, abundance and quality with a discussion of the possible significance of a detrital-based microbial food web in the tidal freshwater-oligohaline reach. Possible interactions between river herring larvae with larvae of other species, primarily gizzard shad and threadfin shad, and with potential predators are then considered. Pertinent literature on potential predators of anadromous and landlocked *Alosa* is reviewed as an overview to potential predation on river herring larvae in the Pamunkey River tidal freshwater-oligohaline reach. Trophodynamics is suggested to be the principal determinant of larval river herring survival, and a model (Fig. 4-56) is presented to facilitate conceptualization of trophodynamic linkages involving river herring larvae and, perhaps, prompt new questions of herring biology and ecology in tidal freshwater habitats. A second model (Fig. 4-57) is presented to conceptualize factors which may influence the distribution of larvae in the tidal freshwater reach, and which may affect trophodynamic interactions. The trophodynamics model also shows potential larva-larva interactions which to suggest that intra- and interspecific interactions between larvae may influence the growth or survival of larvae.

Habitat utilization by river herring larvae

Distribution between potential nursery habitats

Initial ichthyoplankton collections made in the five potential nursery habitats in 1989 showed that river herring larvae were abundant in Holts and Big creeks and that larval river herring abundance differed between habitats suggesting that larvae may have been nonrandomly distributed throughout the study area. Consequently, these areas were sampled with greater frequency in 1990 and sampling effort along the river channel was reduced. In 1989, larval river herring abundance in the tidal creeks was higher in mid-May than in mid-April or late May. In 1990, larval river herring abundance in the tidal creeks was highest from 8 May to 12 May. These results suggest that river herring larvae utilize these tidal creeks only for a brief time from about mid- to late April to about mid-May. However, gear avoidance by larger larvae and juveniles and unknown patchiness of larvae limits the interpretation of tidal creek utilization by river herring. Additional sampling using techniques able to capture larger larvae and young juveniles, from about 11 mm SL to about 25 mm SL, extended through May and June is needed to evaluate further the utilization of tidal creeks in the Pamunkey River and to detect possible differences in the distribution of alewife and blueback herring.

Differences in larval river herring abundances between 1989 and 1990 may have been influenced by the timing and frequency of sampling events, but similarities were observed between the two seasons despite different sampling schedules (Fig. 4-36). Late preflexion and postflexion larval river herring abundances were highest in Holts Creek, and the apparent progressive increase in larval river herring abundance in Holts Creek suggest an immigration of larvae into this creek. However, sampling gear avoidance or inaccessibility of larvae to the gear in other habitats is not known and may have influenced observed abundances. Mean abundances of early preflexion larvae between 1989 and

1990 were more similar in Holts Creek than in remaining habitats suggesting that events in 1989, possibly associated with higher rainfall and river flow, might have caused greater mortality of larvae in the other habitats. High abundance of late preflexion and postflexion larvae in the tidal creeks, especially Holts Creek, suggests that river herring larvae may have selected the tidal creeks as nursery habitat for access to higher zooplankton abundances and possibly as refuge from adverse environmental conditions and predators. However, gear avoidance may also have affected the results.

Early preflexion larval river herring distribution appeared to shift between habitats in 1990. Abundances in Big Creek, the mainstem river, and Cumberland Thoroughfare showed simultaneous maxima on 22 April and maximal abundance over the shoulder was observed on 29 April. Observed abundances in Holts Creek were highest from 29 April to 8 May indicating that maximal abundance occurred between these dates (Fig. 4-54). That maximal abundances over the shoulder and in Holts Creek occurred later than in the other areas suggests that the distribution of larvae shifted toward shallow-water, protected areas as the season progressed. A similar result was not observed for yolk-sac larvae, however, suggesting that the distributions of these two stages may be determined by different factors. Different hatch date distributions for larvae in the tidal creeks and mainstem river may indicate altered larval herring distribution resulting from a change in spawning by adults rather than a redistribution of larvae by physical processes or by directed movement.

Early preflexion larval river herring abundances declined following maximal abundance in all habitats, but a second increase was observed in the thoroughfare from 8 May to 12 May coincident with declining abundance in Holts Creek. Cumberland Thoroughfare provides the only direct access to Holts Creek (Fig. 4-4), hence larvae in the thoroughfare may be more likely to enter Holts Creek while larvae in the

channel may be more likely to move onto the river shoulder. Coincident increase of larval river herring abundance in the thoroughfare with decrease of abundance in Holts Creek from 8 May to 12 May suggests that early preflexion larvae may not have entered the creek, possibly affected by large numbers of late preflexion and postflexion larvae.

The present research found relatively large numbers of late preflexion and postflexion river herring larvae in Holts Creek, primarily, and in Big Creek which raises questions regarding the potential significance of habitat selection by alewife and blueback herring adults or larvae. Adult spawning behavior may be one factor influencing larval river herring distributions (Fig. 4-57). In New England, alewife spawn in lentic or slower-flowing lotic habitats and blueback herring spawn in faster-flowing lotic habitats (Loesch 1987). In the south Atlantic region, where alewife are few in number or are absent, blueback herring spawn in lentic and slower-flowing lotic habitats (Loesch 1987; Osteen et al. 1989). Loesch (1987) hypothesized that spawning site selection by blueback herring varies in a south-north cline but this has not been confirmed. In southern Chesapeake Bay tributaries, site selection by spawning alewife and blueback herring is poorly known (Odom et al. 1986; Odom et al. 1988a, 1988b; Uzee and Angermeier 1993). Anecdotal observations suggest that alewife and blueback herring may spawn in tidal creeks, lakes and ponds, and the mainstem river. Of the river herrings, only blueback herring are known to migrate into Herring Creek, Virginia. Both blueback herring eggs and *Dorosoma* eggs were collected on submerged aquatic vegetation at the same site in Herring Creek (Chapter 1). Only alewife were observed in Massaponax Creek, Virginia (Chapter 1). Adult migrations into tidal creeks for spawning or passage to lentic habitats as well as the dispersal and advection of larvae may depend on prevailing hydrologic conditions. Advection of larvae from spawning areas (Wang and Kernehan 1979; Boreman 1981; Johnston and Cheverie 1988) may, however, produce

larval river herring distributions with little association to spawning sites.

Alternatively, habitat selection may be mediated by ontogeny (Werner and Gilliam 1984). In nontidal freshwater ecosystems, gizzard shad larvae occur in creek and backwater areas often more frequently than in open waters (Hess and Winger 1976; Chubb and Liston 1986; Sager 1987). Mean larval gizzard shad density was 2.5 times higher in main-channel borders than in backwaters of the Kanawha River, West Virginia, but larger larvae (≥10 mm) were more abundant in the backwaters (Scott and Nielsen 1989). A greater proportion of larger *Dorosoma* spp. were found in beds of panic grass (*Panicum* spp.) than in open water of Orange Lake, Florida, although no larvae were captured in hydrilla (*Hydrilla verticillata*) beds nor among floating emergent vegetation (Conrow et al. 1990). Consistent use of out-of-channel or protected habitats by larger gizzard shad larvae in diverse ecosystems and by larger river herring larvae in the Pamunkey River tidal freshwater reach suggests that habitat selection may be common to clupeid larvae possibly to access higher prey densities or to reduce predation risk (see below).

Distribution along the mainstem channel

Highest early preflexion larval river herring abundances occurred in late April-early May in 1989 and 1990. Isopleths of larval river herring abundance showing the distribution of larvae along the mainstem Pamunkey River on two-dimensional plots of location and time suggest that early preflexion larvae were advected downstream in early May 1989, but a similar isopleth pattern was observed in late April 1990 when river flow was relatively low (Fig. 4-22). If higher river flow was the proximate cause of reduced early preflexion larval river herring abundance in early May 1989, then the distribution and abundance of yolk-sac larvae might have been affected similarly (Fig. 4-21). There is some evidence for downstream advection of yolk-sac larvae in early

May 1989, but yolk-sac larval river herring abundance began to decline before the high flow-event. Yolk-sac larval river herring abundances remained relatively constant and were relatively higher upstream during the high-flow event. Yolk-sac larvae often were more abundant in upper strata of the study area in 1990 suggesting reduced advection downstream compared to 1989, but sampling in 1990 was too infrequent to detect short-term advection events. Yolk-sac larval river herring distribution in might have been affected by other factors, possibly including differential vertical distribution of larvae. Vertical distribution of river herring larvae in the Pamunkey River is unknown, but yolk-sac larvae may remain near the bottom following hatching. Ichthyoplankton collections made for this research were integrated samples of the water column and vertical distributions of larvae could not be ascertained. Differential vertical distribution might influence potentially the advection of larvae and the exposure of larvae to different predator assemblages, e.g. demersal or pelagic. Use of tidal creeks may be a mechanism by which some larvae avoid advection downstream during high flow periods, and tidal creeks may be important refugia during periods of adverse flow conditions (Fig. 4-57.).

Potential significance of river flow to larval river herring survival

Freshwater inflow is the primary abiotic factor establishing order in the tidal freshwater-oligohaline reach of coastal rivers. High flow creates a high-energy system characterized by short residence time and elevated turbidity while low flow creates a low-energy system with characteristics similar to a large reservoir on which tidal movement is superimposed (Jones et al. 1992). Water residence time in the Potomac River tidal freshwater reach in May 1989 was less than one day because of high river flow (Jones et al. 1992). The Pamunkey River is smaller than the Potomac River, hence residence time in the Pamunkey River tidal

freshwater reach was likely to be short, possibly only a few hours, during the highest flows of the 1989 high-flow event.

River flow, rainfall, and water temperature are integral factors in lotic ecosystems directly or indirectly affecting fish egg and larva survival, development, behavior, and vital rates (Pepin 1991; Batty et al. 1993), phytoplankton and zooplankton productivity (Anderson 1986; Schuchardt and Schirmer 1991), advection and dispersal of organisms (Pace et al. 1992), and water quality (Hall et al. 1985; McGovern 1991). These factors are likely to be major determinants of recruitment variability in anadromous herring populations and are known to affect American shad egg and larva development and vital rates (Marcy 1976; Leggett 1977; Crecco et al. 1983, 1986; Crecco and Savoy 1984, 1987a, 1987b; Savoy and Crecco 1988) as well as the onset and duration of spawning (Leggett 1976) in the Connecticut River. An environment-dependent stock-recruitment model based on parent stock size, river flow and rainfall explained 80% to 90% of recruitment variability in this population (Crecco et al. 1986). Egg and early larva mortality rates of Connecticut River American shad are positively correlated to river flow and inversely correlated to water temperature (Crecco and Savoy 1987b; Savoy and Crecco 1988). River flow has been implicated as a significant determinant of clupeid reproductive success in other systems. River flow below about 0.8 $m \cdot s^{-1}$ increased egg mortality of Azov-Don shad (*Alosa pontica pontica*) due to settling of eggs to the river bottom (Kovtun and Nikul'shin 1989). Imposition of river regulation lowered river flow and reduced reproduction of Azov-Don shad (Kovtun and Nikul'shin 1989) and of blueback herring in the Santee-Cooper river system (Thomas et al. 1992).

Abiotic and biotic heterogeneity in the tidal freshwater-oligohaline reach affects vital rates of eggs and larvae thereby contributing to establishment of year-class strength in alewife and blueback herring populations of southern Chesapeake Bay tributaries.

The Pamunkey River in 1989 and 1990 was characterized by contrasting conditions of freshwater inflows in 1989 and 1990. River flow was higher in 1989, with a major high-flow event (>8000 cfs) occurring in early May. Water temperature ranged from about 11 °C to about 20 °C in both 1989 and 1990 which was suitable for adult spawning and egg and larva development (Loesch 1987; Klauda et al. 1991a). Alterations of other variables in association with high river flow, such as reduced acidity and zooplankton concentrations and higher turbidity, might affect adversely the physiology of early preflexion larvae increasing the minimum daily energy requirement and potentially causing malnourishment. Malnourishment alters behavior and the chemical composition of the body. Although Atlantic herring *Clupea harengus* larvae are adapted for extended larval stage duration, malnourishment is detectable after only 3 days of starvation (Blaxter and Ehrlich 1974; Ehrlich 1974). The larval stage duration of alewife and blueback herring is relatively short, and larvae transform into juveniles at about 18 mm TL compared to about 34 mm TL for Atlantic herring larvae (Wang and Kernehan 1979). Anadromous river herring larvae may be relatively more susceptible to short-term food deprivation which potentially may increase susceptibility to advection and various sources of mortality.

Numerous factors may be altered by high river flow which may then affect, directly or indirectly, larval river herring growth and survival. Some of these may include dissolved oxygen, turbidity, and acidity. Mean daily dissolved oxygen concentration in 1989 along the mainstem river was higher (range: 7.6-9.0 $mg \cdot \ell^{-1}$) before the high-flow event and remained depressed throughout May (range: 6.5-7.4 $mg \cdot \ell^{-1}$). Mean daily dissolved oxygen concentration in the five potential nursery habitats showed a similar trend. In comparison, mean daily dissolved oxygen concentration in 1990 was generally high (>7.5 $mg \cdot \ell^{-1}$) throughout the sampling season, except during late April. Alewife larvae require a

minimum dissolved oxygen concentration of 5.0 mg·ℓ^{-1}, but a minimum DO was not reported for blueback herring larvae. Assuming similar minimum requirements for alewife and blueback herring, dissolved oxygen appears to have been sufficient for survival of river herring larvae in the Pamunkey River in 1989 and 1990 (Klauda et al. 1991a).

Acidity in the Pamunkey River typically ranged from pH 7.0 to pH 8.5 in 1989, but several periods of lower acidity were associated with rainfall events (McGovern 1991). Acidity fell to about pH 6.4 during early May 1989 in association with the high-flow event. Low acidity (<pH 6.9) occurred between 9 May and 19 May with levels falling below pH 6.3 on two days (17-18 May) (McGovern 1991). Acidity in 1990 was not measured. Blueback herring yolk-sac larvae are susceptible to death when acidity falls below about pH 6.2 (Klauda et al. 1991a), but the aluminum concentration during acidic pulses may modulate larva mortality (Hall et al. 1985; Klauda and Palmer 1987). River herring larvae were exposed to potentially lethal acidity levels during May 1989 (McGovern 1991), but reduced acidity levels did not occur until after early preflexion larvae abundance declined and yolk-sac larvae abundance remained relatively stable through early May. Consequently, reduced acidity may not have affected early preflexion larva abundance in 1989.

Higher flow in May 1989 reduced water transparency in the study area with transparency in the lower study area returning levels observed from mid-March to mid-April. In comparison, water transparency in 1990 progressively improved throughout the sampling season. Increased turbidity may have reduced prey visibility thereby increasing energy utilization by larvae searching for food. Young larvae have little stored energy so that increased energy utilization during suboptimal conditions may hasten malnourishment.

Hatch dates in relation to larval river herring abundance

Reproduction in anadromous fishes is environmentally constrained by interannual variability in the onset and duration of salubrious environmental conditions promoting egg and larva survival (Cushing 1975; Rothschild 1986). The timing of spawning activities (migration, reproduction) by anadromous herrings, therefore, is linked to the time period when such conditions are likely (i.e. the spawning season). The timing of adult spawning is adapted so that some fraction of the annual reproductive output coincides with salubrious conditions; consequently, the proportion of offspring hatching and initiating feeding during optimal conditions varies between years (Cushing 1975). The fraction of the total reproductive effort which establishes the year class may show little correspondence to maximal larva production (Methot 1983).

River herring spawning is temperature dependent. Alewife begin spawning between 5 °C and 10 °C and blueback herring begin between 10 °C and 15 °C (Loesch 1987). Spawning seasons of these species overlap considerably with peak alewife spawning preceding peak blueback herring spawning by only 2 to 3 weeks (Loesch 1987). In southern Chesapeake Bay tributaries, alewife spawning migrations begin about mid-March and blueback herring spawning migrations begin about early April (Loesch 1987). Spawning migrations of these species are not continuous, rather groups of spawning adults, called 'waves', migrate at intervals of about 5 days or less (Fay et al. 1983).

Hatch date frequency distributions showed two groups of river herring larvae in the study area in 1989 and 1990: an early-spawned group associated primarily with the mainstem river and a late-spawned group associated primarily with the tidal creeks, although some early- and late-spawned larvae were found in each area. In 1990, similar timing of maximal preflexion larvae abundance in Big Creek, the channel and the thoroughfare suggests that the early-spawned larvae in Big Creek were of the early-hatch 'channel' group rather than of the late-hatch

'tidal creek' group. Inconsistency between the hatch date frequency distribution and the time of maximal early preflexion larval river herring abundance suggests that few early preflexion larvae remained or survived in Big Creek. The composition of the early- and late-spawned groups, whether a single species or a mixture of alewife or blueback herring larvae, could not be determined because most larvae were too small to identify. The few identifiable larvae were captured only in the tidal creeks and were all alewife, but this does not imply that only alewife larvae occurred in the tidal creeks since blueback herring larvae may not have developed sufficiently to show diagnostic pigment.

Growth of river herring larvae

Larval river herring growth in 1989 and 1990 did not differ within the younger or older age groups (<11 days and ≥11 days after hatching) but was significantly greater for older larvae, 0.59 $mm \cdot d^{-1}$, than for younger larvae, 0.35 $mm \cdot d^{-1}$. The estimated length at which the growth trajectory changed was about 8 mm SL, estimated from the WLS regression model for older larvae, and corresponds approximately to the length at onset of dorsal fin development (Chapter 2). Growth acceleration coincident with dorsal fin formation may be determined ontogenetically, but faster growth must be accompanied by increased energy stores. Dorsal fin formation may enhance swimming ability providing larvae with improved control over movement thereby increasing the efficiency of prey pursuit and capture with a consequential increase in daily ration.

Larvae from age 3 d to age 14 d grew faster in the tidal creeks, 0.47 $mm \cdot d^{-1}$, than in the mainstem river, 0.35 $mm \cdot d^{-1}$. Differences in growth of larvae between these areas may be associated with differences in the potential prey field. Faster growth of larval fishes in the presence of high prey abundances has been documented in laboratory experiments (Houde and Schekter 1981; Buckley et al. 1987) as well as from field observations (Govoni et al 1985). Larval Atlantic herring

growth is about 0.27-0.30 mm·d^{-1} on Georges Bank (Lough et al. 1980), and is about 0.29 mm·d^{-1} for 10-40 mm larvae in Sheepscot estuary, Maine (Townsend and Graham 1981). In the River Blackwater Estuary, Atlantic herring yolk-sac larvae from 1978 to 1980 grew about 0.18 mm·d^{-1} and post yolk-sac larvae grew about 0.43 mm·d^{-1} (Henderson et al. 1984). In contrast, larval Connecticut River American shad growth is about 0.7 to 0.9 mm·d^{-1} from hatching to about age 20 d but only 0.3 to 0.5 mm·d^{-1} from age 20 d to age 30 d based on the Gompertz equation (Crecco et al. 1983).

Faster growth reduces stage duration and mortality of larvae (Shepherd and Cushing 1981; Houde 1987; McNamara and Houston 1987; Pepin 1991). Faster growing larvae would gain a size advantage, and potentially a competitive advantage, over slower growing larvae. The estimated duration of the larval river herring stage in the tidal creeks, 32 days, is about 12 days shorter than the estimated stage duration in the mainstem river, 44 days, assuming that larvae grow about 15 mm before transforming into juveniles and that the estimate growth rates remains constant throughout the larval stage. Consequently, relatively more river herring larvae potentially survive to the juvenile stage in the tidal creeks than in the mainstem river. In absolute terms, however, numbers of larvae surviving to the juvenile stage in the mainstem river may be much greater than the numbers in out-of-channel areas simply because of greater larval river herring abundance in the mainstem river given its greater volume compared to out-of-channel nursery habitats. Nevertheless, loss of out-of-channel areas as nursery habitat may have potentially deleterious consequences for river herring using these areas during the larval stage.

Zooplankton abundance and the potential prey field

Potential prey of river herring larvae

Larval alewife and blueback herring foraging habits in the Pamunkey River are not documented, and prey preferences are known only for areas where these species do not coexist. Larval alewife diets in Lake Michigan (Norden 1968) and in Claytor Lake, Virginia, (Nigro and Ney 1982) are similar. Small larvae (<15 mm SL) primarily consume cyclopoid copepods (primarily *Cyclops* spp.) and nauplii, with increased consumption of cladocerans (primarily *Bosmina* spp.) and rotifers by larger larvae and juveniles. Lake Michigan alewife larvae reared in aquaria consumed copepodite and small adult stages of cyclopoid copepods and the cladoceran *Bosmina longirostris* (Heinrich 1981). Blueback herring larvae (5 mm to 16+ mm SL) in the Connecticut River showed positive selection for rotifers (*Keratella* spp. and *Polyarthra* spp.) and cladocerans (*Bosmina* spp.), and generally did not select for copepod nauplii or copepodites (Crecco and Blake 1983). Temporal changes in prey preference by blueback herring larvae followed changes in the river zooplankton community (Crecco and Blake 1983). Crecco and Blake (1983) suggested that intraspecific competition for food was likely more important than interspecific competition between coexisting blueback herring and American shad larvae in the Connecticut River.

Composition of the potential prey field in 1989 and 1990

Zooplankton composition in the mainstem Pamunkey River differed between 1989 and 1990. High rotifer, copepod nauplii and copepodite, and cladoceran abundances were found downstream in the study area, but temporal and spatial distributions of these groups differed intra- and interannually. Rotifer abundances were similar spatially and temporally in 1989 and 1990. Cladocerans appeared to be more abundant in 1989 than in 1990, but different sampling schedules make this comparison speculative. Copepod nauplii and copepodite abundance was higher in the

upper reach of the study area in late April 1990 than from mid-April to mid-May 1989. Maximal cladoceran and rotifer abundances in 1989 occurred simultaneously with maximal early preflexion larval river herring abundance before the high-flow event of early May 1989. Highest observed abundances of cladocerans and copepod nauplii and copepodites occurred in 1990 simultaneously with highest early preflexion river herring larval abundance, but copepod nauplii and copepodite abundance was much higher than cladoceran abundance at this time. Cladocerans and rotifers in 1989 and copepod nauplii and copepodites in 1990 appear to have been the dominant zooplankton when river herring early preflexion larvae were most abundant.

The temporal progression of mean total-zooplankton abundances within the study area was similar to that reported by McGovern (1991) for the mainstem Pamunkey River from P53 to P88 in April-May 1989. Observed total-zooplankton abundances were higher for the present research farther upstream due to different sampling technique and enumeration of rotifers. McGovern (1991) found higher percentage of cladocerans than copepod nauplii in 1988, 73.3% and 12.6%, respectively, but similar percentages in 1989, 45.1% and 41.7%, respectively. However, McGovern (1991) did not identify separate cladoceran or copepod nauplii distributions or temporal progressions of abundance. In the present research, cladocerans were abundant from late April to early May 1989 while copepod nauplii and copepodites were abundant in late March and late May 1989.

Zooplankton abundances in the five potential nursery habitats varied, but trends were similar over the channel, on the shoulder and in the thoroughfare and were similar in the tidal creeks. Copepods were usually dominant in the mainstem river and in the thoroughfare, although rotifers became dominant in May. Rotifers were usually the dominant group in the tidal creeks. Cladocerans were always subordinate in number. The reason for dominance by cladocerans in the along-channel

data set and by early copepod life stages in the between-habitats data set in 1989 is not apparent since the same gear and sampling procedure were used at all locations.

Potential significance of a variable potential prey field

Patchy spatial distribution and variable abundance of zooplankton permute the potential prey field so that river herring larvae hatching at different times or locations encounter varying concentrations and combinations of potential prey groups (Fig. 4-56). Average abundance of river herring yolk-sac larvae ranged from about 100 to about 400 yolk-sac larvae·100 m^{-3} during the 1989 season, but high abundances of early preflexion larvae were found only during late April-early May. Larval river herring hatch dates and zooplankton abundances observed in the Pamunkey River suggest that larval river herring survival in the mainstem river was associated with the high cladoceran abundance in late April 1989, whereas survival in the tidal creeks was independent of prey abundances in the mainstem river (Fig. 4-53).

Differences in abundance and composition of the potential prey field may influence larval fish nutrition, growth and mortality (Martin et al. 1985; Buckley and Lough 1987). However, prey quality, including factors such as particle size distribution (Frank and Leggett 1986) and nutritional value (Theilacker and Kimball 1984), may be more important than abundance or composition in determining the relationship between the zooplankton prey field and larval fish nutrition and vital rates (Boisclair and Leggett 1989a, 1989b). Inferior quality zooplankton dominating the potential prey field may increase the incidence of malnourishment among larval fishes leading to prolonged stage duration and increased mortality.

Anadromous herring larvae in Chesapeake Bay tributaries might be susceptible to malnourishment when appropriate conditions prevail. One line of evidence supporting this hypothesis is the occurrence of starved

striped bass larvae in the Choptank River (Setzler-Hamilton et al. 1987) and the Potomac River (Martin et al. 1985). Martin et al. (1985) related poor nutritional condition of striped bass larvae with a prey field dominated by copepods and improved nutritional condition with a prey field dominated by cladocerans. Striped bass larvae are developmentally advanced compared to clupeid larvae and may be more resistant to malnourishment than clupeid larvae; consequently, malnourishment of striped bass larvae strongly suggests the potential for malnourishment of clupeid larvae in Chesapeake Bay tributaries when appropriate conditions prevail. Other evidence is the occurrence of starved gizzard shad larvae in Lake Texoma (Oklahoma-Texas) coincident with lower zooplankton abundance following the spring maxima (Kashuba and Matthews 1984) indicating that larvae similar to river herring, both morphologically and with respect to feeding habits, experience malnourishment during suboptimal feeding conditions.

Differences in zooplankton abundances found during in this research provide only an indication of the potential prey field available to river herring larvae at a given time. The rotifer group, for example, was comprised of at least 8 identifiable genera, including *Keratella* spp., *Polyarthra* spp., *Notholca* spp., *Lepadella* spp., *Filinia*, *Lecane* spp., *Trichocera* spp., and *Asplanchna* spp. Blueback herring in the Connecticut River ingest *Keratella* spp. and *Polyarthra* spp. (Crecco and Blake 1983). Norden (1968), Heinrich (1981), and Nigro and Ney (1982) ascribe even less significance to rotifers in the diet of alewife larvae, and cladoceran and copepod species may be more or less preferred by alewife larvae. Juvenile blueback herring (Burbidge 1974) and juvenile alewife (Weaver 1975) select against the cladoceran *Diaphanosoma* spp. but select for *Bosmina* spp. Dettmers and Stein (1992) found that larval gizzard shad in Knox Lake, Ohio, never selected *Diaphanosoma* spp., although it was a predominant component of the zooplankton community. Dettmers and Stein (1992) also showed an

increased proportion of rotifers in the diet as crustacean zooplankton (primarily cyclopoid copepodites and copepod nauplii) decreased in abundance in the plankton. Analysis of larval alewife and blueback herring feeding habits are needed to identify important prey groups and determine whether diets of these larvae in Chesapeake Bay tributaries differ. The potential prey field and its importance to the nutrition and growth of river herring larvae may be evaluated more thoroughly once feeding habits of these larvae are determined.

Patchy spatial distribution and variable abundance of zooplankton in the Pamunkey River are factors which may affect larval river herring survival. Zooplankton abundance from late April to mid-May in 1989 and 1990 differed between habitats when river herring early preflexion larvae were most abundant in a manner suggesting a gradient from lower abundance in the channel to higher abundance in the tidal creeks. Differences in zooplankton abundance between habitats might influence larval river herring distribution and survival if larvae utilize such a gradient either as an environmental cue or as a consequence of food searching behavior to locate suitable nursery habitats such as Holts Creek, but this hypothesis does not explain why early preflexion larvae apparently emigrated from Big Creek even though zooplankton abundance appeared to be relatively high. Predation on larvae in Big Creek might account for this discrepancy.

Larval fish predation may affect zooplankton community composition, species abundances, and factors determining prey quality. Larval fish predation may affect demographics of zooplankton populations resulting in altered community composition, species abundance, and prey quality (e.g. particle size distribution). *Bosmina longirostris*, for example, is prey for larvae, juveniles, and adults of many fishes, including river herring, gizzard shad, and striped bass. Reproduction in *B. longirostris* increases at low to moderate levels of predation through reduced size-at-maturity and reduced size-at-birth enabling the

completion of the life cycle before becoming vulnerable to predation (Vonder Brink and Vanni 1993). Consequently, predation may shift the particle size distribution of zooplankton prey affecting their vulnerability to predation. Mortality losses in *B. longirostris* populations cannot be offset, however, by decreased size-at-maturity at high levels of predation (Vonder Brink and Vanni 1993). High levels of larval fish predation, therefore, may lead to altered zooplankton community composition. Additionally, such alterations in the potential prey field might influence potential intra- and interspecific competition. Last, food availability supports predation-induced demographic changes in *Bosmina longirostris* populations; *B. longirostris* birth rates increase as fish biomass increases in response to increasing food biomass (Vonder Brink and Vanni 1993). The relative importance of phytoplankton and microbial food sources to cladocerans, or other zooplankton, in different areas of tidal freshwater ecosystems (see below) might influence zooplankton productivity and body composition thereby affecting prey availability, abundance and quality for river herring larvae.

Coincident, high abundances of river herring larvae and potential zooplankton prey suggests that the two tidal creeks, especially Holts Creek, are significant nursery areas for river herring larvae. River herring larvae appear to utilize the tidal creeks for only a brief time from about mid- to late April to about mid-May, about three to four weeks. Larvae benefit from high prey abundances in the tidal creeks as evidenced by faster growth, and it remains to be determined whether river herring utilize the tidal creeks for longer periods especially after transformation to the juvenile stage.

Utilization of tidal creeks may be one mechanism by which river herring larvae access high prey abundances, and variable prey abundances between microhabitats of the tidal freshwater reach suggests that such differences affect the quality of nursery habitat for river herring.

Faster growth of river herring larvae in the tidal creeks than in the mainstem river supports this hypothesis. It remains to be determined whether alewife and blueback herring larvae partition available prey and habitat resources and, therefore, benefit equitably from potentially higher quality nursery habitats. Analyses of foraging behavior, nutritional condition and distribution of alewife and blueback herring larvae in tidal freshwater is needed to understand better the trophodynamics of these larvae on at least three levels: between seasons, between time periods or larval cohorts, and between locations including levels of the mainstem river and out-of-channel habitats.

Zooplankton production within the tidal freshwater ecosystem

High abundances of rotifers, copepod nauplii and copepodites, and cladocerans in the lower tidal freshwater-oligohaline reach are suggested to result from higher reproduction rates supported by high concentrations of diatoms, detritus, and nutrients (Anderson 1986; Marshall and Alden 1990; Moon and Dunstan 1990). High zooplankton abundances appear to coincide with high concentrations of detritus in the mainstem Pamunkey River from about P56 to about P93 (Van Engel and Joseph 1968). Downstream advection of plankton, detritus, and nutrients from upstream areas and export from adjacent tidal marshes also may contribute to higher zooplankton concentrations in this zone (Odum 1984; Odum et al. 1984; Findlay et al. 1990). The significance of nutrient exchange between tidal marshes and the mainstem river is questionable, however. Heinle and Flemer (1976) found little export of organic carbon from a poorly flooded tidal marsh, although dissolved nitrogen and dissolve phosphorous were exported. Microbial communities at land-water interface zones may reduce nutrient concentrations available for export through nutrient cycling and recycling (Wetzel 1992). Movement of river herring larvae, as well as by other species, may provide an important

mechanism for nutrient and energy exchange between tidal marsh and mainstem river components of the tidal freshwater-oligohaline ecosystem.

According to Pennak (1989), most rotifers are omnivorous consuming all organic particles of appropriate size, and cladocerans consume all organic particles of appropriate size with organic detritus and bacteria comprising the bulk of ingested material. Detritus also may be a significant component of the diet of copepods in estuaries and tidal marshes (Heinle et al. 1974; Heinle and Flemer 1976; Pennak 1989). Bacteria, protists, and pico- and nanoplankton in the detritus may contribute to tidal freshwater-oligohaline ecosystem productivity (Fenchel 1989). Bacteria have been suggested to be an important food for zooplankton (Hessen and Andersen 1990) and to play a primary role in nutrient regeneration (Heinle et al. 1973; Morris et al. 1978; Odum et al. 1984; Sellner 1988; Wylie and Currie 1991). Garman (1992), examining the decomposition of blueback herring carcasses, concluded that microbes rather than macroinvertebrates were responsible for initial decomposition. This finding suggests that microbes may remove a substantial quantity of particulate organic carbon in nontidal, and possibly tidal, freshwater reaches of coastal plain rivers. The significance of microbe trophic pathways as energy or nutrient sinks is an important, controversial question (Sherr et al. 1986, 1987), but accumulating evidence suggests that bacteria, ciliates, protists, and pico- and nanoplankton may provide important trophic links between the microbial food web and the traditional food web in some ecosystems (Sherr et al. 1986; Stoecker and McDowell Capuzzo 1990; Carlough and Meyer 1991).

Detrital-based food webs may be more important in lower order streams and creeks than in large rivers, embayments, or offshore and may be highly site specific (Odum 1984). Consequently, food webs of many tidal freshwater wetlands and associated creeks may be primarily detritus-based (Odum et al. 1984). In contrast to low to moderate

quality detritus produced by salt marsh vascular flora, detritus produced by tidal freshwater vascular flora is of high nutritional quality characterized by relatively high nitrogen concentration and relatively low crude fiber content (Odum 1988). The contribution of a detrital-based microbial food web to zooplankton dynamics in tidal freshwater-oligohaline ecosystems has not been well documented, but it may affect the dynamics of river herring larvae as one link in the production cycles of their zooplankton prey (Fig. 4-56). The significance of a microbial food web as a carbon source for zooplankton, river herring larvae and other metazoan consumers may depend on the composition of the zooplankton community. Bacteria and picoplankton may be a significant carbon source when cladocerans dominate the crustacean community but not when copepods are dominant (Wylie and Currie 1991).

Species Interactions

References to early life history studies of gizzard shad and threadfin shad have been made to support observations and conclusions regarding the early life histories of alewife and blueback herring. These four clupeid species coexist in Chesapeake Bay tributaries, although threadfin shad are limited primarily to the James and Rappahannock rivers (Wass 1972). Potential intraspecific and interspecific interactions between these clupeid larvae may be most probable when morphology and ecological requirements are most similar and might affect vital rates and influence recruitment.

Crecco and Blake (1983) suggested that intraspecific competition might be more important than interspecific competition in determining foraging success among coexisting blueback herring and American shad larvae. However, differences between blueback herring larvae and American shad larvae, including size-at-hatching and mouth development and size, may affect feeding behavior and prey selection. In contrast, alewife and blueback herring larvae are identical morphologically and

are virtually identical morphologically to larval gizzard and threadfin shad (Chapter 3). Additionally, gizzard shad and threadfin shad are zooplanktivores during the larval stage and ingest the same prey as alewife larvae and blueback herring larvae. Gizzard shad larvae ingest protozoans, copepod nauplii and copepodites (including *Cyclops* spp.), cladocerans (including *Daphnia* spp. and *Bosmina* spp.), and rotifers (primarily *Keratella* spp.) (Miller 1960; Cramer and Marzolf 1970; Scott and Crossman 1973; Guest et al. 1990; Dettmers and Stein 1992). Threadfin shad appear to ingest these same zooplankton and suppress zooplankton populations in closed systems, and threadfin shad larvae and juveniles may reduce larval and juvenile gizzard shad abundance and may displace young gizzard shad (Guest et al. 1990).

Similarities in morphology and feeding habits suggest that competition potentially might occur between these species during the larval stage. However, one species must be able to control access of the other species to a limiting resource, and it is questionable whether conditions might exist in tidal freshwater ecosystems which would enable one species to limit the remaining species. Resource limitation, most probably prey availability, may influence larval herring growth and survival rates especially in areas or during time periods characterized by environmentally-determined suboptimal conditions or when larvae are restricted to the same refuge habitats (Werner and Gilliam 1984). The potential for resource limitation and for intra- and interspecific larval herring interactions to affect the year class for herring species in tidal freshwater-oligohaline systems is unknown.

Differing diets, feeding behaviors (e.g. feeding chronology), and larva distributions are mechanisms which may reduce potential intra- and interspecific interactions between sympatric alewife, blueback herring and gizzard shad larvae. Feeding behaviors of alewife and blueback herring larvae may be quite similar especially early in ontogeny when stored energy reserves are minimal and when fast growth is an important

determinant of survival. Juvenile alewife and blueback herring in the James River, Virginia, have virtually identical diets (Burbidge 1974; Weaver 1975) supporting the hypothesis of diet overlap between the larvae. Spatial segregation between groups of river herring larvae is suggested based on different hatch date frequency distributions for larvae captured in the mainstem river (early-hatch) and in the tidal creeks (late-hatch), but the nature of these groups, either as single or multiple species, could not determined.

Species interactions may have important implications for fishery management (Lasker 1987), and may be relevant for river herring fishery management. Anadromous herring stock abundances in Chesapeake Bay are at historically low levels (Klauda et al. 1991a, 1991b). Reduced alewife and blueback herring stock sizes coincident with favorable environmental conditions may have provided an opportunity for gizzard shad and threadfin shad population expansion. Anecdotal evidence based on observations at Conowingo Dam on the Susquehanna River suggests that reduced *Alosa* population abundance for some stocks is associated with increased gizzard shad population abundance (Klauda et al. 1991a). The status of gizzard shad or threadfin shad populations in most Chesapeake Bay tributaries is unknown so that the relationship between *Alosa* and *Dorosoma* populations can not be evaluated. Interactions among and between alewife, blueback herring, and gizzard shad larvae might affect larval growth and survival for each species. Potential intra- and interspecific interactions between larval, and potentially juvenile, anadromous and freshwater herring may affect the establishment of year-class strength among river herring spawning populations in the Chesapeake Bay, but direct tests of this hypothesis are needed.

Predation and potential predators

Predation is one of the most important biological forces structuring and regulating the distribution and abundance of fishes

(Mittlebach and Chesson 1985; Anderson 1988; Bailey and Houde 1989). Small fishes modify their behavior in the presence of predators by preferentially utilizing refuge habitats to reduce predation risk (Mittlebach and Chesson 1985). Predation is likely to influence significantly the year-class strength of alewife and blueback herring populations. Savoy and Crecco (1988) estimate that density-dependent mortality may comprise up to about 40% of total mortality of American shad eggs and early larvae in the Connecticut River, although sources of mortality were not specified. Predation on river herring eggs and larvae was not examined for the present research, but utilization of Holts Creek (primarily) and Big Creek by older river herring larvae may indicate predator-mediated habitat selection, predation-induced differential mortality, or a combination of these affects. Because of the importance of predation as a determinant of year class success in fishes, literature pertinent to potential predation of river herring eggs and larvae is reviewed. McGovern (1991) studied the distributions and abundance of larval striped bass potential predators in the Pamunkey River in 1988 and 1989, and his results are examined relative to larval river herring distribution and abundance.

McGovern and Olney (1988) list ten species of fishes (blueback herring, satinfin shiner, spottail shiner, white catfish, channel catfish, tessellated darter, bluegill, pumpkinseed, white perch, and striped bass) as potential vertebrate predators of striped bass larvae in the Pamunkey River. They also identify several species which may be potential predators of striped bass, including bay anchovy, Atlantic menhaden, other clupeids, yellow perch, inland silverside *Menidia beryllina*, other cyclopoid copepod species, and insect larvae. Many of these may be predators of river herring eggs and larvae.

Predation of river herring eggs and larvae by clupeids, both river herring and *Dorosoma* spp., may be an under-recognized source of mortality. Creed (1985) found fish eggs, suggested to be probably

alewife and blueback herring, as the most abundant dietary item of blueback herring migrating to spawning grounds in the Chowan River, North Carolina, but egg predation was low on a known spawning ground. Egg predation by migrating blueback herring decreased rapidly from >85% of ingested prey early in the spawning season to <5% late in the spawning season suggesting that egg predation might be of limited significance. Freshwater feeding habits of blueback herring are poorly documented (Frankenstein 1976; Creed 1980), and are unknown for alewife.

Gizzard shad and threadfin shad predation on fish eggs and larvae also has been reported (Dendy 1946). Guest et al. (1990) suggest that gizzard shad and threadfin shad may have preyed on white crappie eggs and larvae, but direct evidence was not presented. Adult gizzard shad ingest detritus (Miller 1960), zooplankton and phytoplankton (Bodola 1964), and benthic prey (Jude 1973). Both adult and juvenile gizzard shad and threadfin shad switch feeding strategies between detritivory (including benthic prey) and zooplanktivory (Ingram and Ziebell 1983). Gizzard shad may exhibit poor nutritional condition when feeding only on detritus, but nutritional condition and growth improve when they also ingest zooplankton (Pierce et al. 1981; Mundahl and Wissing 1987). Consequently, predation on river herring eggs and larvae and cannibalism of their own eggs might supplement the nutritional value of detritus ingested by gizzard shad during the spawning season. Detection of gizzard shad or threadfin shad predation on fish eggs or larvae may be difficult due to maceration and rapid digestion and to the transient nature of predation on larval fish (Guest et al. 1990). Predation on fish eggs and larvae may be common to clupeids under appropriate conditions or feeding stimuli (Daan et al. 1985).

Circumstantial evidence suggests a possible relationship in the decline of some river herring populations with increased abundance of gizzard shad (Klauda et al. 1991a). Gizzard shad predation on river herring eggs and larvae may be one mechanism which may contribute to

such a relationship (Fig. 4-56), but evidence supporting this hypothesis is lacking. Predation on river herring eggs and yolk-sac larvae by gizzard shad and threadfin shad, possibly coincidental with ingestion of detritus, may be a significant source of river herring mortality.

Direct evidence of predation on river herring eggs or larvae in the Pamunkey River is lacking. Johnson and Dropkin (1992) found 15 fish species ate cultured American shad larvae (age 18 d) following release of larvae into the Susquehanna and Juanita rivers (Table 4-31). At least seven of these species exist in southern Chesapeake Bay tributaries (Table 4-31). Johnson and Dropkin (1992) also showed increased predation by two cyprinid species, spotfin shiner *Cyprinella spiloptera* and mimic shiner *Notropis volucellus*, with increasing number of released American shad larvae suggesting a density-dependent response. Wild and reared fish larvae differ (Blaxter 1975), so high predation on reared larvae does not imply necessarily a similar predator response to wild larvae. Johnson and Dropkin (1992) show, however, that larval *Alosa* abundance may be reduced rapidly when predators are provided an adequate food signal.

Invertebrates may also be important predators of river herring larvae. McGovern and Olney (1988) list two invertebrates, the cyclopoid copepod *Acanthocyclops vernalis* and the hydra *Craspedacusta sowerbyi*, as potential predators of striped bass larvae in the Pamunkey River. Hartig et al. (1982) identify two cyclopoid copepods, *Diacyclops thomasi* and *A. vernalis*, as major predators of young alewife larvae (3-8 mm TL) in Lake Michigan. Of six species of fish larvae examined by Hartig et al. (1982), 98 percent of cyclopoid predation was directed toward alewife. Ninety-nine percent of the cyclopoid predators were adult females of *D. thomasi* and *A. vernalis* suggesting that predation on fish larvae may be important for cyclopoid copepod egg production and that increased predation might occur in conjunction with cyclopoid copepod reproductive activity. Smith and Kernehan (1981) found *Cyclops*

bicuspidatus thomasi (=*D. thomasi* [Kiefer 1978]) on larvae of striped bass (*Morone saxatilis*) and white perch (*M. americana*) in the Chesapeake and Delaware canal. Younger river herring larvae, including yolk-sac larvae and early preflexion larvae, may be poor swimmers (Blaxter and Hunter 1982) especially vulnerable to predatory copepods (Hartig et al. 1982). McGovern and Olney (1988), based on published reports, identify four other cyclopoid copepod species in Chesapeake Bay including *Eucyclops agilis*, *Halicyclops fosteri*, *Mesocyclops edax*, and *M. leukardti* (=*M. americana* Dussart 1984).

Potential fish and invertebrate predators of striped bass larvae in the Pamunkey River were investigated in 1988 and 1989 by McGovern (1991). Potential fish predator abundances, primarily of bay anchovy and menhaden, were relatively low (<5 individuals·100 m^{-3}) above the 1‰ isohaline which occurred well below the study area (about P63) from early April to late May. In contrast, cyclopoid copepod abundances, primarily *A. vernalis* and *M. edax*, were high (>100 copepods·m^{-3}) from about P59 to about P86 in early May when river herring larvae were most abundant. High cyclopoid copepod abundances were also observed upstream from about P66 in late May. McGovern (1991) found little temporal coincidence of striped bass larvae and cyclopoid copepods in 1988 compared to 1989 suggesting that variable spatial and temporal predator distributions might affect larval fish mortality.

Documentation of predation on river herring eggs and larvae is necessary to establish the importance of predation as a determinant of the distribution, abundance, and habitat utilization by river herring early life stages. Analyses of potential predator distributions, abundances and diet composition will potentially indicate the relative importance of various habitats as refuge for river herring larvae. Potential fish predator abundances reported by McGovern (1991) may not reflect the distributions or abundances of potential fish predators on river herring eggs or larvae. River herring eggs are semidemersal or

demersal and are adhesive and yolk-sac larvae may remain relatively close to the bottom after hatching. River herring eggs and yolk-sac larvae may be more vulnerable to demersal predators such as hogchokers, catfishes, cyprinids, or gizzard shad than to pelagic predators such as anchovy or menhaden. Coincident cyclopoid copepod and larval river herring distributions demonstrates the potential for predation by cyclopoid copepods on river herring larvae in the tidal freshwater reach. River herring larvae advected into meso- and euryhaline estuarine zones (Dovel 1971; Johnston and Cheverie 1988) in Chesapeake Bay and its tributaries may not contribute significantly to the year class due to high predation in these areas. Behavior mechanisms, such as immigration to out-of-channel areas, may be important for limiting downstream advection into higher salinity zones. Loss of refuge habitats might affect adversely the retention of river herring larvae when high-energy conditions prevail in the tidal freshwater reach.

Conclusion

Anadromous herrings spawning populations in Chesapeake Bay currently are at historically low levels of abundance and there is little evidence of recovery of these stocks. Current knowledge of the early life histories of these species in Chesapeake Bay is poorly developed to facilitate management of these species during their freshwater residency. Additionally, the milieu of the tidal freshwater ecosystem in which anadromous herring year classes are established is relatively poorly known compared to other estuarine ecosystems. Continued investigations of tidal freshwater ecosystems and of anadromous herring early life histories in these ecosystems are warranted to facilitate fisheries and habitat management promoting the economic viability of river herring populations, as well as other anadromous herring populations, for commercial and recreational exploitation.

Table 4-1. Status of alewife spawning populations in the major Chesapeake Bay tributaries (Klauda et al. 1991a). Rivers in which alewife have never spawned and for which no data were reported are excluded. Populations for which data were available but no status was indicated were classified as established populations.

River	Population Status	Abundance	Trend
Susquehanna River			
Deer Creek	Remnant	Very low	
Octoraro Creek	Remnant	Very low	
Bush River	Remnant	Very low	Stable
Gunpowder River	Remnant	Low	Stable
Patapsco River	Remnant	Very low	
Magothy River	Extinct		
Severn River	Remnant	Low	
South River	Remnant	Low	
West River	Remnant		
Patuxent River	Remnant	Low	Stable
Potomac River			
Wicomico River	Extinct		
Port Tobacco River	Extinct		
Nanjemoy River	Remnant		Declining
Mattawoman River	Established	Moderate	Stable

Table 4-1 (continued). Alewife spawning populations in Chesapeake Bay.

River	Population Status	Abundance	Trend
Potomac River (cont.)			
Piscataway Creek	Remnant		Stable
Anacostia River	Extinct		
Rock Creek	Remnant		Stable
Rappahannock River	Established	Low	Stable
York River			
Mattaponi River	Established	Low	Declining
Pamunkey River	Established	Low	Stable
Pocomoke River	Remnant		Declining
Nanticoke River	Established	Moderate	Increasing
Honga River	Extinct		
Choptank River	Remnant	Low	Declining
Wye River	Extinct		
Chester River	Remnant	Low	Declining
Sassafras River	Remnant	Very low	
Bohemia River	Remnant	Very low	
Elk River	Remnant	Very low	Declining
Northeast River	Remnant	Low	Declining

Table 4-2. Status of blueback herring spawning populations in major Chesapeake Bay tributaries (Klauda et al. 1991a). Rivers in which blueback herring have never spawned and for which no data were reported are excluded. Populations for which data were available but no status was indicated were classified as established populations.

River	Population Status	Abundance	Trend
Susquehanna River			
Deer Creek	Remnant		Declining
Octoraro Creek	Remnant		Declining
Bush River	Remnant	Very low	Declining
Gunpowder River	Remnant	Low	
Patapsco River	Remnant	Very low	Stable
Magothy River	Extinct		
Severn River	Remnant	Low	
South River	Remnant	Low	
West River	Remnant	Very low	
Patuxent River	Remnant		Stable
Potomac River			
Wicomico River	Remnant	Very low	Declining
Port Tobacco River	Remnant	Very low	
Nanjemoy River	Remnant		Declining
Mattawoman River	Established	Moderate	Stable

Table 4-2 (continued). Blueback herring spawning populations in Chesapeake Bay.

River	Population Status	Abundance	Trend
Potomac River (cont.)			
Piscataway Creek	Remnant		Stable
Anacostia River	Remnant		Stable
Rock Creek	Extinct		
Rappahannock River	Established	Moderate	Stable
York River			
Mattaponi River	Established	Moderate	Declining
Pamunkey River	Established	Moderate	Stable
Pocomoke River	Remnant		Declining
Nanticoke River	Established	Moderate	Increasing
Honga River	Remnant		Declining
Choptank River	Established	Moderate	Stable
Wye River	Extinct		
Chester River	Established	Moderate	Stable
Sassafras River	Remnant	Low	
Bohemia River	Remnant	Low	
Elk River	Remnant	Low	Increasing
Northeast River	Remnant		Declining

Table 4-3. Summary of status of spawning populations of alewife and blueback herring populations in major Chesapeake Bay tributaries based on Tables 4-1 and 4-2.

Current Status	Alewife		Blueback Herring	
	Population			
Established	5 (17%)		7 (23%)	
Remnant	19 (63%)		20 (67%)	
Extinct	6 (20%)		3 (10%)	
	Abundance			
High	0		0	
Moderate	2 (11%)		7 (39%)	
Low	10 (53%)	(89%)	6 (33%)	(61%)
Very low	7 (37%)		5 (28%)	
	Trend			
Increasing	1 (6%)		2 (10%)	
Stable	8 (50%)		9 (45%)	
Declining	7 (44%)		9 (45%)	

Table 4-4. Mean monthly water temperature, daily air temperature, Pamunkey River flow, and dissolved oxygen during March, April, and May in 1989 and 1990. Mean water temperature and dissolved oxygen were computed from mean values for collection events made in each season. The number of measurements used to compute mean monthly water temperature and dissolved oxygen is shown in parentheses.

Month	Year	
	1989	1990
Mean water temperature (°C)		
March	10.9 (1)	14.3 (1)
April	15.7 (8)	17.9 (2)
May	19.3 (6)	21.5 (1)
(Mean)	15.3	17.9
Mean daily air temperature (°C)		
March	8.8	11.2
April	13.2	14.4
May	17.8	18.8
(Mean)	13.3	14.8
Mean daily Pamunkey River flow (cfs)		
March	2243	1262
April	1258	1970
May	2634	2303
(Mean)	2022	1860
Mean dissolved oxygen ($mg \cdot \ell^{-1}$)		
March	9.0 (1)	8.6 (1)
April	8.2 (7)	7.1 (2)
May	6.9 (6)	8.1 (1)
(Mean)	8.0	7.9

Table 4-5. Dissolved oxygen concentrations ($mg \cdot \ell^{-1}$) in potential nursery habitats of the Pamunkey River tidal freshwater reach in 1989 and 1990.

Location	Date							Mean
	1989							
	April			May				
	20			18		30		
Holts Creek	6.3			6.2		6.5		6.3
Big Creek	8.1			7.7		6.0		7.3
Channel	7.9			7.7		7.6		7.7
Shoulder	8.2			7.6		7.8		7.9
Thoroughfare	8.1			7.2		8.3		7.9
Mean	7.7			7.3		7.4		
	1990							
	March	April				May		
	17	8	16	22	29	8	12	
Holts Creek	7.8	8.7	8.1	8.7	6.4	9.2	7.2	8.0
Big Creek	8.4	8.9	9.0	8.3	7.2	8.0	8.1	8.3
Channel	8.4	8.8	8.2	8.1	5.6	7.2	7.2	7.6
Shoulder	8.3	8.9	8.1	8.4	6.2	7.6	8.1	7.9
Thoroughfare	8.6	8.6	8.5	8.7	7.0	8.0	8.3	8.2
Mean	8.3	8.8	8.4	8.5	6.2	7.7	7.9	

Table 4-6. Water transparency (cm) in potential nursery habitats of the Pamunkey River tidal freshwater reach in 1989 and 1990.

Location	Date							Mean
	1989							
	April		May					
	20		18		30			
Holts Creek	40		37		55			44
Big Creek	55		48		50			51
Channel	62		50		56			56
Shoulder	50		54		48			51
Thoroughfare	54		50		43			49
Mean	52		48		51			
	1990							
	March	April				May		
	17	8	16	22	29	8	12	
Holts Creek	30	40	38	45	54	38	35	40
Big Creek	55	40	40	50	52	47	38	46
Channel	50	65	65	45	56	56	30	52
Shoulder	30	42	40	50	32	53	50	42
Thoroughfare	35	40	47	49	50	50	31	43
Mean	40	45	46	47	52	49	36	

Table 4-7. Herring egg abundances ($100 \cdot m^{-3}$) in the Pamunkey River and Cumberland Thoroughfare in 1989 and 1990.

Stratum	Date																Mean
	1989																
	March		April								May						
	22	28	4	6	12	14	18	22	25	28	3	5	11	16	20	25	
1	0	.	196	1365	0	0	0	396	16	0	12	0	0	0	0	0	132
2	0	0	4	60	0	0	24	0	0	0	0	0	0	0	0	0	6
3	0	0	11	58	0	0	0	0	10	0	0	0	0	0	0	0	4
4	0	0	7	116	0	0	0	0	0	0	0	0	0	0	0	0	8
5	12	389	0	0	0	0	0	0	0	0	36	7	0	62	0	0	32
6	0	0	0	206	0	0	0	0	0	0	9	142	0	7	0	0	23
CT	.	.	84	.	37	.	1523	1007	64	0	0	241	0	0	0	0	246

	1990				
	March	April		May	
	21	10	27	9	
1	0	31	23	0	14
2	0	0	61	0	15
3	0	0	3	0	<1
4	0	0	36	0	9
5	0	301	39	0	85
6	0	220	24	0	61
CT	43	161	917	0	280

Table 4-8. Analysis of variance of yolk-sac larval river herring abundances (natural logarithm transformed) in 1989 and 1990 to determine the significance of main effects and interactions between strata along the mainstem river channel (Location), time intervals of the spawning season (Time), and sampling season (Year).

Source of Variation	df	SS	MS	F	p
Within cells error	71	53.46	0.75		
Location	5	5.20	1.04	1.38	0.241
Time within Year	3	13.46	4.49	5.96	0.001*
Year	1	102.41	102.41	136.01	<0.000*
Location by Time	15	7.40	0.49	0.66	0.818
Location by Year	5	4.46	0.89	1.18	0.326
Time by Year	3	1.71	0.57	0.76	0.521
Location by Time by Year	15	6.47	0.43	0.57	0.886

Table 4-9. Analysis of variance of early preflexion larval river herring abundances (natural logarithm transformed) in 1989 and 1990 to determine the significance of main effects and interactions between strata along the mainstem river channel (Location), time intervals of the spawning season (Time), and sampling season (Year).

Source of Variation	df	SS	MS	F	p
Within cells error	71	47.41	0.67		
Location	5	1.38	0.28	0.41	0.838
Time within Year	3	35.28	11.76	17.61	<0.000*
Year	1	74.00	74.00	110.82	<0.000*
Location by Time	15	12.78	0.85	1.28	0.240
Location by Year	5	3.87	0.77	1.16	0.337
Time by Year	3	1.17	0.39	0.59	0.627
Location by Time by Year	15	3.64	0.24	0.36	0.984

Table 4-10. Analysis of variance of total zooplankton abundance (natural logarithm transformed), including rotifers, copepodites and nauplii, and cladocerans, in 1989 and 1990 to determine the significance of main effects and interactions between strata along the mainstem river channel (Location), time intervals of the spawning season (Time), and sampling season (Year).

Source of Variation	df	SS	MS	F	p
Within cells error	57	9.04	0.16		
Location	5	7.36	1.47	9.29	<0.000*
Time within Year	3	8.35	2.78	17.56	<0.000*
Year	1	100.17	100.17	631.93	<0.000*
Location by Time	15	2.81	0.19	1.18	0.311
Location by Year	5	0.51	0.10	0.64	0.669
Time by Year	3	0.61	0.20	1.28	0.290
Location by Time by Year	15	3.33	0.22	1.40	0.179

Table 4-11. Herring egg abundance ($100 \cdot m^{-3}$) in potential tidal freshwater habitats of the Pamunkey River, Virginia, in 1989 and 1990.

Location	Date							Mean
	1989							
	April			May				
	20			18		30		
Holts Creek	0			0		7		2
Big Creek	14			0		0		4
Channel	0			0		0		0
Shoulder	0			0		0		0
Thoroughfare	11			3		173		62
Mean	5			<1		38		
	1990							
	March	April				May		
	17	8	16	22	29	8	12	
Holts Creek	0	0	0	0	0	0	0	0
Big Creek	0	0	0	2	3	0	0	<1
Channel	0	0	2	0	0	0	0	<1
Shoulder	0	0	3	0	0	0	0	<1
Thoroughfare	0	30	3	10	0	0	0	6
Mean	0	5	1	2	1	0	0	

Table 4-12. Analysis of variance of yolk-sac larval river herring abundance (natural logarithm transformed) in potential tidal freshwater nursery habitats of the Pamunkey River in 1989 and 1990 to determine the significance of main effects and interactions between potential nursery habitats (Habitat), time intervals of the sampling season (Time), and sampling seasons (Year).

Source of Variation	df	SS	MS	F	p
Within cells error	10	1.18	0.12		
Habitat	4	0.17	0.04	0.37	0.828
Time within Year	1	6.94	6.94	58.78	<0.000*
Year	1	11.29	11.29	95.64	<0.000*
Habitat by Time	4	1.17	0.29	2.47	0.112
Habitat by Year	4	0.74	0.18	1.56	0.259
Time by Year	1	2.24	2.24	19.01	0.001*
Habitat by Time by Year	4	1.29	0.32	2.72	0.091

Table 4-13. Analysis of variance of early preflexion, late preflexion and postflexion larval river herring abundances (natural logarithm transformed) in potential tidal freshwater nursery habitats of the Pamunkey River between mid- to late April and early to mid-May time periods in 1989 and 1990 to determine the significance of main effects and interactions between potential nursery habitats (Habitat), time intervals of the sampling season (Time), developmental group (Group), and sampling seasons (Year).

Source of Variation	df	SS	MS	F	p
Within cells error	30	7.49	0.25		
Habitat	4	12.11	3.03	12.12	<0.000*
Time interval within year	1	0.21	0.21	0.85	0.364
Year	1	13.57	13.57	54.36	<0.000*
Group	2	21.71	10.86	43.48	<0.000*
Habitat by Time	4	10.47	2.62	10.48	<0.000*
Habitat by Year	4	0.49	0.12	0.49	0.743
Time by Year	1	<0.00	<0.00	0.02	0.890
Group by Habitat	8	1.12	0.14	0.56	0.802
Group by Time	2	8.65	4.33	17.33	<0.000*
Group by Year	2	0.48	0.24	0.96	0.393
Habitat by Time by Year	4	0.75	0.19	0.75	0.564
Habitat by Time by Group	8	1.33	0.17	0.67	0.715
Habitat by Year by Group	8	1.92	0.24	0.96	0.484
Time by Year by Group	2	1.17	0.58	2.34	0.114
Habitat by Time by Year by Group	8	0.73	0.09	0.37	0.930

Table 4-14. Analysis of variance of rotifer, nauplius and copepodite, and cladoceran abundances (natural logarithm transformed) in potential tidal freshwater nursery habitats of the Pamunkey River between mid-to late April and early to mid-May time periods in 1989 and 1990 to determine the significance of main effects and interactions between potential nursery habitats (Habitat), time intervals of the sampling season (Time), zooplankton group (Group), and sampling seasons (Year).

Source of Variation	df	SS	MS	F	p
Within cells error	30	2.94	0.10		
Habitat	4	8.57	2.14	21.88	<0.000*
Time interval within season	1	0.05	0.05	0.49	0.490
Year	1	40.48	40.48	413.45	<0.000*
Group	2	14.95	7.47	76.34	<0.000*
Habitat by Time	4	1.38	0.34	3.52	0.018*
Habitat by Year	4	0.41	0.10	1.06	0.394
Time by Year	8	2.15	0.27	2.74	0.021*
Group by Habitat	1	0.06	0.06	0.60	0.444
Group by Time	2	4.63	2.32	23.66	<0.000*
Group by Year	2	6.72	3.36	34.30	<0.000*
Habitat by Time by Year	4	0.41	0.10	1.06	0.396
Habitat by Time by Group	8	0.35	0.04	0.45	0.881
Habitat by Year by Group	8	1.07	0.13	1.36	0.253
Time by Year by Group	2	0.08	0.04	0.39	0.683
Habitat by Time by Year by Group	8	0.21	0.03	0.27	0.970

Table 4-15. Summary statistics for analyses of the precision of increment enumerations by sampling season and by habitat.

Group	Index of Precision	Coefficient of Variation	
	Mean	Mean[a]	95% C.I.
1989	0.0553	0.0782	0.0775-0.0790
1990	0.0385	0.0544	0.0539-0.0549
River	0.0572	0.0809	0.0798-0.0820
Creek	0.0409	0.0578	0.0574-0.0582

a. Values for the coefficient of variation and the average percent error were equal; therefore, only values for the coefficient of variation are shown.

Table 4-16. Summary of sample sizes of larvae by habitat and spawning season.

Group		River Herring	Gizzard Shad	Unidentified[a]
		Habitat		
Tidal Creek		140	41	3
River channel		96	19	0
		Spawning Season		
1989	Cohort I	60	11	1
	Buffer[b]	13	6	0
	Cohort II	32	20	0
1990	Cohort I	122	20	2
	Buffer	9	3	0
	Cohort II	0	0	0

a. The three larvae classified as 'unidentified' by the SVL/SL ratio were identified as alewife larvae based on pigment characters observed during length measurement.

b. This refers to the 8-day interval separating cohorts I and II.

Table 4-17. Test for statistical significance of extreme observations[a]: comparison of age 11 d specimens of the 1990 'early-spawn' cohort.

	X_i	$X_i-(\bar{X})$	$\{X_i-(\bar{X})\}^2$
possible outlier	12.0	4.11	16.91
	6.2	-1.69	2.85
	6.2	-1.69	2.85
	6.4	-1.49	2.21
	6.5	-1.39	1.93
	7.2	-0.69	0.47
	7.6	-0.29	0.08
	7.7	-0.19	0.04
	7.8	-0.09	0.01
	8.0	0.11	0.01
	8.1	0.21	0.05
	8.1	0.21	0.05
	8.2	0.31	0.10
	8.3	0.41	0.17
	8.8	0.91	0.83
	9.1	1.21	1.47
Mean (X_i)	7.9		
$\sum \{X_i-(\bar{X})\}^2$ (A)			30.02
$\sqrt{}$ (A)			5.48
Maximum Normed Residual			0.75
5% probability			0.668
1% probability			0.672
			(0.01>p)

a. Snedecor and Cochran (1980), p. 279-282.

Table 4-18. Test for statistical significance of extreme observations[a]: comparison of standard lengths among age 11 d specimens from the river channel mainstem.

	X_i	$X_i-(\bar{X})$	$\{X_i-(\bar{X})\}^2$
possible outlier	12.0	4.11	20.89
	6.2	-1.22	1.49
	6.2	-1.22	1.49
	6.2	-1.22	1.49
	6.5	-0.92	0.85
Mean (X_i)	7.4		
$\sum \{X_i-(\bar{X})\}^2$ (A)			26.29
$\sqrt{}$ (A)			5.13
Maximum Normed Residual			0.89
5% probability			0.642
1% probability			0.780
			(0.01>p)

a. Snedecor and Cochran (1980), p. 279-282.

Table 4-19. Test for statistical significance of extreme observations[a]: comparison of maximum otolith diameter for all age 16 d to age 19 d specimens.

	Age group	X_i	$X_i-(\bar{X})$	$\{X_i-(\bar{X})\}^2$
possible outlier	18 d	163	57.6	3314.5
	19 d	150	44.6	1986.6
	17 d	109	3.6	12.8
	17 d	79	-26.4	698.5
	17 d	78	-27.4	752.3
	16 d	106	0.6	0.3
	16 d	84	-21.4	459.2
	16 d	91	-14.4	208.2
	16 d	81	-24.4	596.8
	16 d	109	3.6	12.8
	16 d	133	27.6	760.2
	16 d	119	13.6	184.2
	16 d	102	- 3.4	11.8
	16 d	72	-33.4	1117.5
Mean (X_i)		105.4		
$\sum\{X_i-(\bar{X})\}^2$ (A)				10115.4
$\sqrt{}$ (A)				100.6
Maximum Normed Residual				0.57
5% probability				0.546
1% probability				0.641
				(0.05>p>0.01)

a. Snedecor and Cochran (1980), p. 279-282.

Table 4-20. Summary of diagnostic tests for ordinary and weighted least-squares regression models relating standard length to estimated age (days after hatching) for river herring larvae of the 1989 'early-spawn' cohort.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	Overall p	F	p	df	F	p	SL	Residuals
Ordinary least-squares										
3-24 (all)	61	Curvature Lack of fit	0.004 0.001	1.90	0.059	47	3.79	<0.001	0.845	0.986
3-10	51	Lack of fit	<0.000	1.76	0.130	43	2.51	0.030	0.913	0.955
11-24	10	None	>0.1	0.13	0.963	4	3.30	0.098	0.995	0.974
Weighted least-squares										
3-24 (all)	61	Curvature	0.010	1.89	0.061	47	1.13	0.370	0.949	0.995
3-10	51	None	>0.1	1.94	0.096	43	0.89	0.520	0.946	0.987
11-24	10	None	>0.1	0.22	0.915	4	1.98	0.208	0.971	0.910

a. Correlation between standard length or studentized residuals with associated normal probability scores.

Table 4-21. Summary of ordinary least-squares and weighted least-squares regression models relating standard length to estimated age (days after hatching) for river herring larvae of the 1989 'early-spawn' cohort.

Age	df	$t_{0.05}$	Regression Statistics								F	SE_{regr}	r^2_{adj}
			α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
Ordinary least-squares													
3-24 (all)	61	2.000	2.90	0.179	2.54	3.26	0.461	0.019	0.423	0.499	582.42	0.7721	0.906
3-10	51	2.009	3.55	0.258	3.03	4.07	0.350	0.042	0.266	0.434	70.57	0.6233	0.582
11-24	10	2.228	0.19	1.527	-3.21	3.59	0.610	0.083	0.425	0.075	54.52	1.0900	0.856
Weighted least-squares													
3-24 (all)	61	2.000	3.48	0.148	3.18	3.78	0.374	0.028	0.318	0.430	178.16	-	-
3-10	51	2.009	3.76	0.187	3.38	4.14	0.311	0.038	0.235	0.387	65.73	-	-
11-24	10	2.228	-0.37	1.300	-3.27	2.53	0.643	0.079	0.467	0.819	66.25	-	-

Table 4-22. Summary of diagnostic tests for ordinary and weighted least-squares regression models relating standard length to estimated age (days after hatching) for river herring larvae of the 1990 'early-spawn' cohort.

Age Range	n	Burn-Ryan Test		Pure error F test			Homogeneity of variances		NPS Correlation[a]	
		Symptom	Overall p	F	p	df	F	p	SL	Residuals
Ordinary least-squares										
4-19 (all)	122	Curvature Lack of fit	<0.001 0.003	4.82	<0.000	107	1.27	0.235	0.980	0.974
4-10	42	None	>0.1	0.62	0.682	35	1.63	0.168	0.961	0.985
11-19	80	Lack of fit	0.048	3.31	0.006	72	0.97	0.462	0.990	0.994
Weighted least-squares										
4-19 (all)	122	Curvature	<0.000	3.13	<0.000	107	2.99	0.001	0.840	0.994
4-10	42	None	>0.1	0.83	0.537	35	1.47	0.217	0.902	0.985
11-10	80	None	>0.1	2.30	0.043	72	2.88	0.010	0.975	0.994

a. Correlation between standard length or studentized residuals and associated normal probability scores.

Table 4-23. Summary of ordinary least-squares and weighted least-squares regression models relating standard length to estimated age (days after hatching) for river herring larvae of the 1990 'early-spawn' cohort.

Age	df	$t_{0.05}$	Regression Statistics								F	SE_{reg}	r^2_{adj}
			α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
Ordinary least-squares													
4-19 (all)	122	1.980	2.46	0.287	1.89	3.03	0.506	0.024	0.458	0.554	439.54	0.8743	0.782
4-10	42	2.019	3.63	0.478	2.66	4.60	0.371	0.061	0.248	0.494	37.07	0.6494	0.468
11-19	80	1.993	0.71	0.671	-0.63	2.05	0.627	0.050	0.527	0.727	158.36	0.8211	0.666
Weighted least-squares													
4-19 (all)	122	1.980	3.19	0.194	2.81	3.57	0.438	0.020	0.398	0.478	473.07	-	-
4-10	42	2.019	3.96	0.384	3.18	4.74	0.328	0.054	0.219	0.437	36.52	-	-
11-19	80	1.993	0.87	0.702	-0.53	2.27	0.615	0.054	0.507	0.723	129.43	-	-

Table 4-24. Weighted analysis of covariance testing the homogeneity of slopes of the standard length-age relationship for younger (<age 11 d) and older (≥age 11 d) river herring larvae between 1989 and 1990 'early-spawn' cohorts.

Source of variation	df	Sums of squares	Mean square	F	p
		Ages less than 11 days			
Age class (Within groups)	1	0.68359	0.68359	89.34	<0.000
Year (Between groups)	1	0.00153	0.00153	0.20	0.656
Age class · year interaction	1	0.00047	0.00047	0.06	0.805
Error	89	0.68099	0.00765		
Total	92				
		Age 11 days and greater			
Age class (Within groups)	1	0.66717	0.66717	163.66	<0.000
Year (Between groups)	1	0.00270	0.00270	0.66	0.418
Age class · year interaction	1	0.00032	0.00032	0.08	0.779
Error	86	0.35059	0.00408		
Total	89				

Table 4-25. Weighted analysis of covariance testing the difference in slopes of regression models relating standard length to age (days after hatching) between younger (<age 11 d) and older (≥age 11 d) river herring larvae pooled across the 1989 and 1990 'early-spawn' cohorts.

Source of variation	df	Sums of squares	Mean square	F	p
Within age classes	1	1.7031	1.7031	279.34	<0.000
Between age classes	1	0.0760	0.0760	12.26	0.001
Age · age group interaction	1	0.1038	0.1038	17.02	<0.000
Error	179	1.0913	0.0061		
Total	182				

Table 4-26. Summary of diagnostic tests for ordinary and weighted least-squares regression models relating standard length to estimated age (days after hatching) for river herring larvae from age 3 d to age 14 d from the mainstem river and tidal creeks.

Regression Model	n	Burn-Ryan Test		Pure error F test			Homogeneity of variance		NPS Correlation[a]	
		Symptom	Overall p	F	p	df	F	p	SL	Residuals
River channel mainstem										
OLS	94	None	>0.1	2.55	0.010	82	2.28	0.017	0.860	0.977
WLS	94	None	>0.1	1.73	0.0818	82	1.94	0.045	0.930	0.987
Tidal creek										
OLS	106	None	>0.1	1.40	0.199	95	1.07	0.393	0.978	0.999
WLS	106	None	>0.1	1.78	0.0869	95	11.63	<0.000	0.865	0.982

a. Correlation standard length and studentized residuals with associated normal probability scores.

Table 4-27. Weighted analysis of covariance testing the difference in slopes of regression models relating standard length to age (days after hatching) for river herring larvae ranging from age 3 d to age 14 d in the mainstem river and tidal creeks.

Source of variation	df	Sums of squares	Mean square	F	p
Within age group	1	4.7656	4.7656	660.79	<0.000
Between habitats	1	0.1673	0.1673	23.19	<0.000
Age · habitat interaction	1	0.1260	0.1260	17.48	<0.000
Error	196	1.4136	0.0072		
Total	199				

Table 4-28. Summary of ordinary and weighted least-squares regression models relating standard length to estimated age (days after hatching) for river herring larvae in tidal creeks.

Age	df	$t_{0.05}$	Regression Statistics								F	SE_{regr}	r^2_{adj}
			α	SE_α	LCL	UCL	β	SE_β	LCL	UCL			
Mainstem river channel													
OLS	94	1.989	3.57	0.1	3.19	3.95	0.346	0.027	0.292	0.400	166.30	0.7009	0.640
WLS	94	1.989	3.63	0.1	3.37	3.89	0.335	0.025	0.285	0.385	177.42	-	-
Tidal creeks													
OLS	106	1.985	2.63	0.1	2.26	3.00	0.472	0.018	0.436	0.508	655.60	0.6187	0.862
WLS	106	1.985	2.68	0.1	2.40	2.96	0.462	0.019	0.424	0.500	594.56	-	-

Table 4-29. Analysis of variance for regression models relating growth-increment width in otoliths to age of river herring larvae from the mainstem river and tidal creeks.

Source of variation	df	SS	MS	F	p	Parameter estimates	
						α (SE_α)	β (SE_β)
River channel mainstem							
Regression	1	0.2329	0.2329	0.93	0.338	2.05 (0.137)	0.018 (0.019)
Error	93	23.3659	0.2512				
Total	94	23.5988					
Tidal creek							
Regression	1	26.665	26.665	115.7	<0.000	1.46 (0.112)	0.099 (0.009)
Error	142	32.724	0.230				
Total	143	59.389					

Table 4-30. Chi-square tests of independence for hatch date frequencies of river herring larvae captured in the mainstem river or in tidal creeks with river flow and relative time interval in 1989. Hatch dates prior to 1 May were classified as the early-hatch groups, and river flow velocities exceeding 1250 cfs were classified as high. Expected values are shown in parentheses.

Contingency Table					χ^2	p
Table 1		Early hatch	Late hatch	Total		
	River	57 (31.6)	12 (37.4)	69	72.169	<0.000
	Creeks	9 (34.4)	66 (40.6)	75		
	Total	66	78	144		
Table 2		High flow	Low flow	Total		
	River	22 (33.1)	47 (35.9)	69	13.645	0.002
	Creeks	47 (35.9)	28 (39.1)	75		
	Total	69	75	144		
Table 3		Early hatch	Late hatch	Total		
	High flow	16 (31.6)	53 (37.4)	69	27.364	<0.000
	Low flow	50 (34.4)	25 (40.6)	75		
	Total	66	78	144		

Table 4-31. Chi-square tests of independence for hatch date frequencies of river herring larvae captured in the mainstem river or in tidal creeks with river flow and relative time interval in 1990. Hatch dates prior to 24 April 1990 were classified as the early-hatch groups, and river flow velocities exceeding 1250 cfs were classified as high. Expected values are shown in parentheses.

Contingency Table					χ^2	p
Table 1		Early hatch	Late hatch	Total		
	River	31 (13.5)	15 (32.5)	46	45.700	<0.000
	Creeks	14 (31.5)	93 (75.5)	107		
	Total	45	108	153		
Table 2		High flow	Low flow	Total		
	River	15 (9.0)	31 (37.0)	46	7.053	0.008
	Creeks	15 (21.0)	92 (86.0)	107		
	Total	30	123	153		
Table 3		Early hatch	Late hatch	Total		
	High flow	23 (8.8)	7 (21.2)	30	40.137	<0.000
	Low flow	22 (36.2)	101 (86.8)	123		
	Total	45	108	153		

Table 4-32. Summary of larval American shad predators in the Susquehanna River system (Johnson and Dropkin 1992).

Species
Central stoneroller *Campostoma anomalum*
Creek chub *Semotilus atromaculatus*
Fallfish *Semotilus corporalis*
Rosyface shiner *Notropis ruellus*
Spotfin shiner *Cyprinella spiloptera*
Spottail shiner *Notropis hudsonius* *
Mimic shiner *Notropis volucellus*
Bluntnose minnow *Pimephales notatus*
Banded killifish *Fundulus diaphanus* *
Rock bass *Ambloplites rupestris*
Redbreast sunfish *Lepomis auritus* *
Bluegill *Lepomis macrochirus* *
Smallmouth bass *Micropterus dolomieu* *
Largemouth bass *Micropterus salmoides* *
Tessellated darter *Etheostoma olmstedi* *

* Species occurring in southern Chesapeake Bay tributaries (Wass 1972).

Figure 4-1. Location of the Pamunkey River in Virginia.

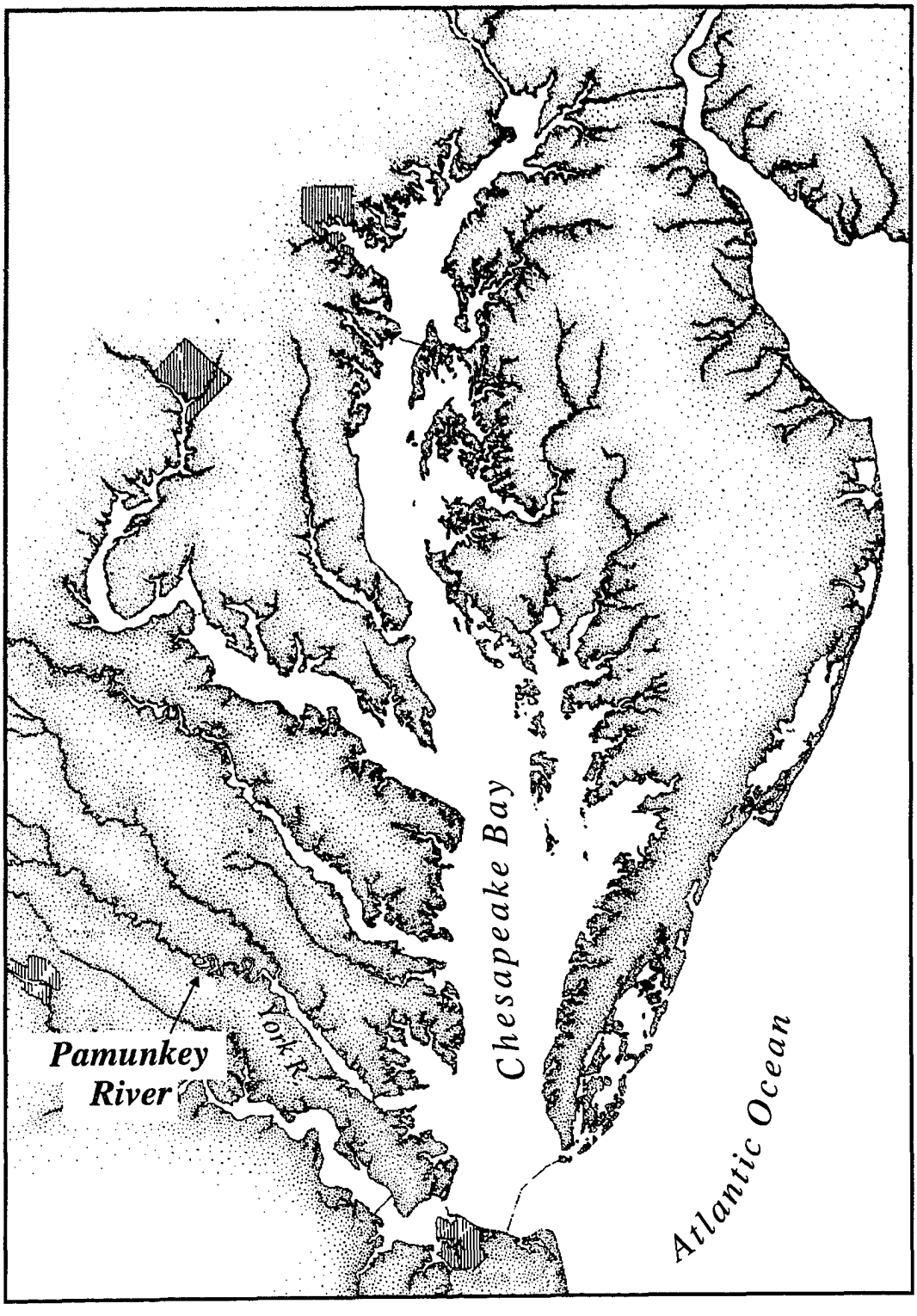


Figure 4-2. Overview of Lilly Point marsh showing Holts Creek (H), Cumberland Thoroughfare (CT), Big Creek (B), and the adjacent Pamunkey River (P).

Figure 4-3. Study area in the Pamunkey River tidal freshwater reach from kilometer 83.4 (P83.4) to kilometer 114.9 (P114.9), inclusive. The inset locates the study area for potential nursery habitats in the vicinity of Lilly Point marsh (see Fig. 4-4).

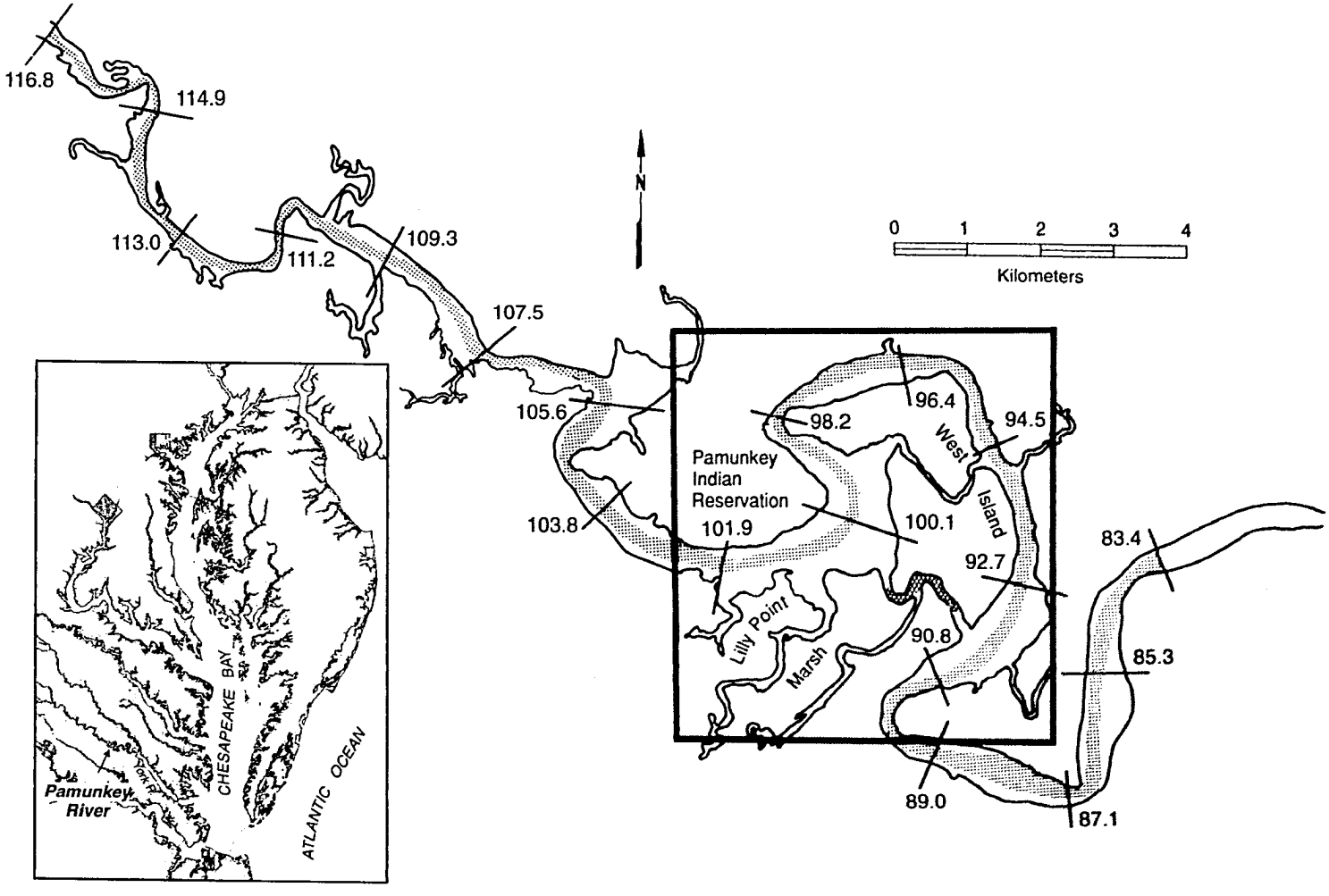
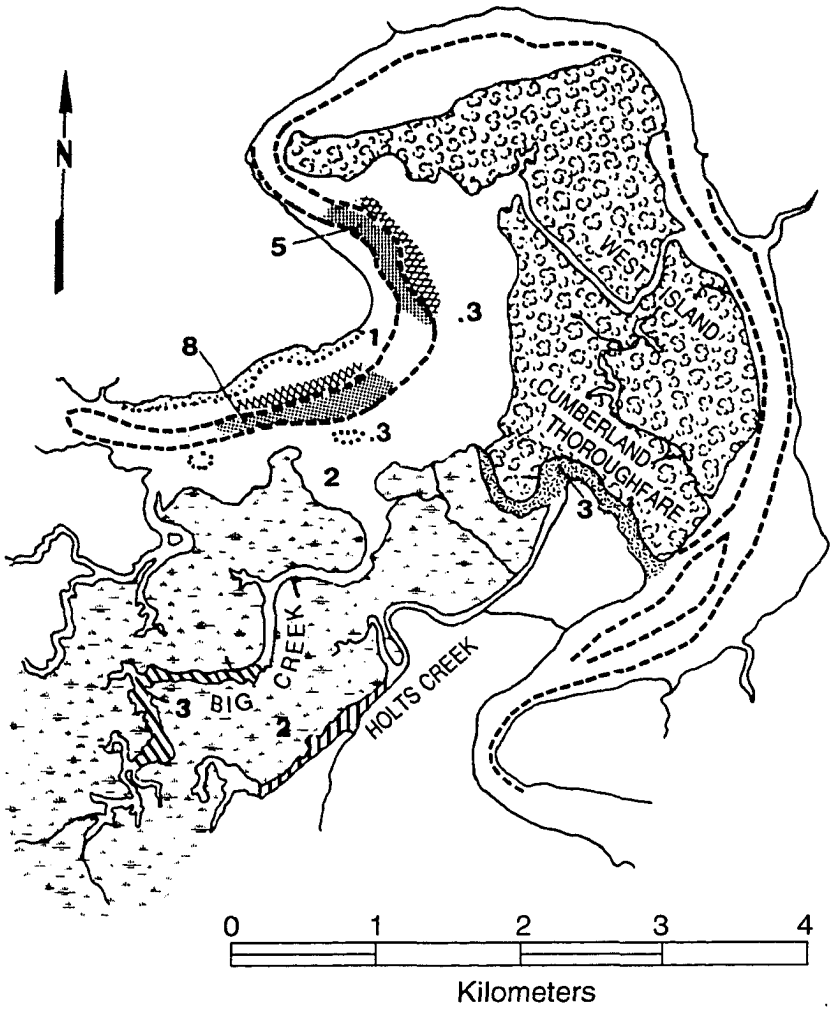


Figure 4-4. The Lilly Point marsh-Cumberland Thoroughfare region study area showing sampling locations in potential nursery habitats.



SAMPLING LOCATIONS

- CUMBERLAND CHANNEL
- TIDAL CREEKS
- CUMBERLAND FLATS
- CUMBERLAND THOROUGHFARE

VALUES INDICATE DEPTH (MEAN LOW WATER) IN METERS

Figure 4-5. Pushnet frame with paired plankton nets used to collect ichthyoplankton from potential tidal freshwater nursery habitats.

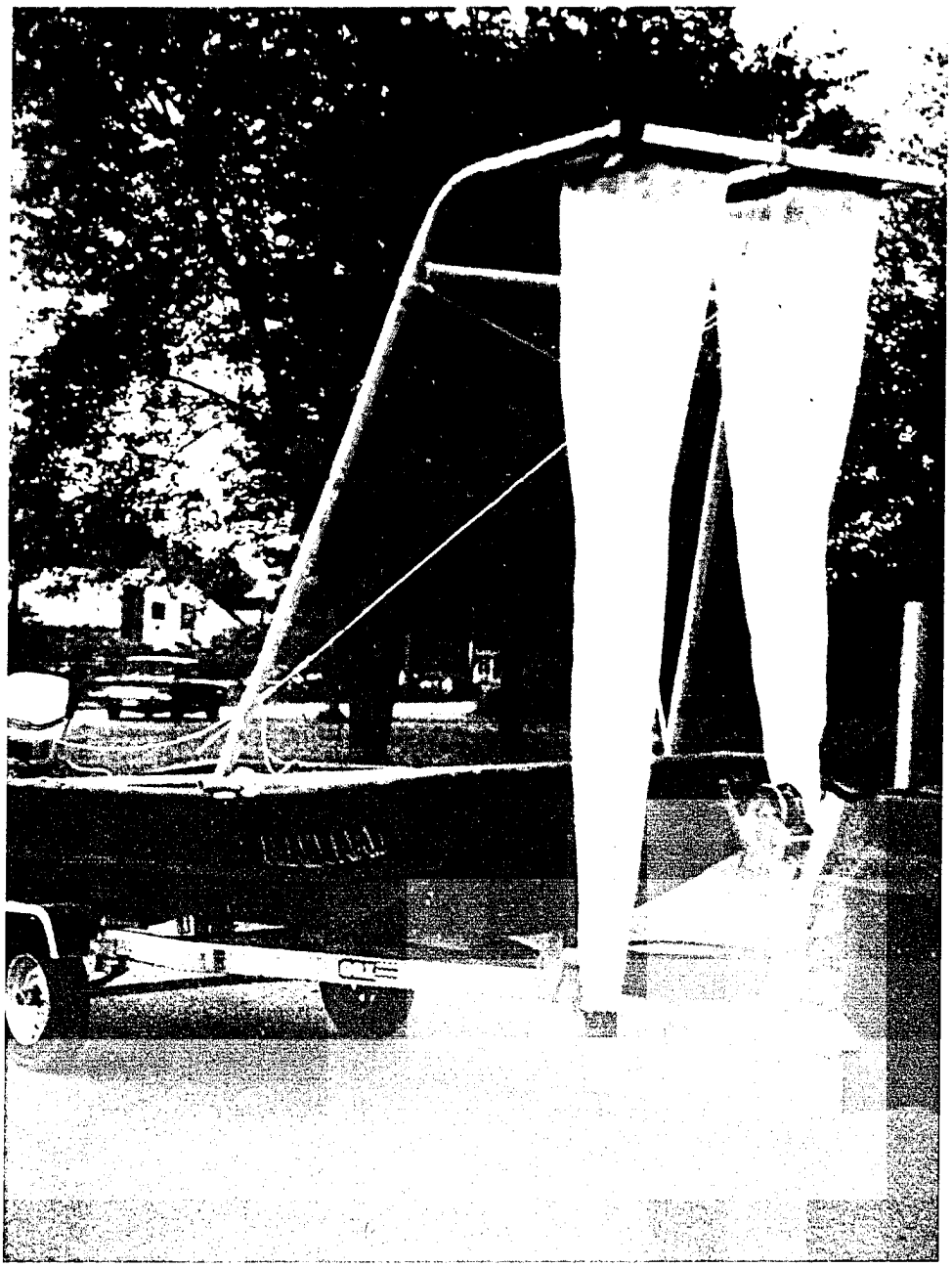


Figure 4-6. Seasonal air and water temperatures (°C) from March to May in 1989 (A) and 1990 (B). Average daily water temperature for the mainstem river (solid) and the potential nursery habitats (dashed), tended to follow the seasonal change in air temperature (dotted). The difference in air temperature between the two seasons (C) was greater and more variable prior to about 16 April. Air temperature was generally warmer in mid-March 1990 as compared to mid-March 1989.

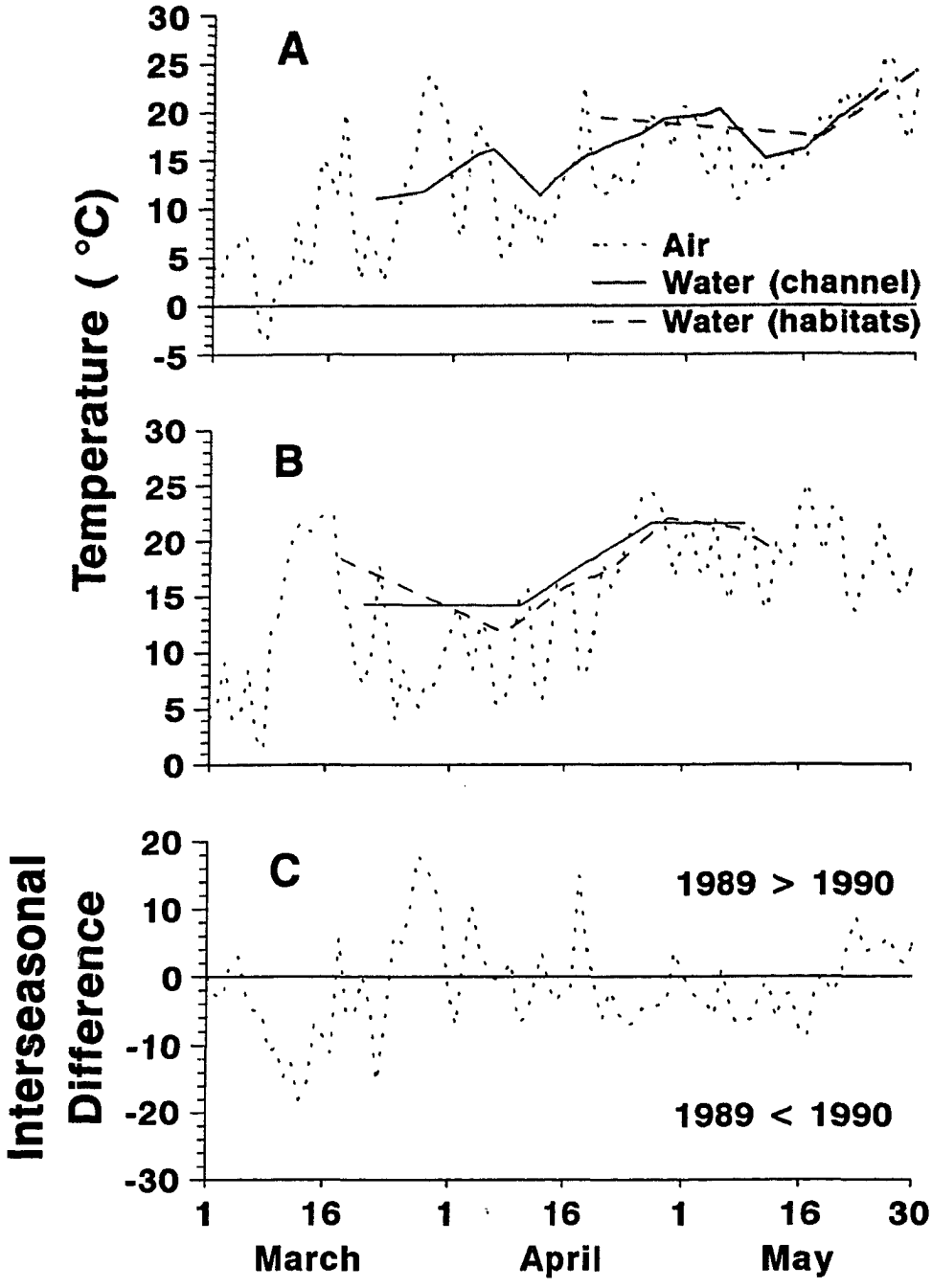


Figure 4-7. Rainfall and river flow from March to May, 1989.

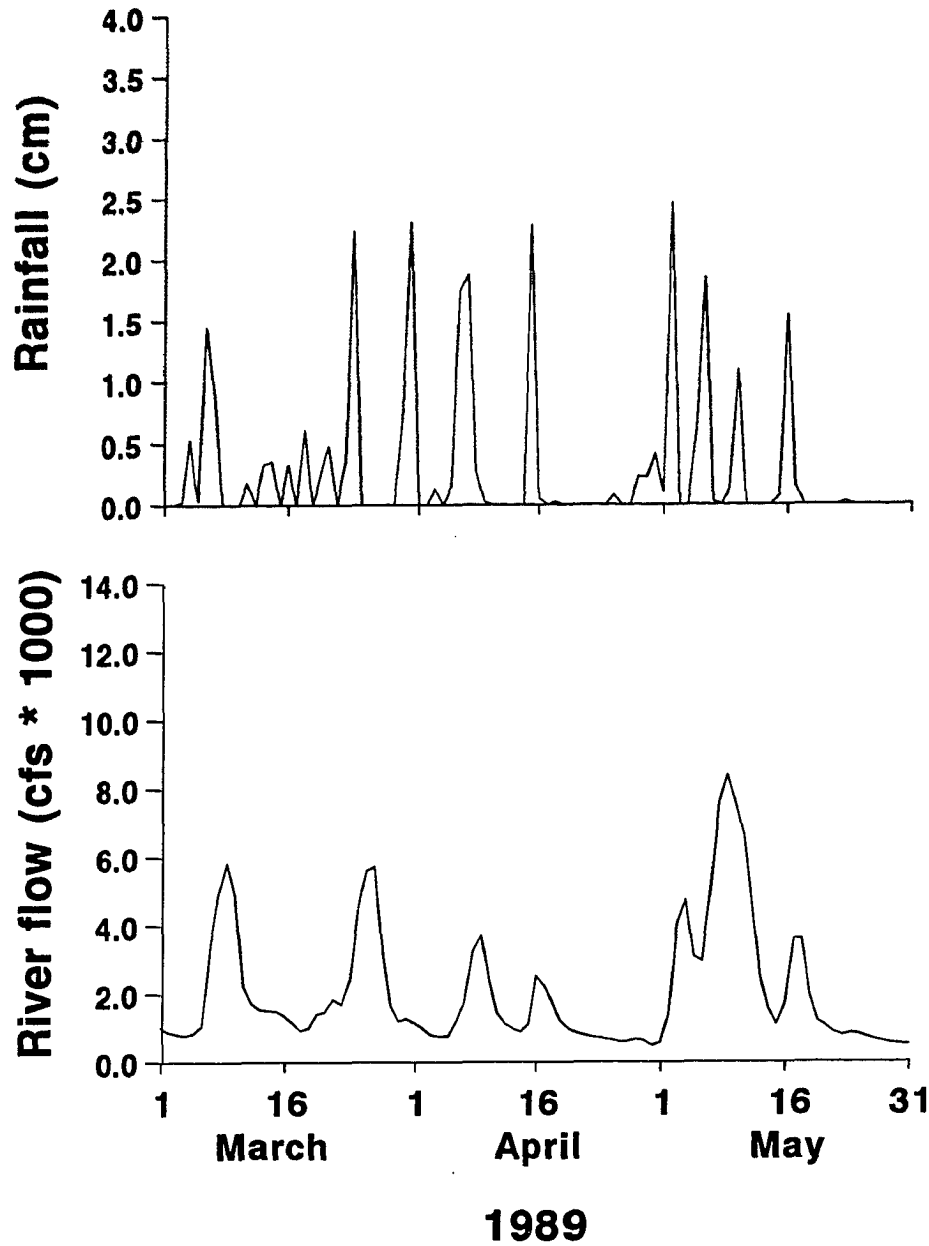


Figure 4-8. Rainfall and river flow from March to May, 1990.

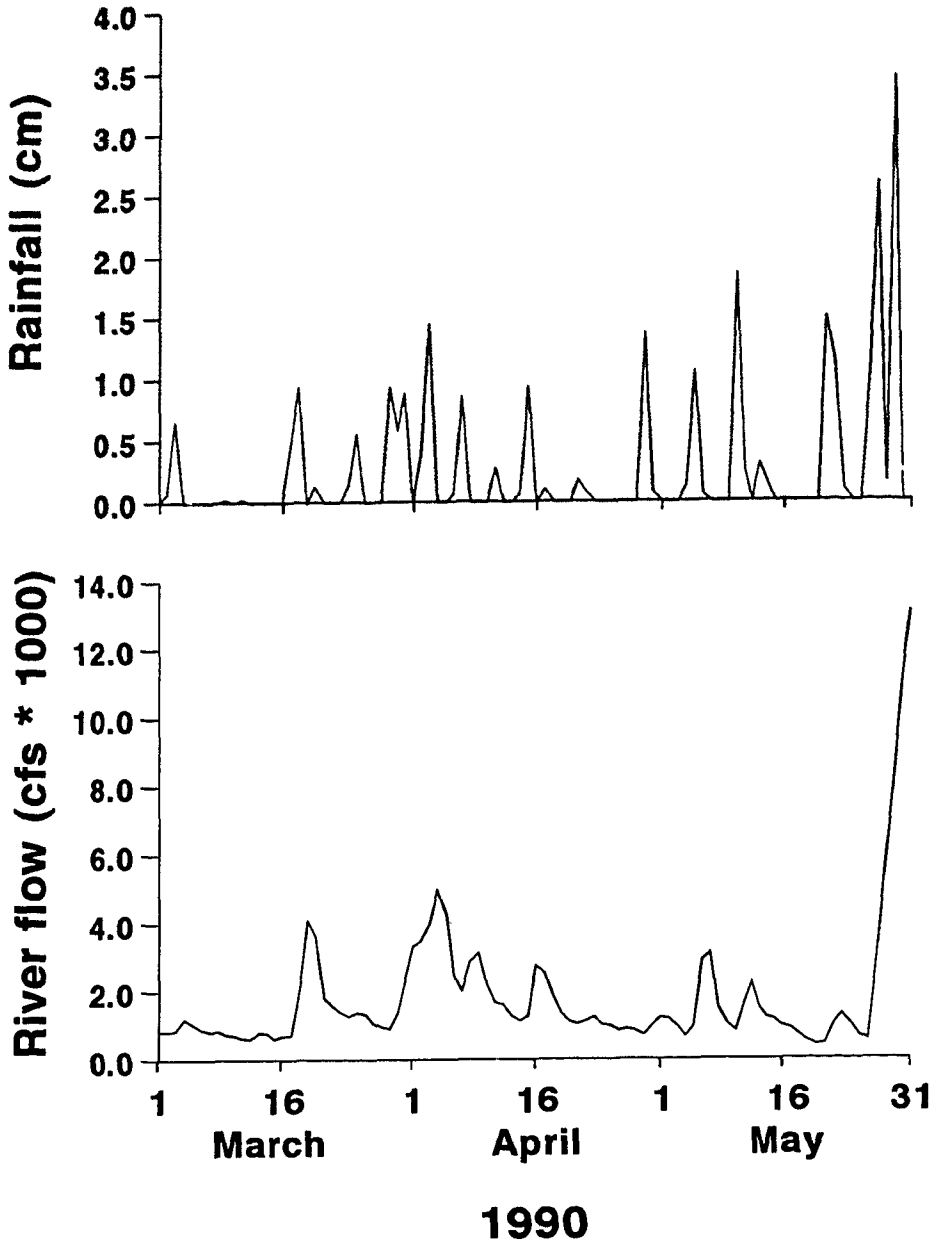


Figure 4-9. Dissolved oxygen concentration ($mg \cdot \ell^{-1}$) along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Open circles indicate locations and dates of missing measurements.

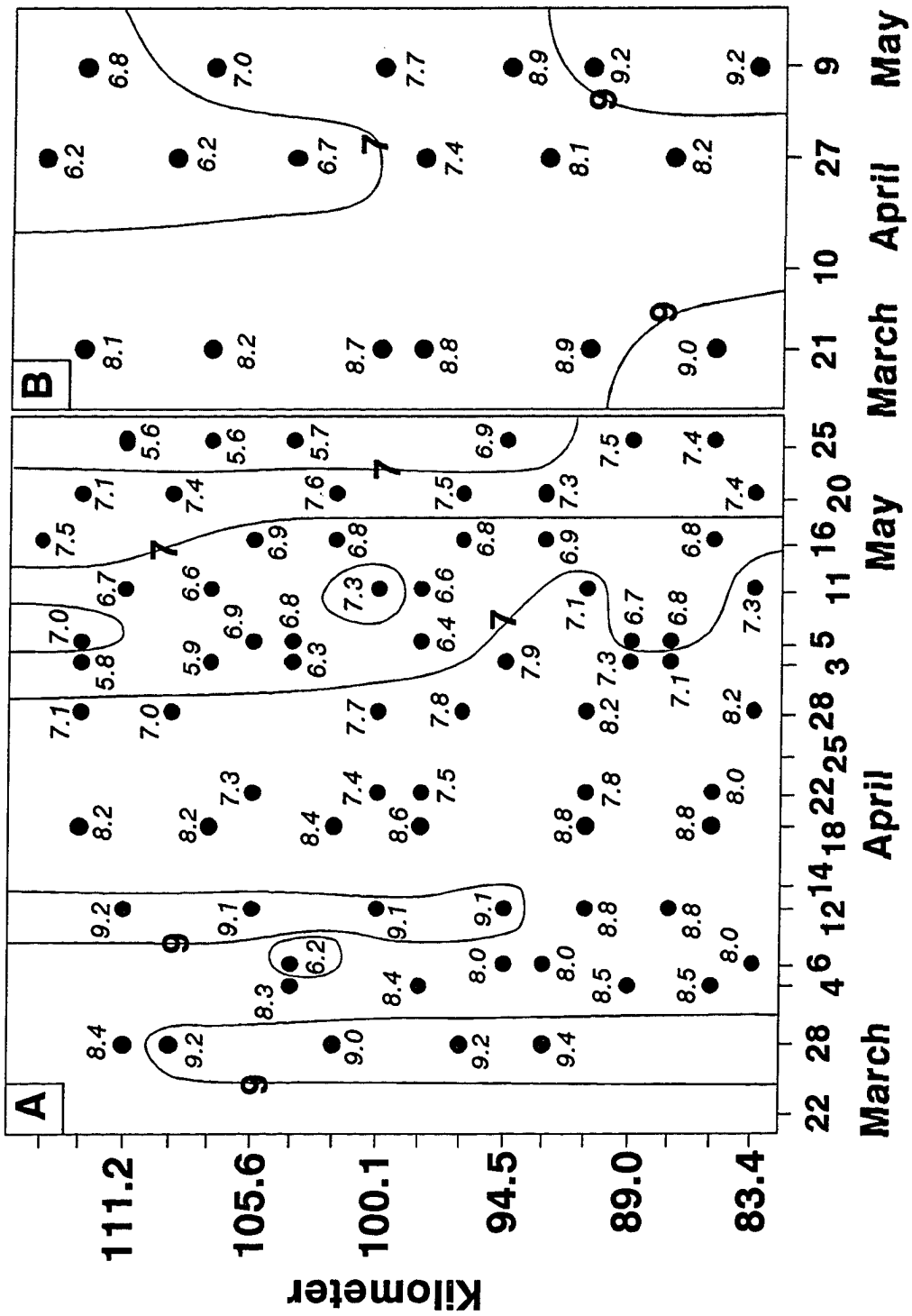


Figure 4-10. Water transparency (cm) along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Open circles indicate locations and dates of missing measurements.

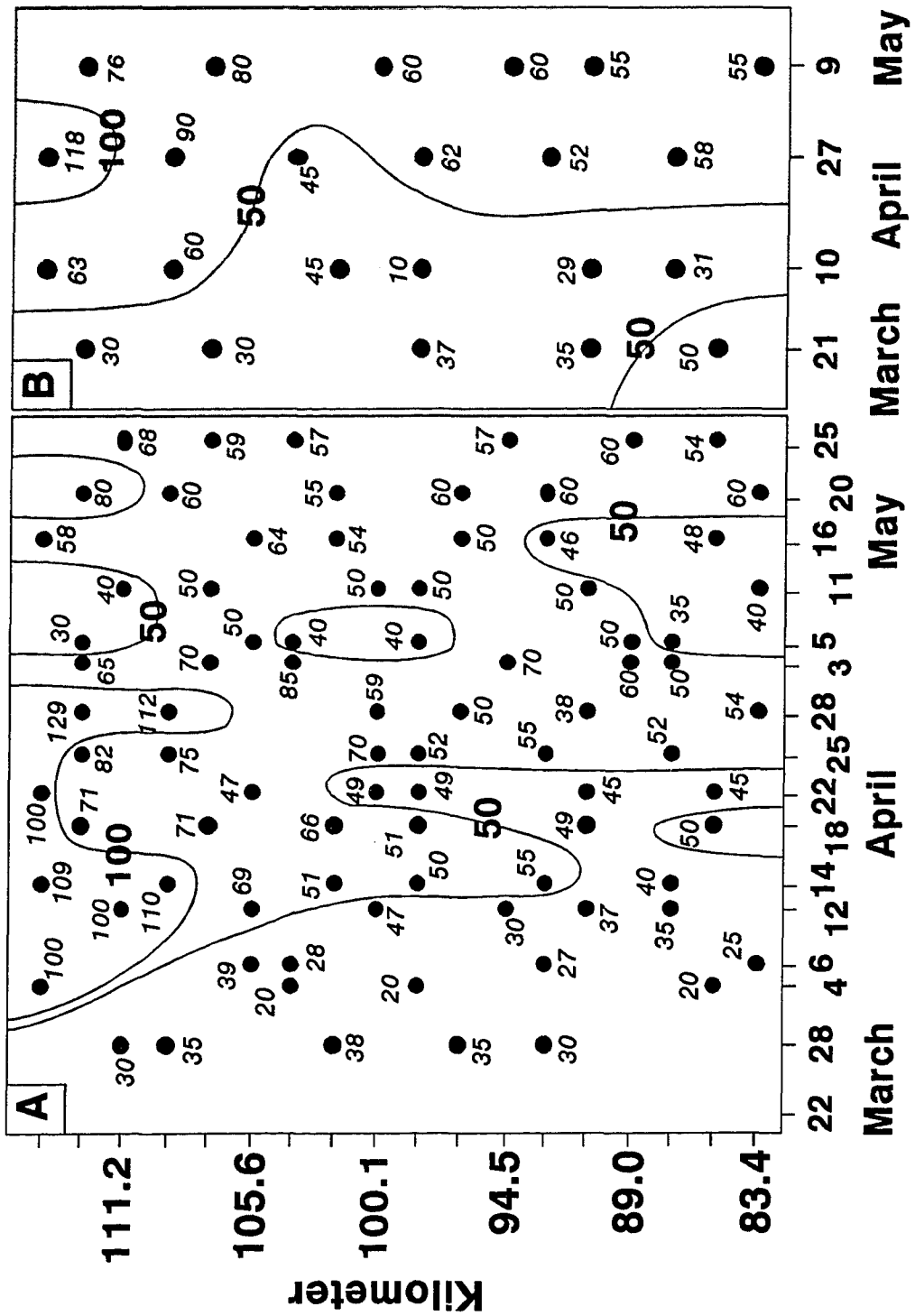


Figure 4-11. Relationship between dissolved oxygen concentration (DO) and river flow in the Pamunkey River, 1989-1990, by quarter-month interval. River flow explained a significant amount of variability in dissolved oxygen concentration when data associated with the high-flow event were excluded from the analysis (Mean DO = 6.85 + 0.000819 Mean flow; F = 14.94; df = 8; p = 0.006; r^2_{adj} = 0.635) but not when these data were included in the analysis (Mean DO = 7.82 - 0.000021 Mean flow; F = 0.01; df = 10; p = 0.917; r^2_{adj} = 0.0).

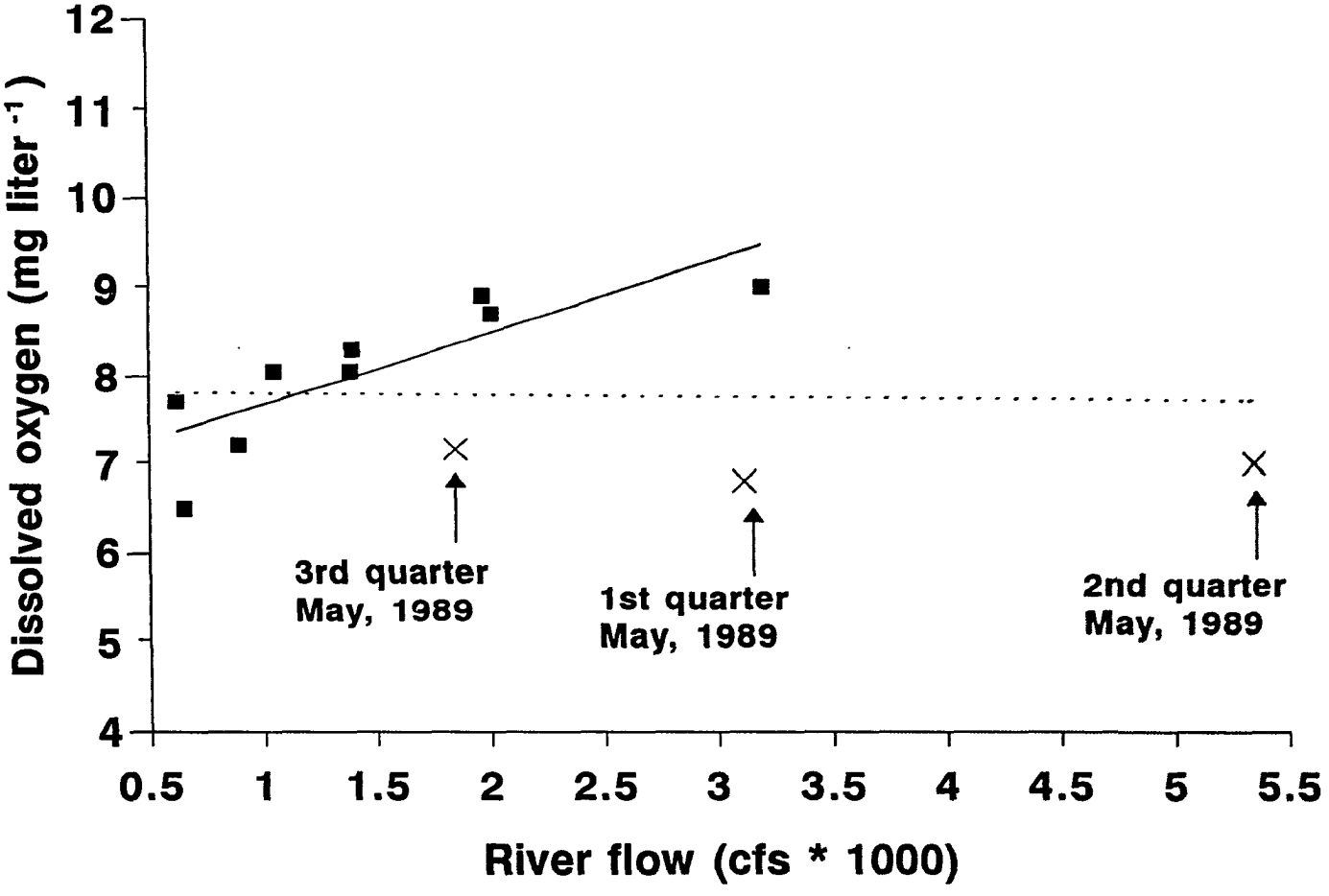


Figure 4-12. Percent composition of river herring (open) and gizzard shad (cross-hatch) yolk-sac larvae (A) and early preflexion larvae (B) in ichthyoplankton collections made along the mainstem Pamunkey River in the tidal freshwater reach in 1989.

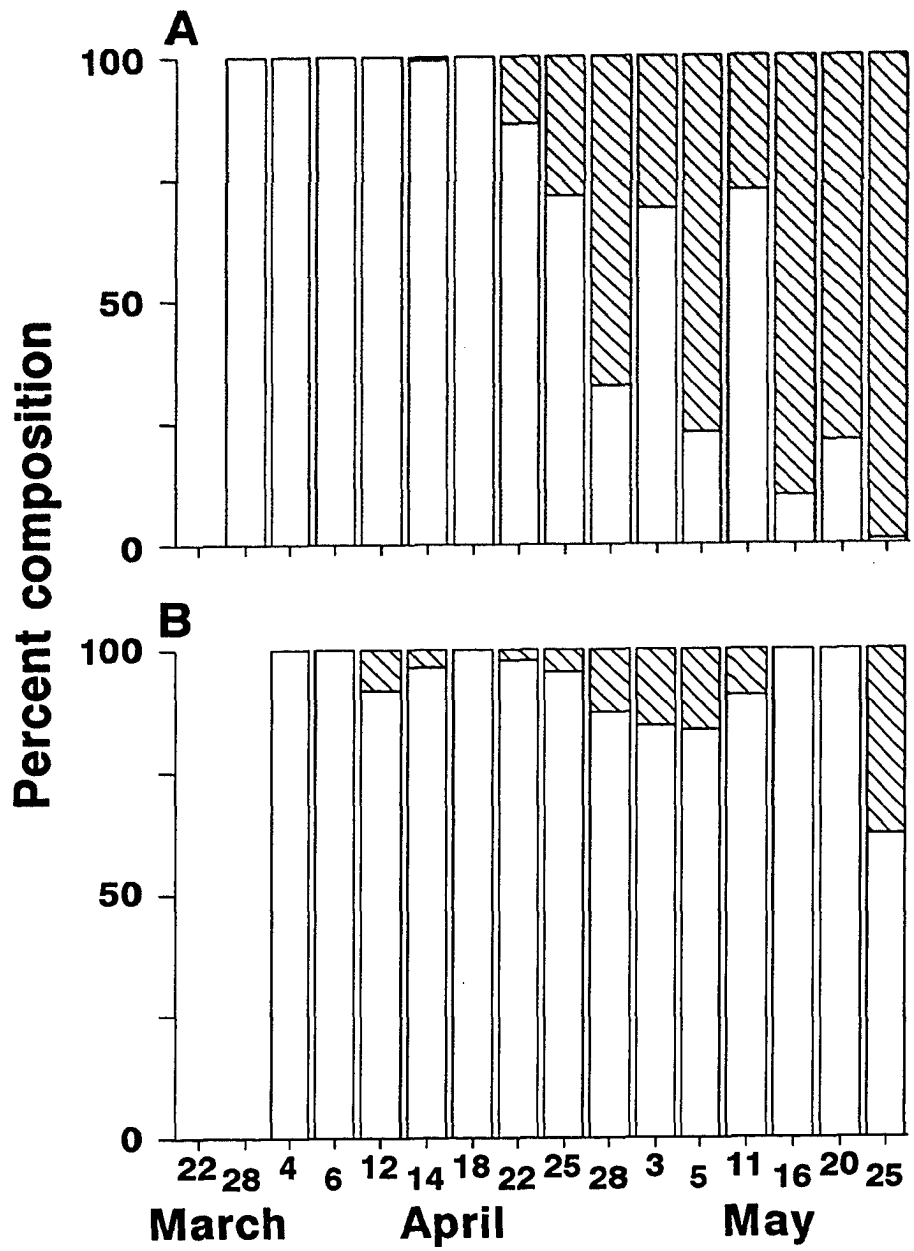


Figure 4-13. Percent composition of river herring (open) and gizzard shad (cross-hatch) yolk-sac larvae (A) and early preflexion larvae (B) in ichthyoplankton collections made along the mainstem Pamunkey River in the tidal freshwater reach in 1990.

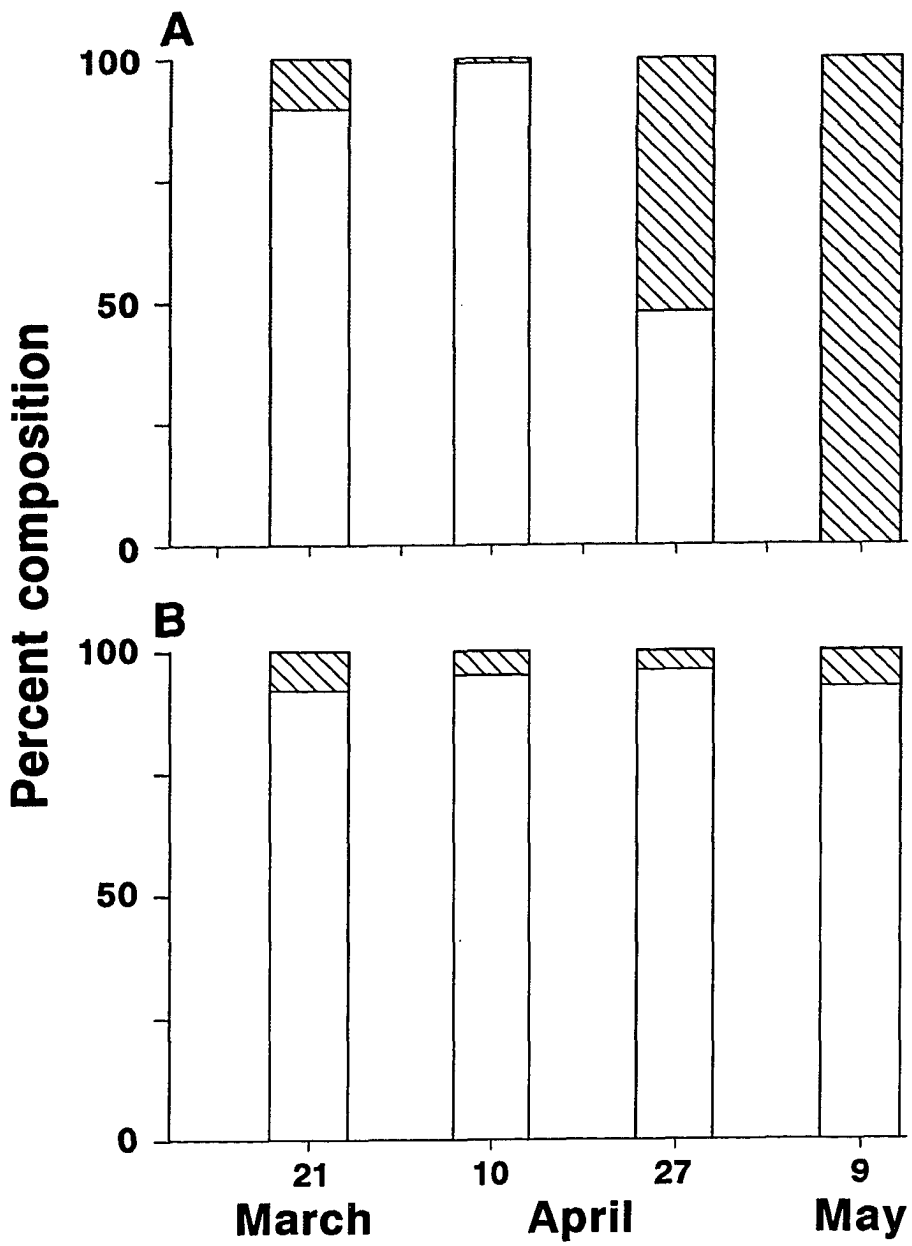


Figure 4-14. Percent composition of river herring (open) and gizzard shad (cross-hatch) yolk-sac larvae (A) and larvae (B) in ichthyoplankton collections made in potential tidal freshwater nursery habitats of the Pamunkey River in 1989.

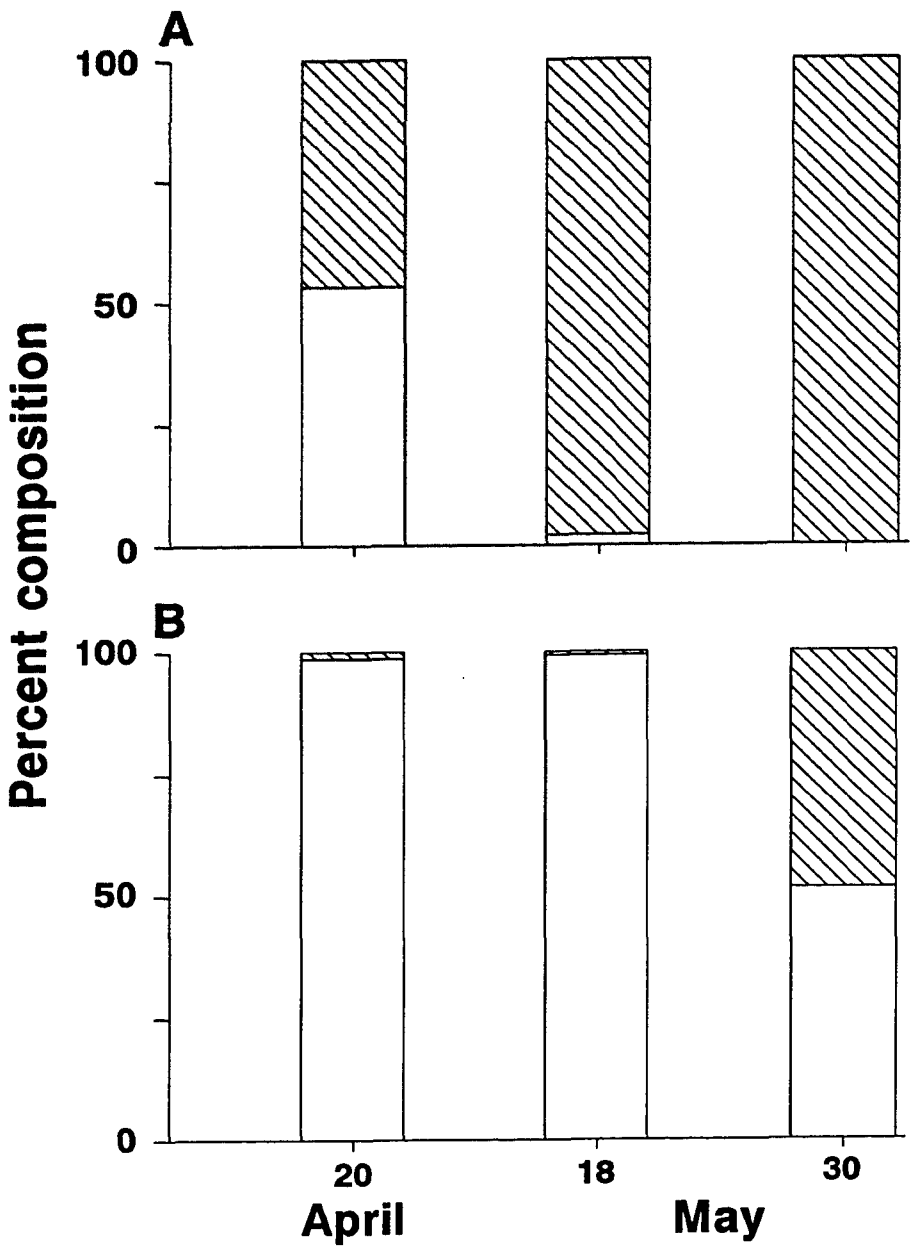


Figure 4-15. Percent composition of river herring (open) and gizzard shad (cross-hatch) yolk-sac larvae (A) and larvae (B) in ichthyoplankton collections made in potential tidal freshwater nursery habitats of the Pamunkey River in 1990.

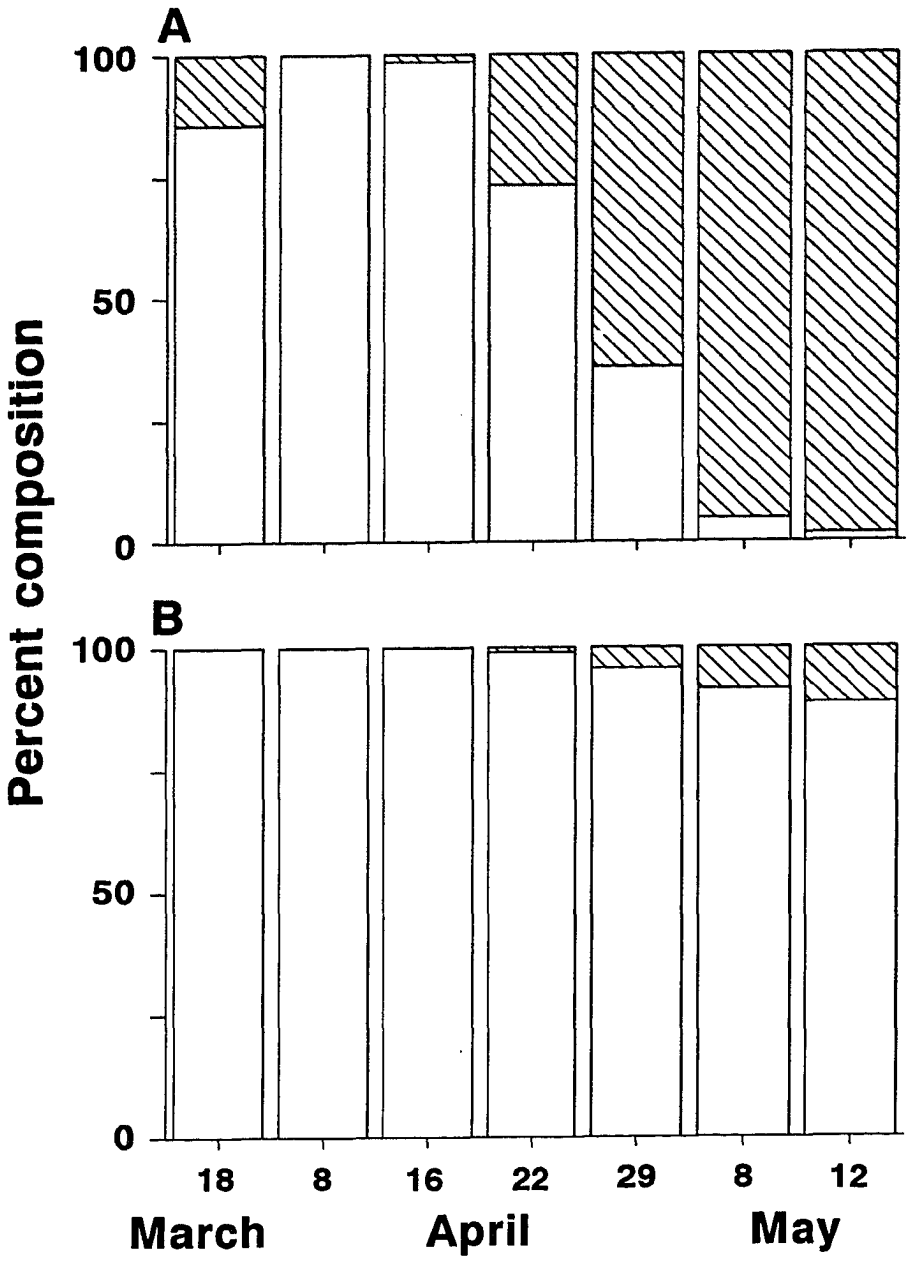


Figure 4-16. Length frequency distributions for river herring and gizzard shad larvae captured in the Pamunkey River tidal freshwater reach in 1989 and 1990: A) river herring larvae, 1989; B) river herring larvae, 1990; C) gizzard shad larvae, 1989; and, D) gizzard shad larvae, 1990. Time intervals refer to: 1) 21 March to 6 April; 2) 10 April to 22 April; 3) 25 April to 5 May; and, 4) 9 May to 30 May. Numbers in plate A are shown to indicate abundances of larvae.

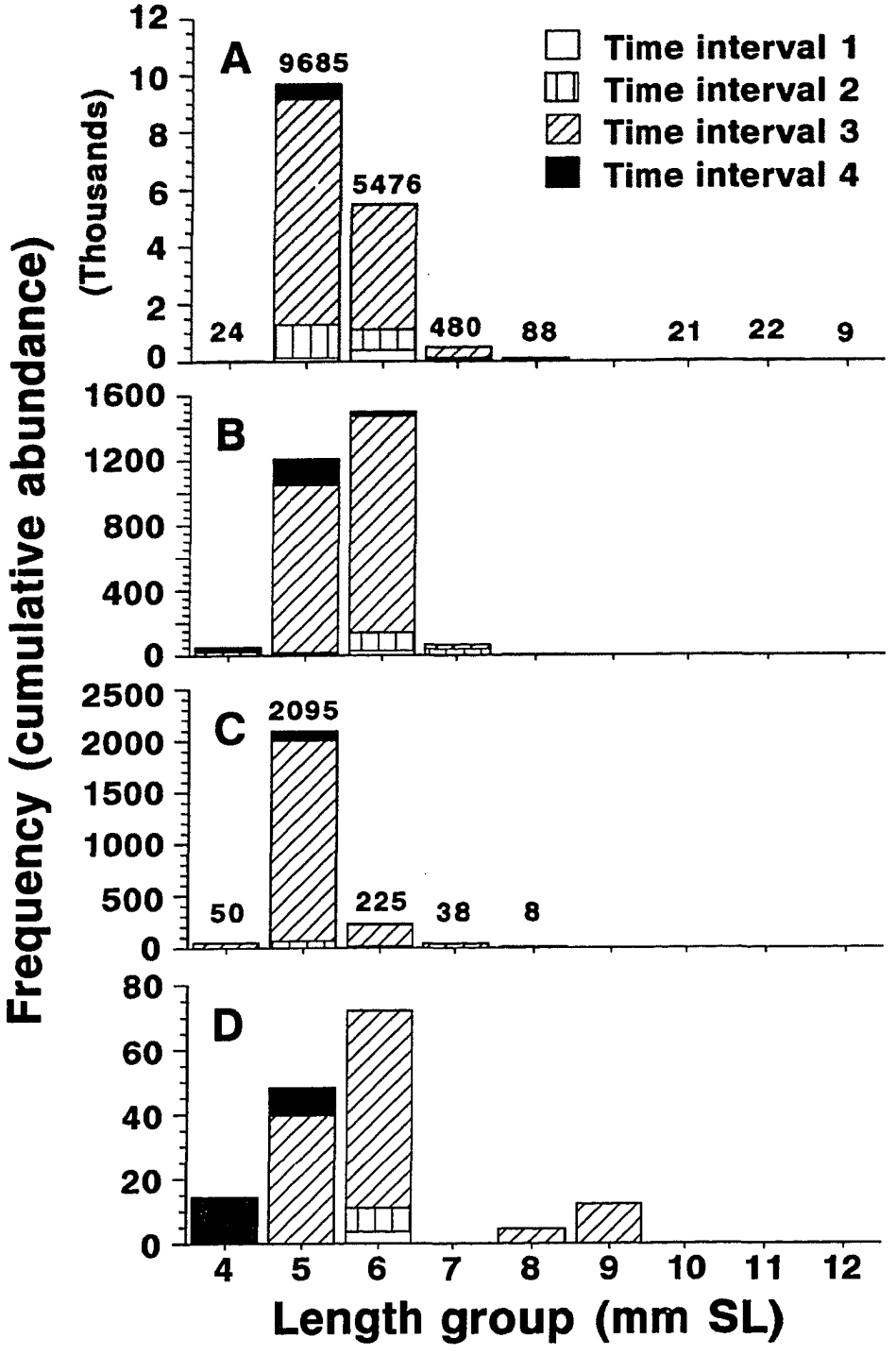


Figure 4-17. Length frequency distributions for river herring and gizzard shad larvae captured in the mainstem river (channel, shoulder, and thoroughfare) and two tidal creeks (Holts Cr. and Big Cr.) of the Pamunkey River tidal freshwater reach in 1989: A) river herring larvae, tidal creeks; B) river herring larvae, mainstem river; C) gizzard shad larvae, tidal creeks; and, D) gizzard shad larvae, mainstem river.

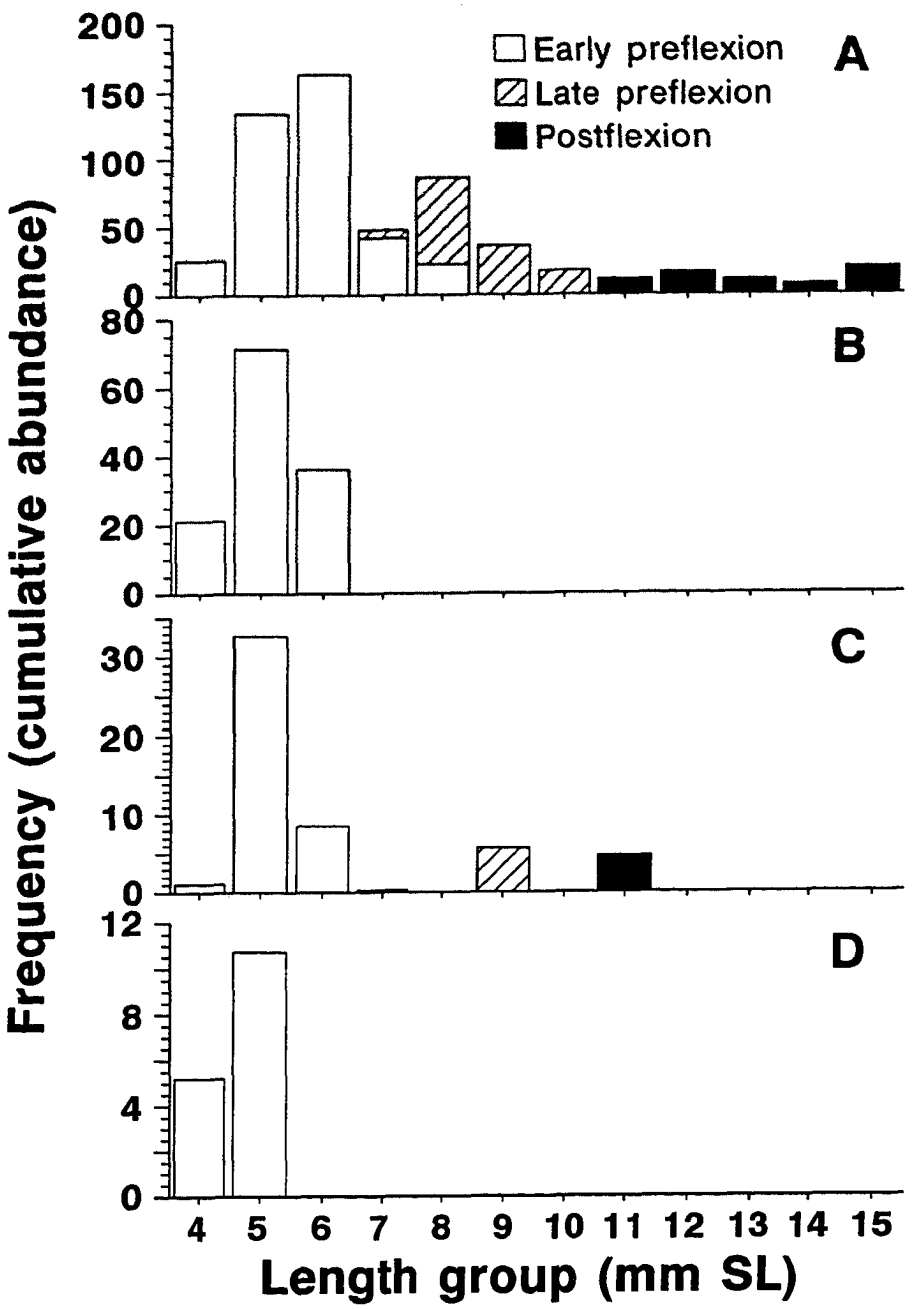


Figure 4-18. Length frequency distributions for river herring larvae and gizzard shad larvae captured in the mainstem river (channel, shoulder, and thoroughfare) and in two tidal creeks (Holts Cr. and Big Cr.) of the Pamunkey River tidal freshwater reach in 1990: A) river herring larvae, tidal creeks; B) river herring larvae, mainstem river; C) gizzard shad larvae, tidal creeks; and, D) gizzard shad larvae, mainstem river.

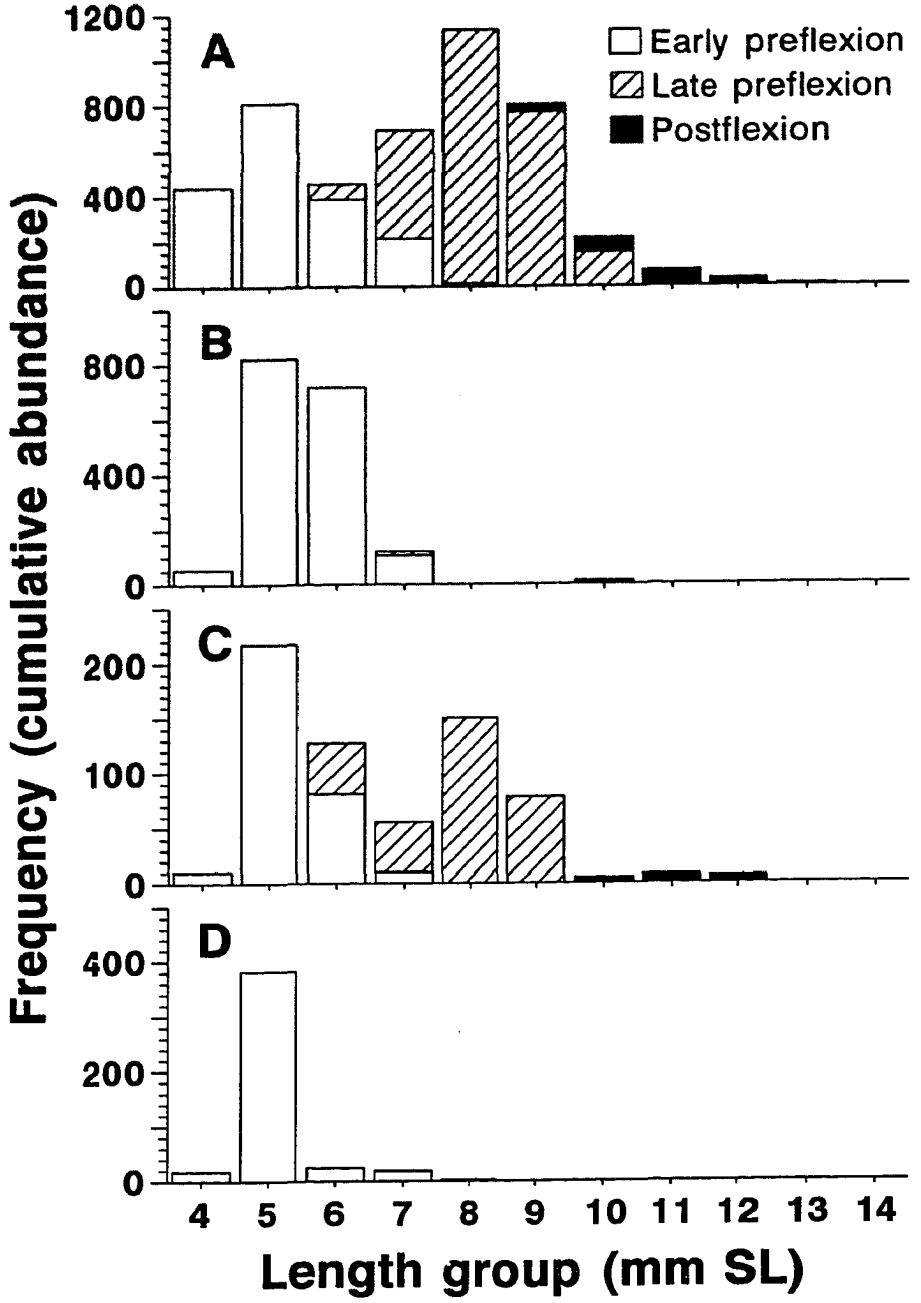


Figure 4-19. Herring egg abundance ($100 \cdot m^{-3}$) and distribution along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Abundances of eggs ares shown (closed circles). Open circles indicate strata where no eggs were captured.

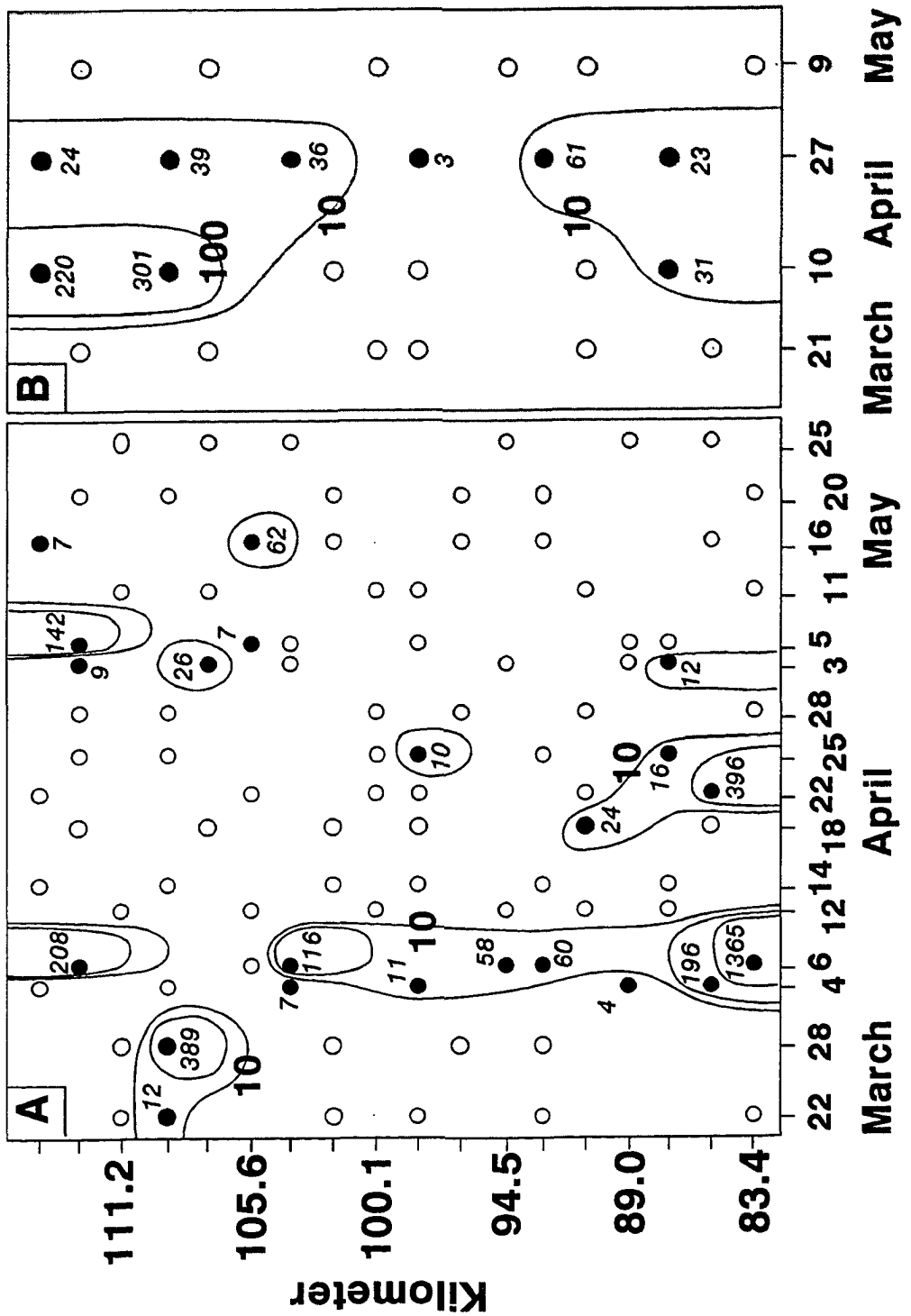


Figure 4-20. Abundances of herring eggs (A), river herring yolk-sac larvae (B), and river herring early preflexion larvae (C) in the Cumberland Thoroughfare in 1989 (-----) and 1990 (- - -).

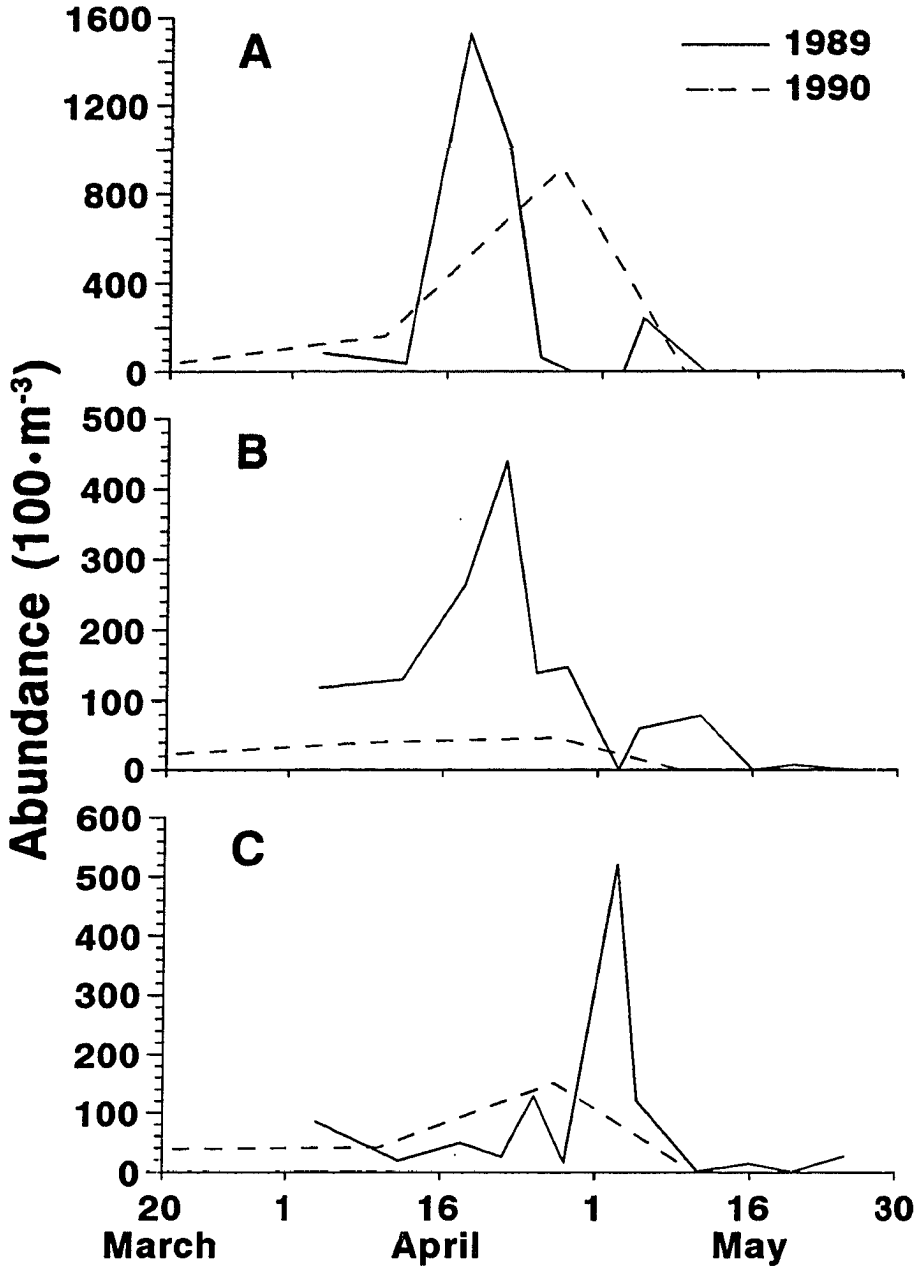


Figure 4-21. Yolk-sac larval river herring abundance ($100 \cdot m^{-3}$) and distribution in the along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Abundances of yolk-sac larvae are shown (closed circles). Open circles indicate strata where no yolk-sac larvae were captured.

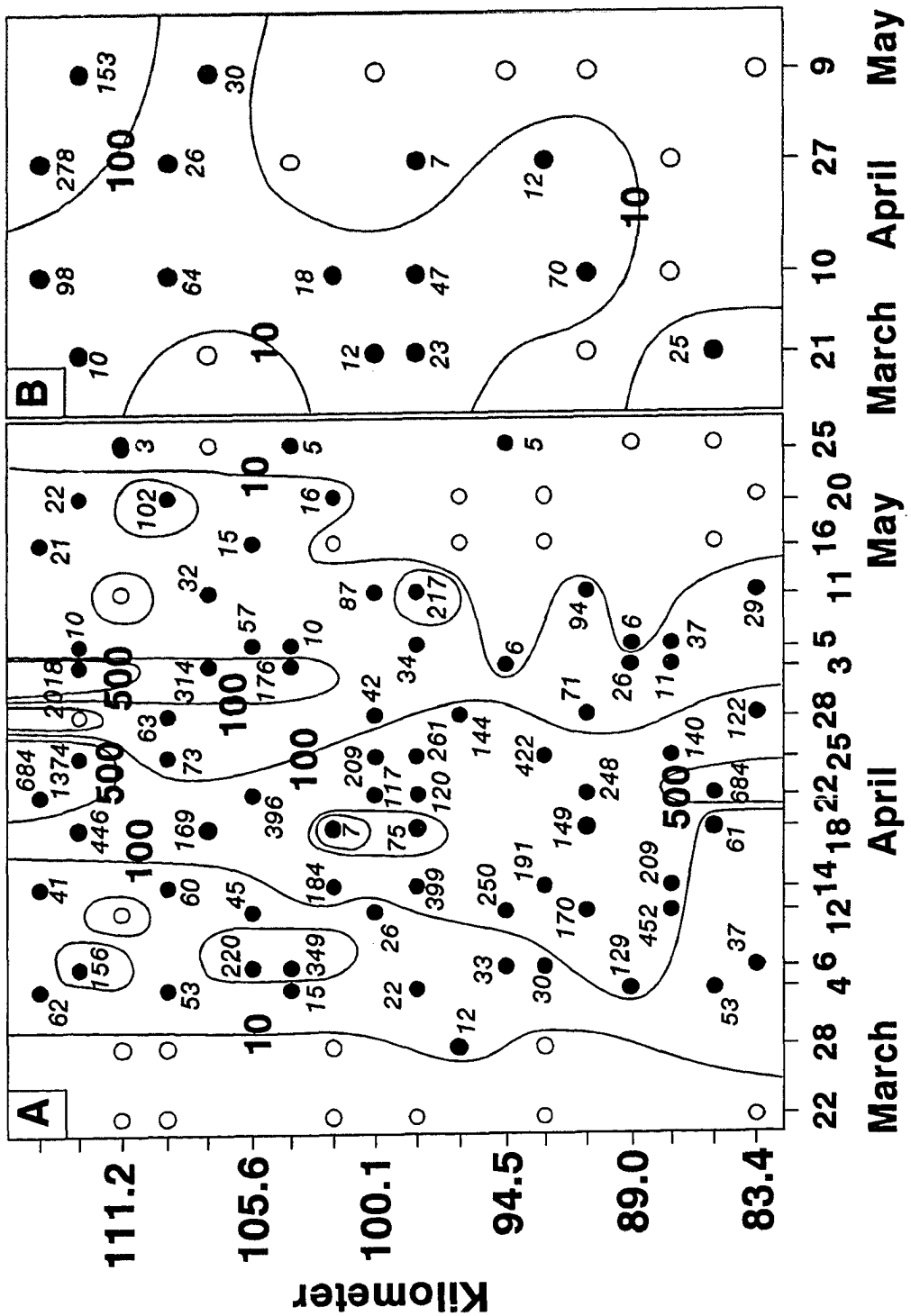


Figure 4-22. Early preflexion larval river herring abundance ($100 \cdot m^{-3}$) and distribution along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Abundances of early preflexion larvae are shown (closed circles). Open circles indicate strata where no early preflexion larvae were captured.

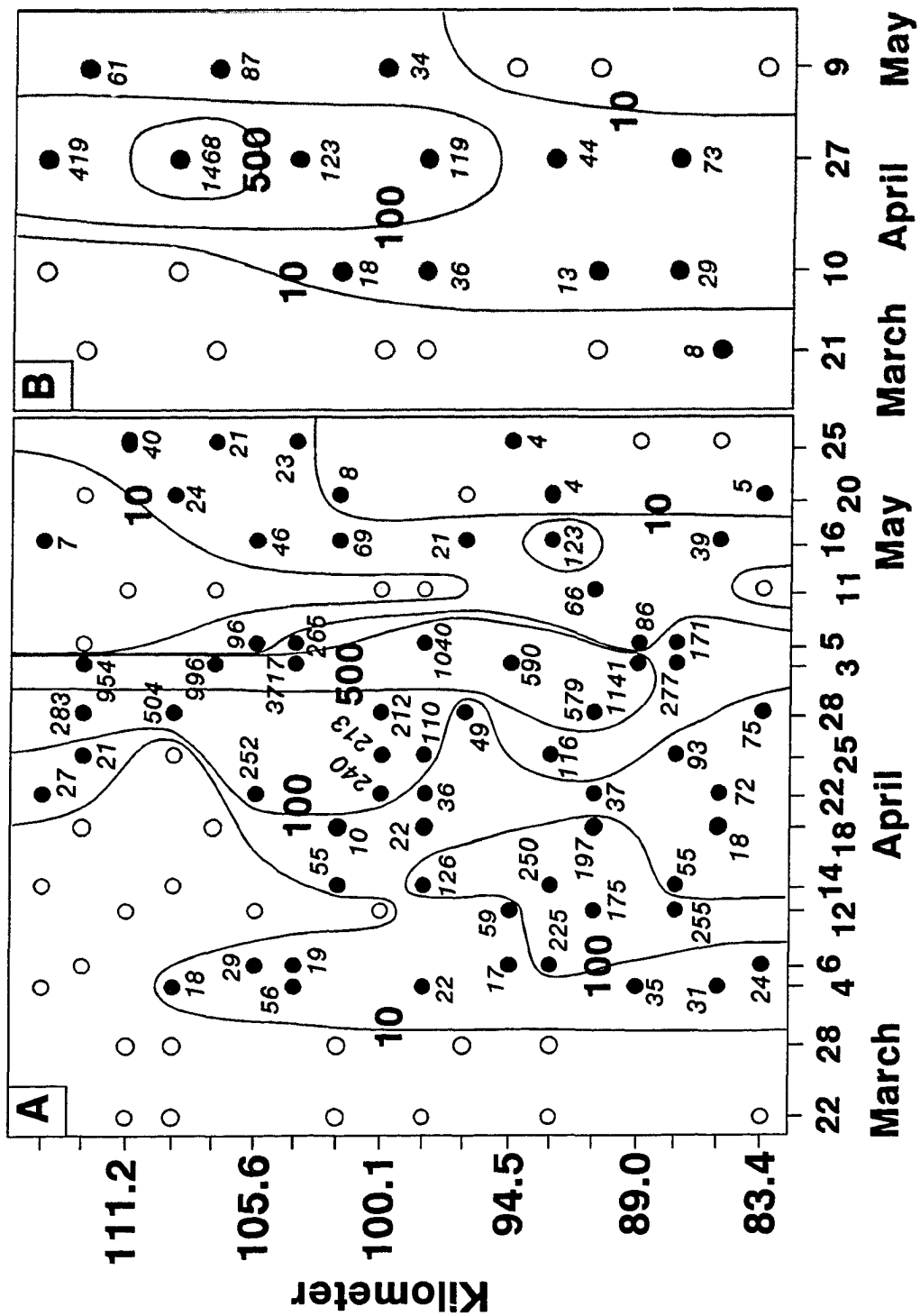


Figure 4-23. Mean observed abundances of yolk-sac and early preflexion larval river herring between strata along the mainstem Pamunkey River (A), between time intervals of the spawning season (B), and between years (C).

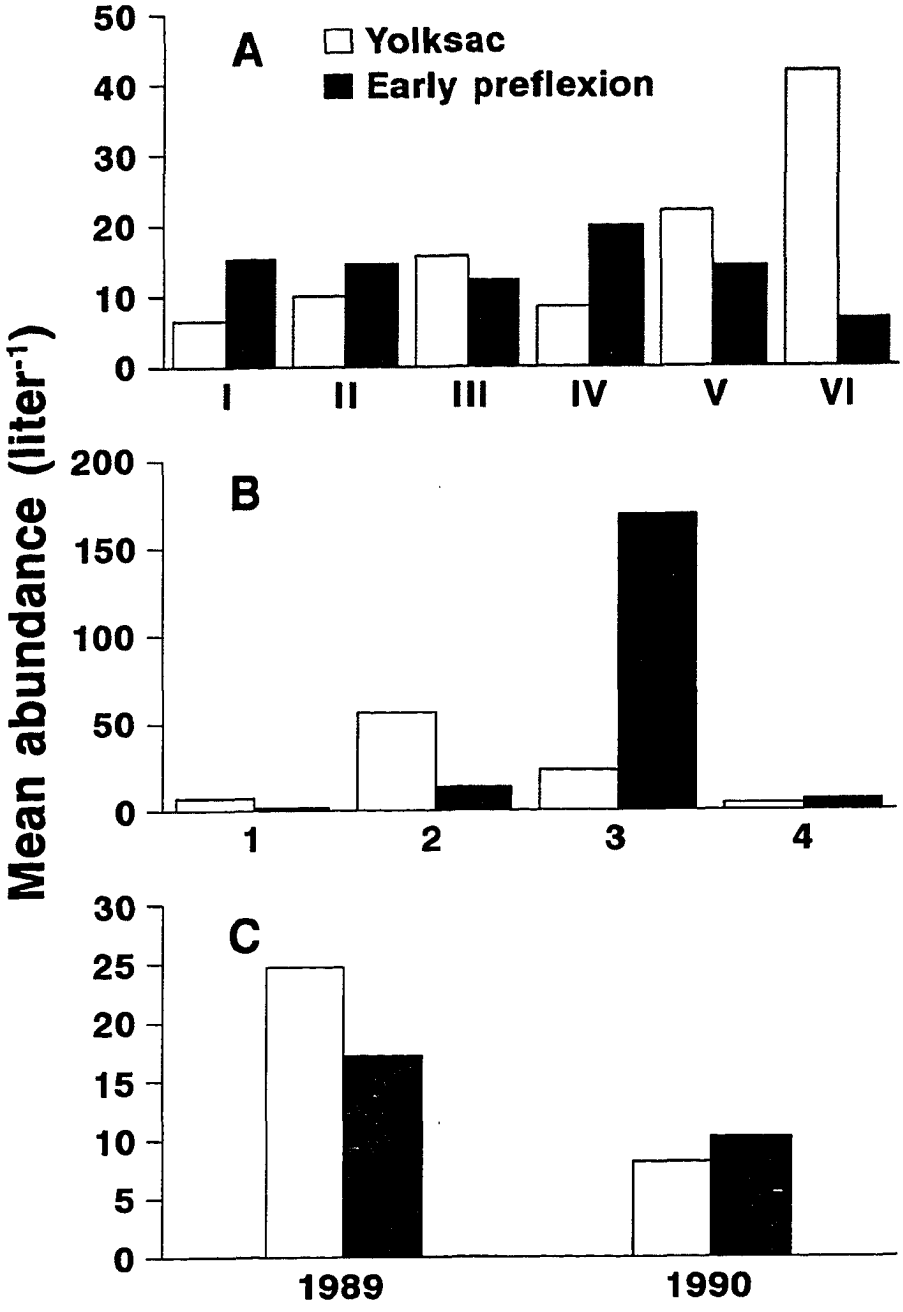


Figure 4-24. Total zooplankton (rotifers, copepod nauplii and copepodites, and cladocerans) abundance (ℓ^{-1}) along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Zooplankton abundances are shown (closed circles).

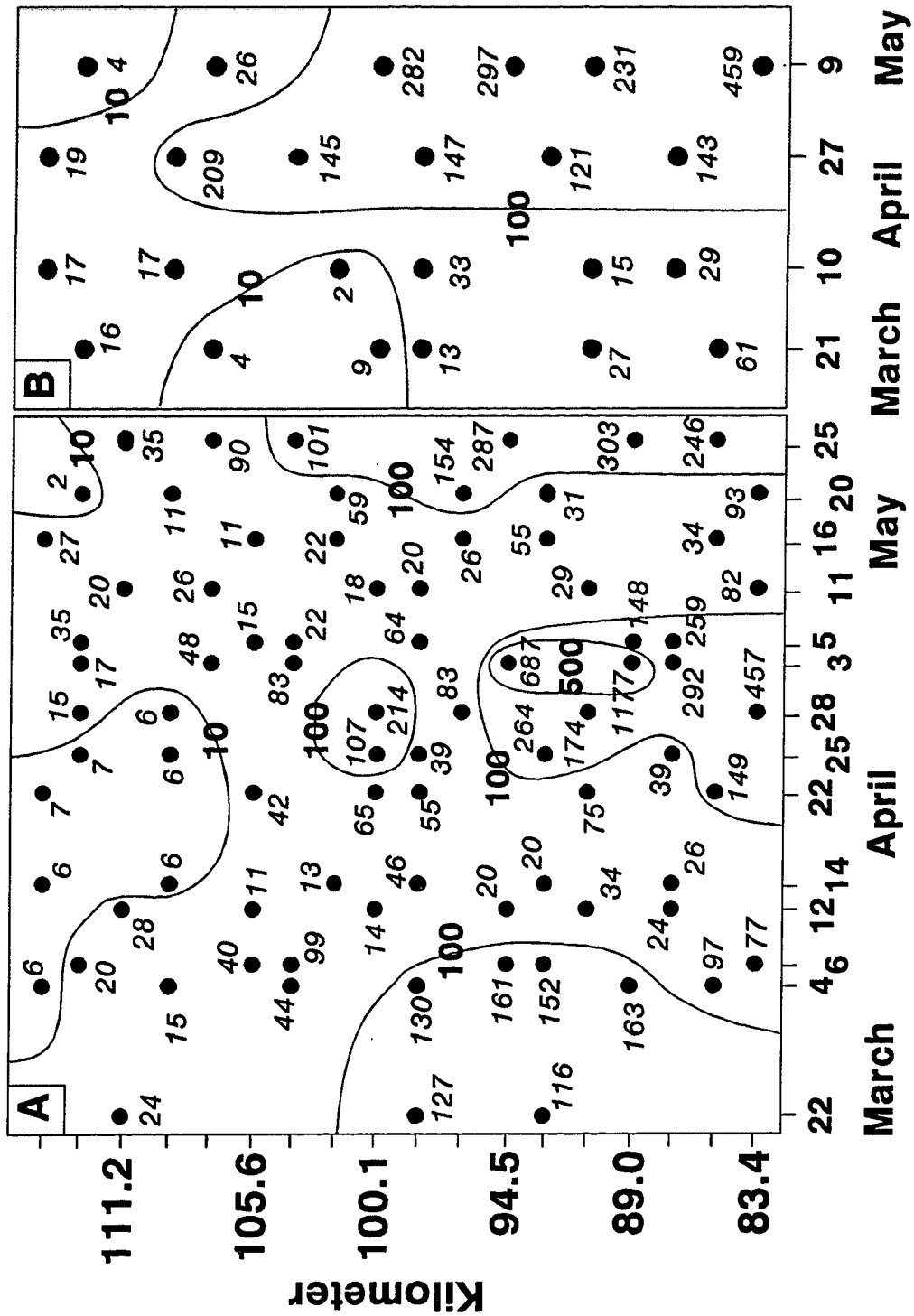


Figure 4-25. Copepod nauplius and copepodite abundance (ℓ^{-1}) and distribution along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Copepod nauplius and copepodite abundances are shown (closed circles). Open circles indicate strata where no copepod nauplii or copepodites were captured.

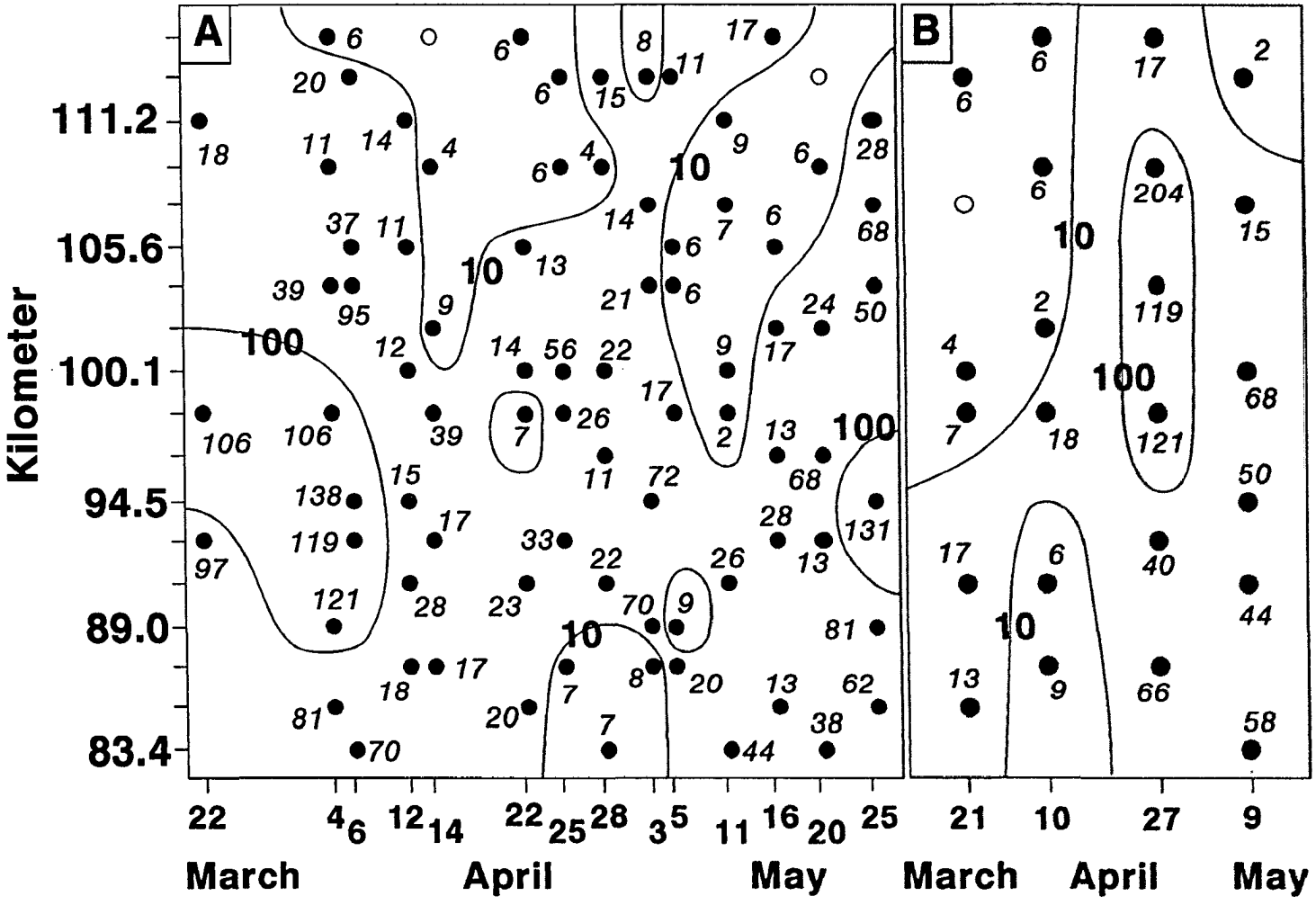


Figure 4-26. Rotifer abundance (ℓ^{-1}) and distribution along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Rotifer abundances are shown (closed circles). Open circles indicate strata where no rotifers were captured.

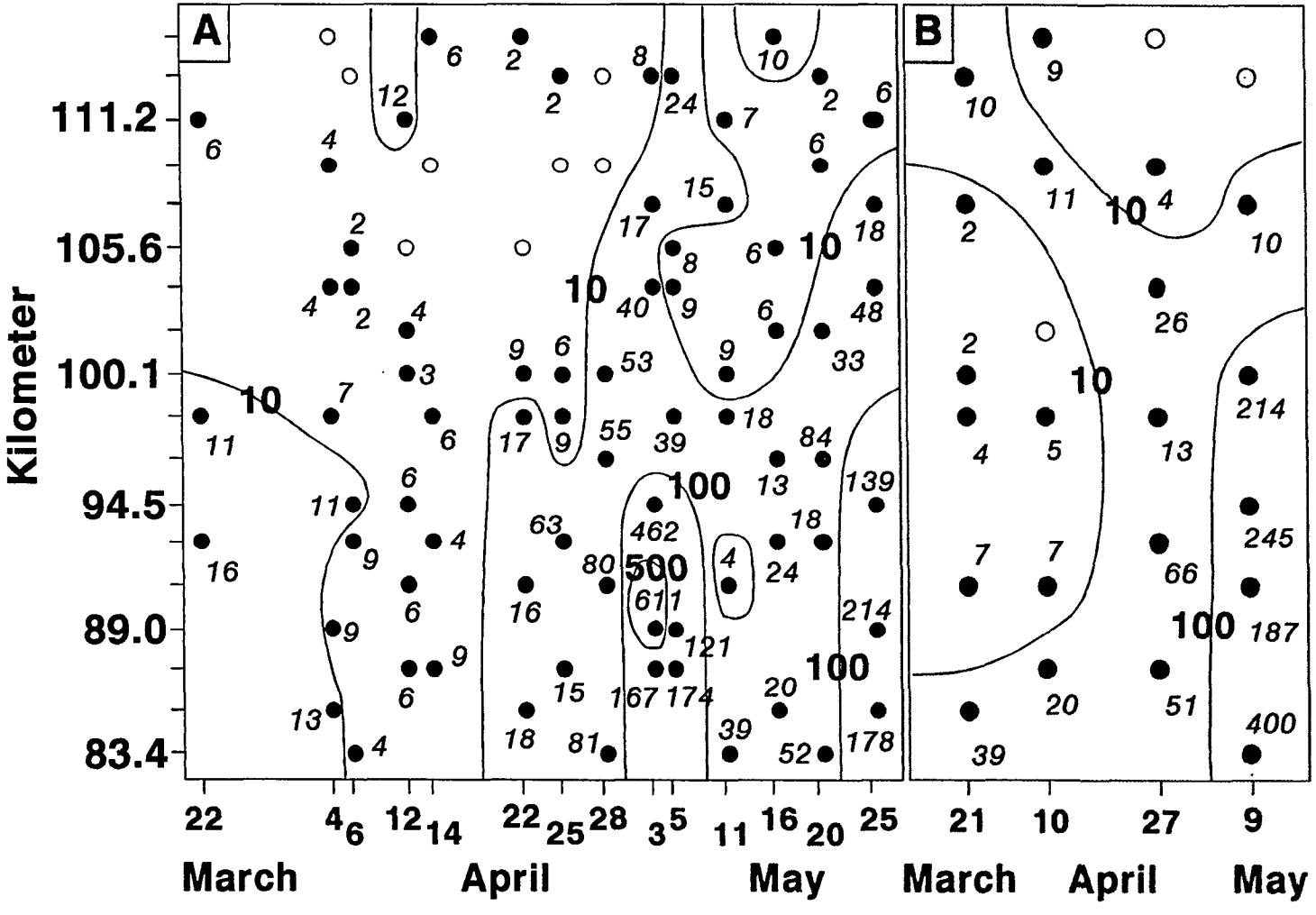


Figure 4-27. Cladoceran abundance (ℓ^{-1}) and distribution along the mainstem Pamunkey River in 1989 (A) and 1990 (B). Cladoceran abundances are shown (closed circles). Open circles indicate strata where no cladocerans were captured.

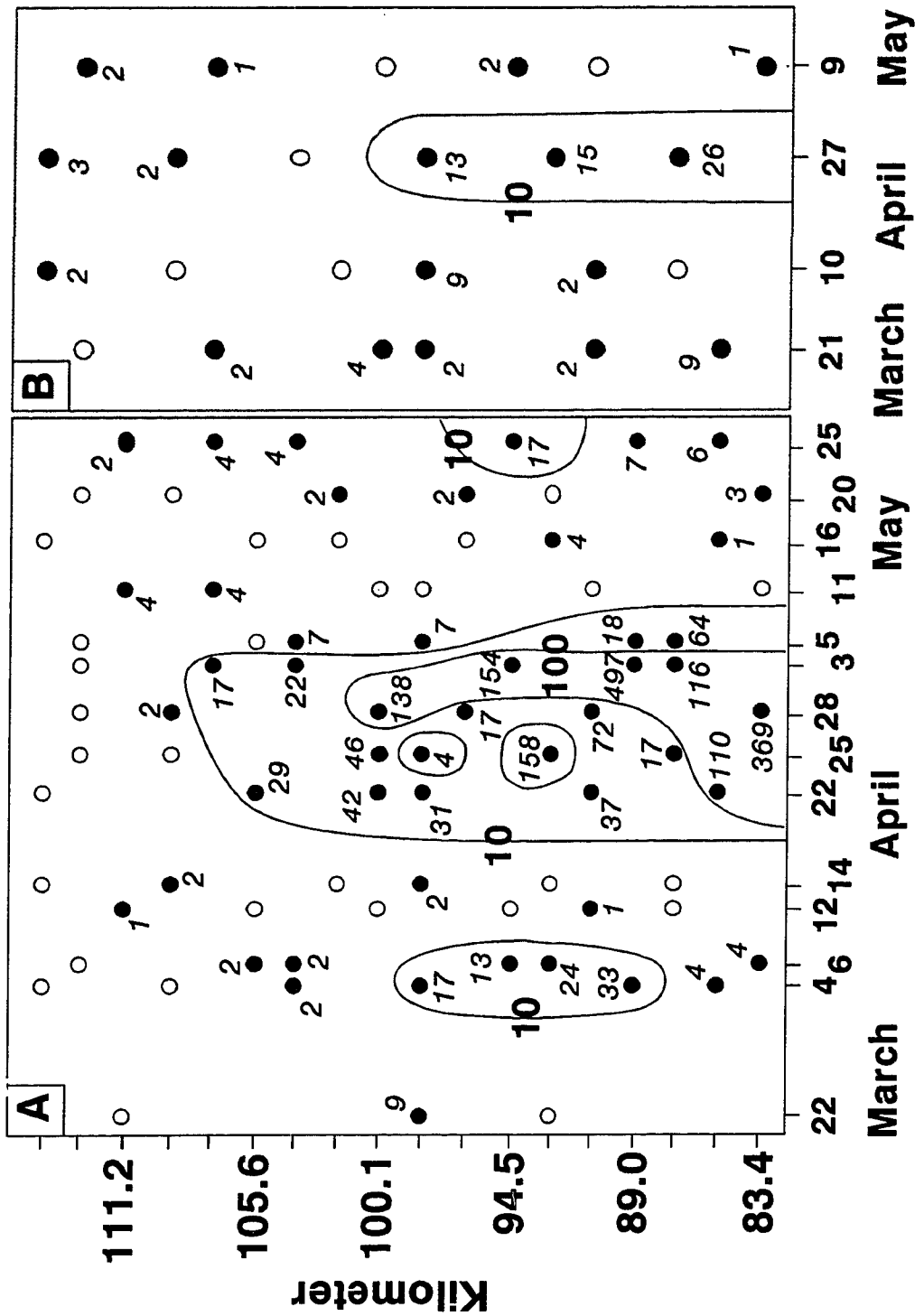


Figure 4-28. Mean observed total zooplankton abundance between strata along the mainstem Pamunkey River (A) and between mid- to late April and early to mid-May time intervals (B).

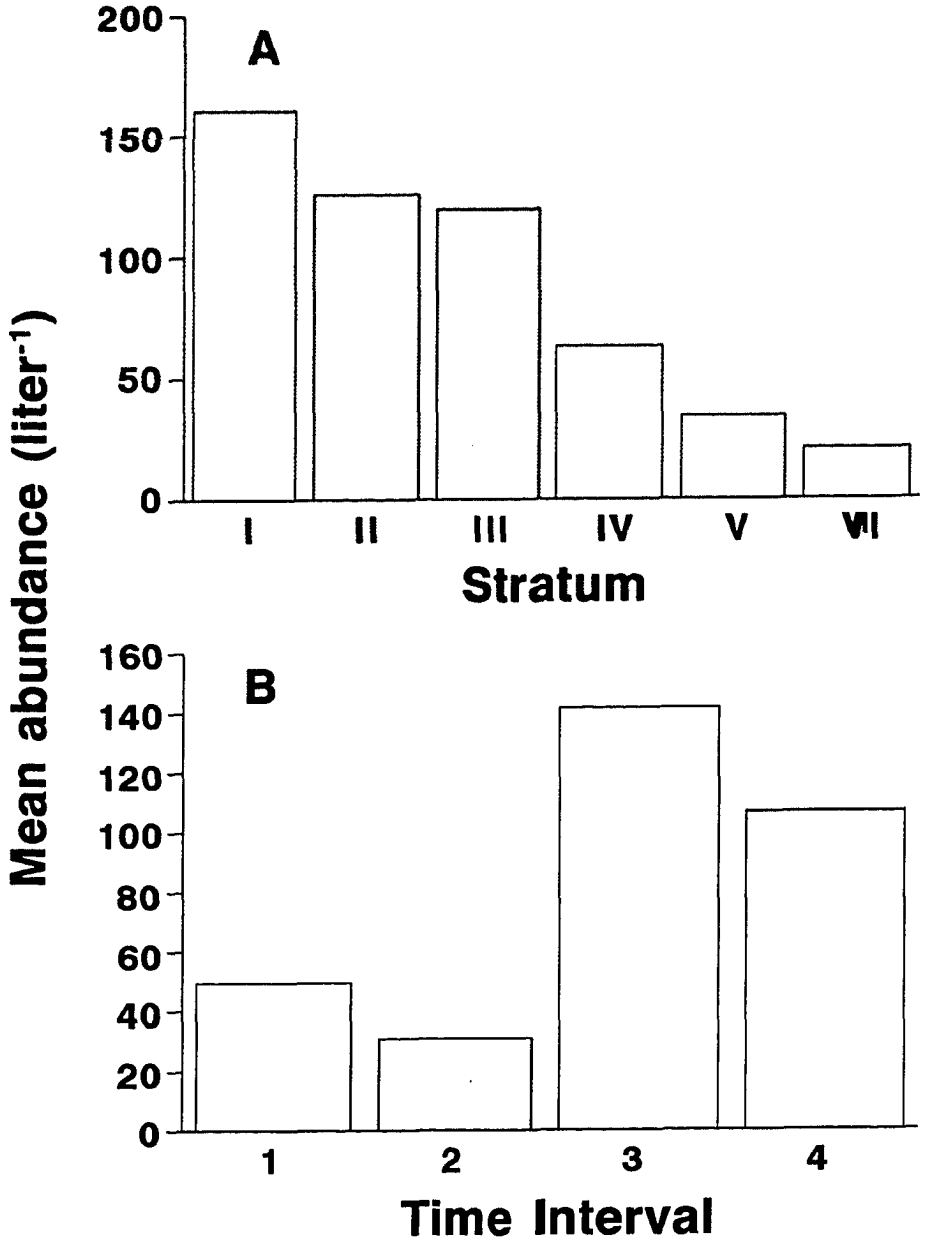


Figure 4-29. Yolk-sac larval and larval river herring abundances in potential tidal freshwater nursery habitats in 1989: A) channel, B) shoulder, C) Cumberland Thoroughfare, D) Big Creek, and E) Holts Creek.

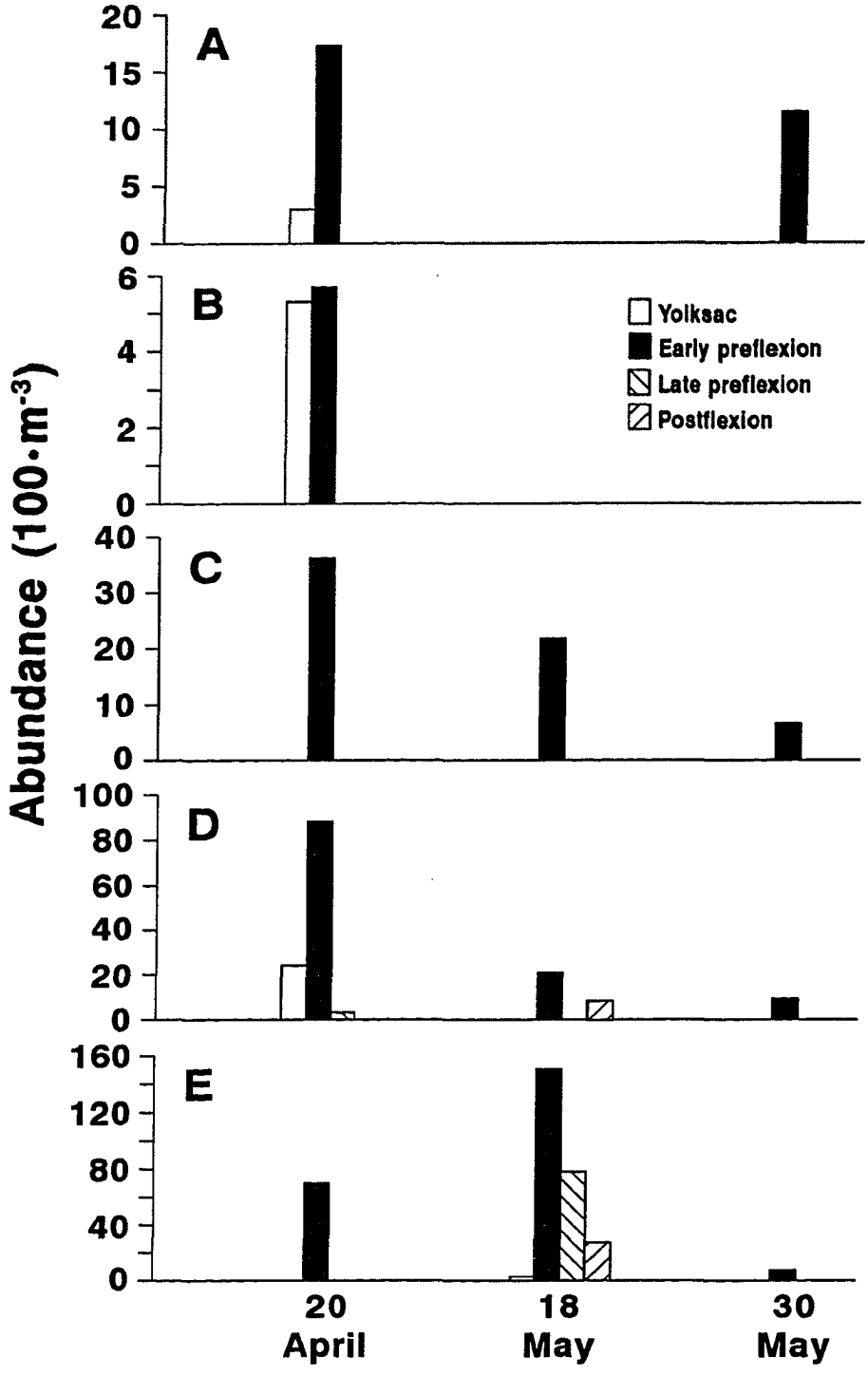


Figure 4-30. Yolk-sac larval river herring abundances in potential tidal freshwater nursery habitats in 1990: A) channel, B) shoulder, C) Cumberland Thoroughfare, D) Big Creek, and E) Holts Creek.

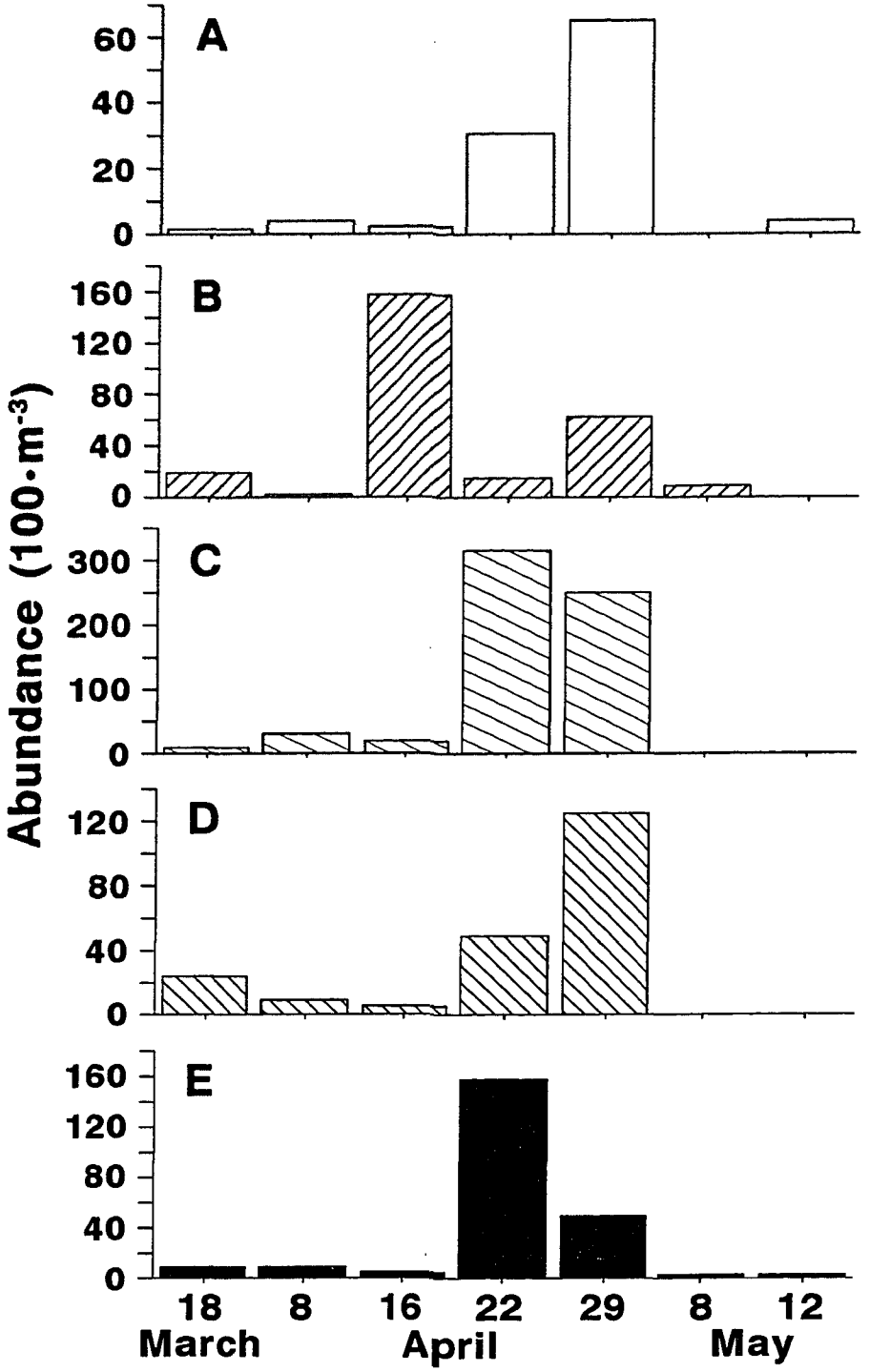


Figure 4-31. Early preflexion larval river herring abundances in potential tidal freshwater nursery habitats in 1989: A) Big Creek, B) channel, C) Cumberland Thoroughfare, D) shoulder, and E) Holts Creek. The ordering of figure plates emphasizes the apparent shift in distribution of larvae from Big Creek, the channel and the thoroughfare on 22 April to the shoulder on 29 April to Holts Creek between 29 April and 8 May.

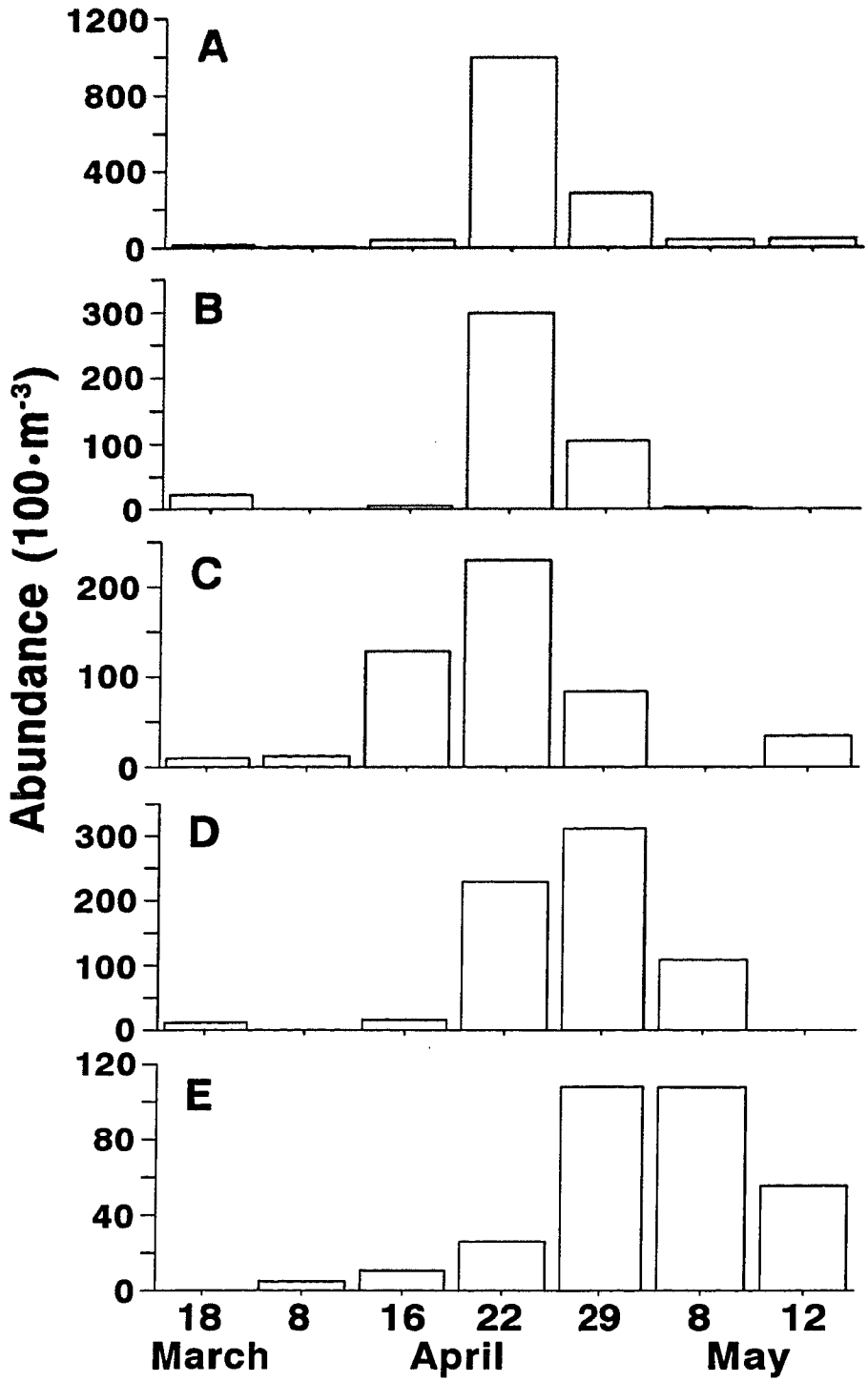


Figure 4-32. Abundances of river herring late preflexion and postflexion larvae in potential tidal freshwater nursery habitats in 1989: A) Big Creek, B) channel, C) Cumberland Thoroughfare, D) shoulder, and E) Holts Creek. The plates are ordered as in Fig. 4-31.

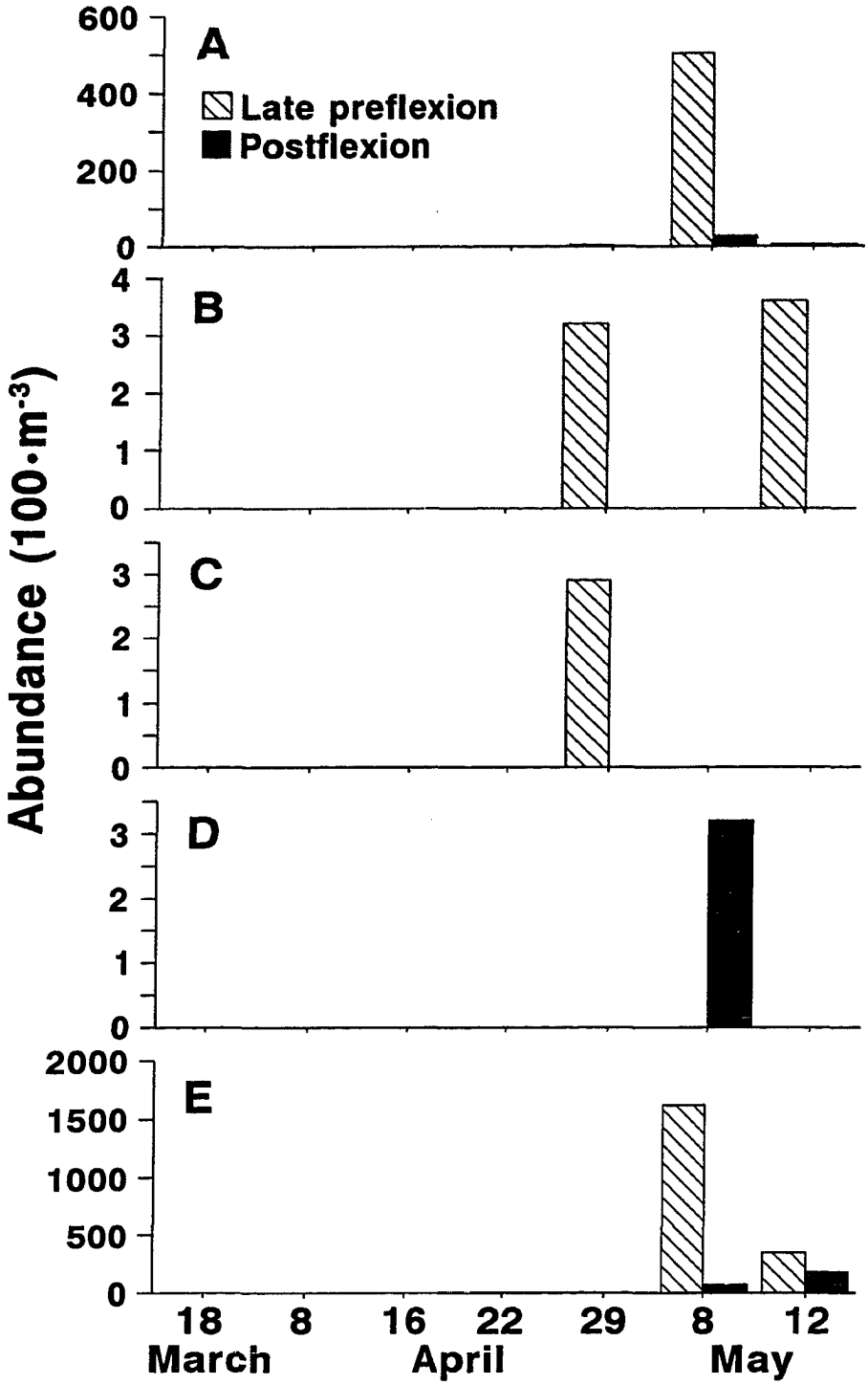


Figure 4-33. Mean observed yolk-sac larval river herring abundance in potential tidal freshwater nursery habitats between mid- to late April and early to mid-May time intervals (A) and years (B).

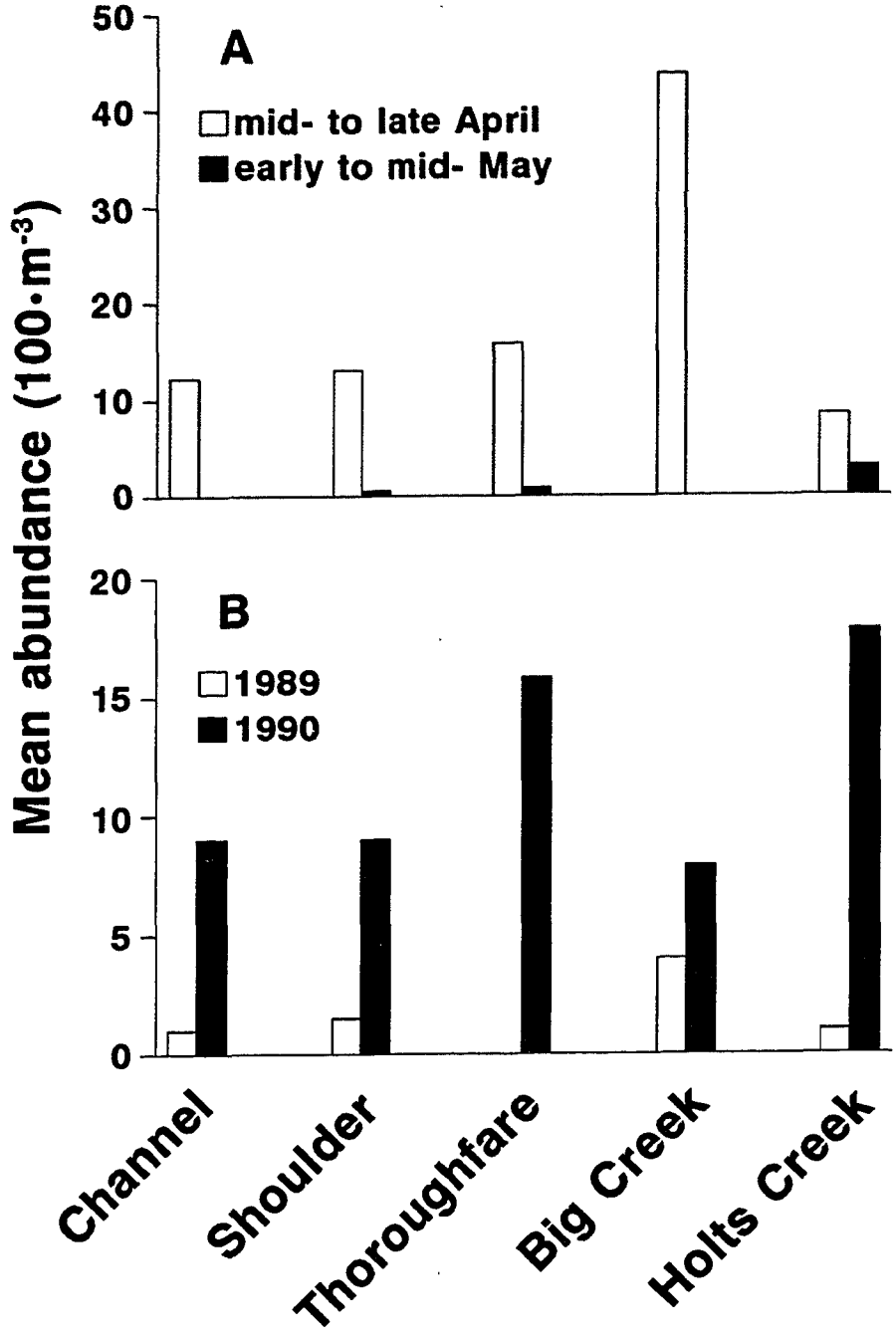


Figure 4-34. Mean observed larval river herring abundances: A) abundance in potential tidal freshwater nursery habitats between time intervals of the spawning season; B) abundance of early preflexion, late preflexion, and postflexion river herring larvae between mid- to late April and early to mid-May time intervals; and, C) abundance of early preflexion, late preflexion, and postflexion river herring larvae between years.

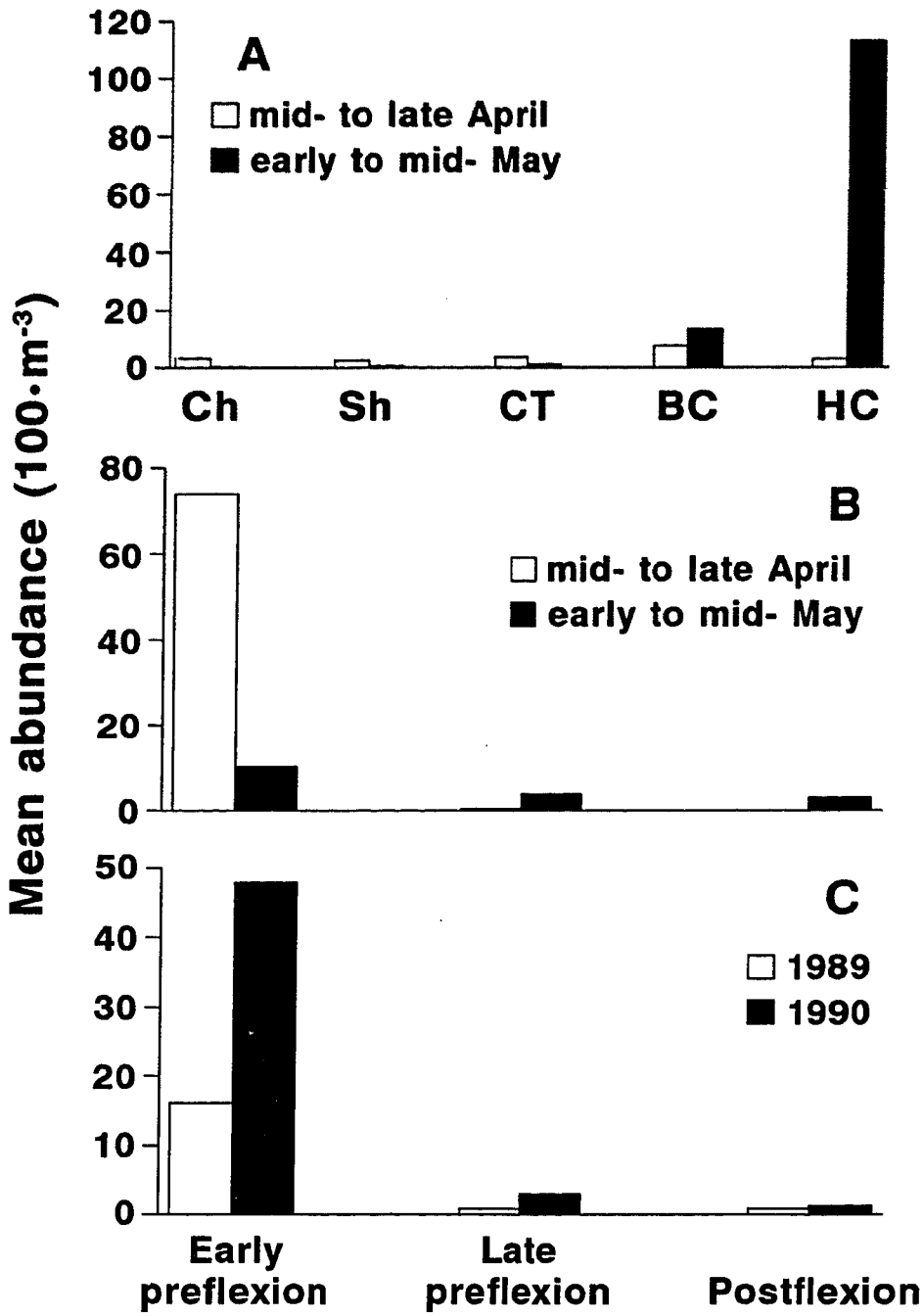


Figure 4-35. Mean observed abundances of early preflexion (A), late preflexion (B), and postflexion (C) river herring larvae in potential tidal freshwater nursery habitats between mid- to late April and early to mid-May time intervals.

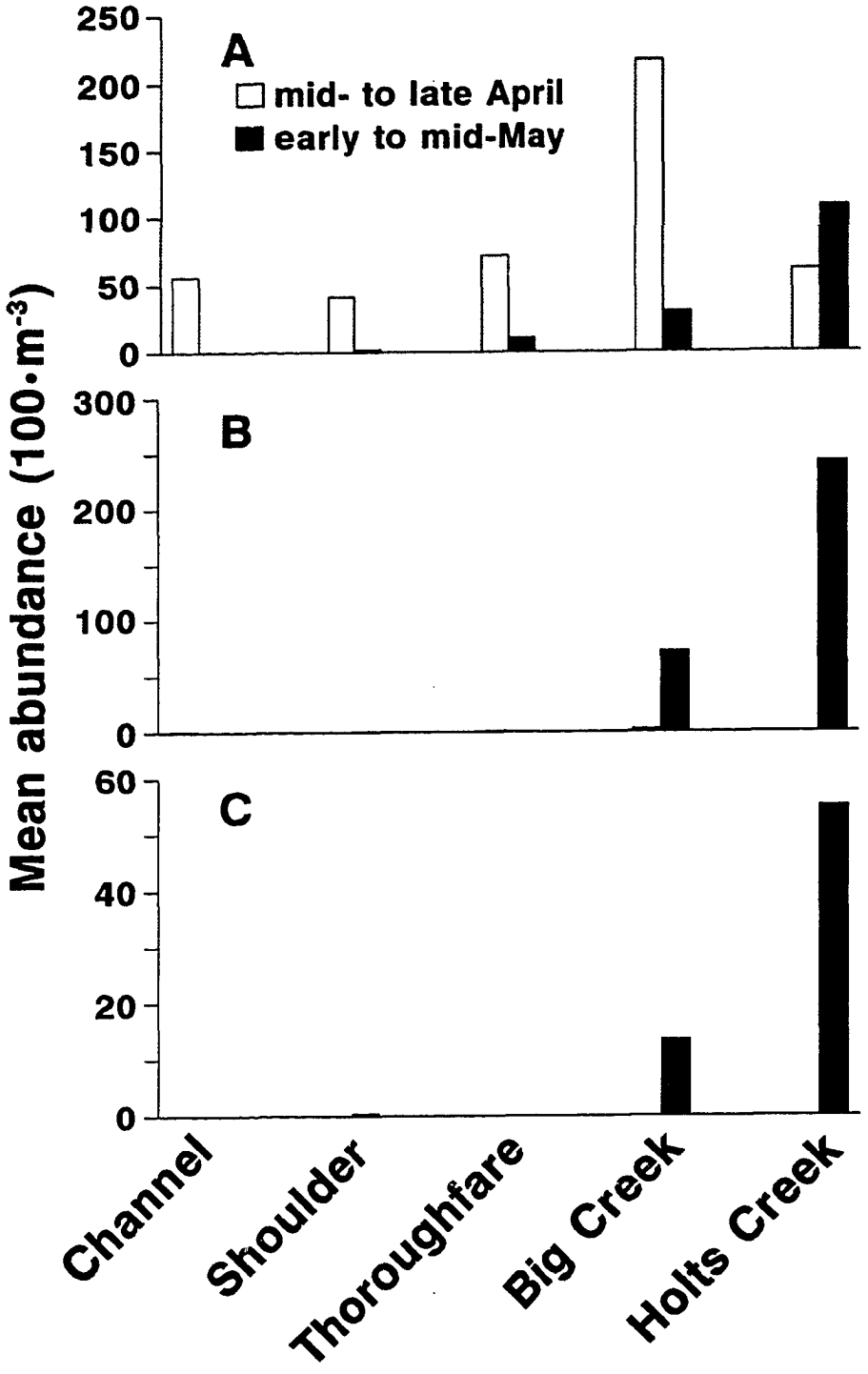


Figure 4-36. Mean observed early preflexion (A), late preflexion (B), and postflexion (C) larval river herring in potential tidal freshwater nursery habitats between years.

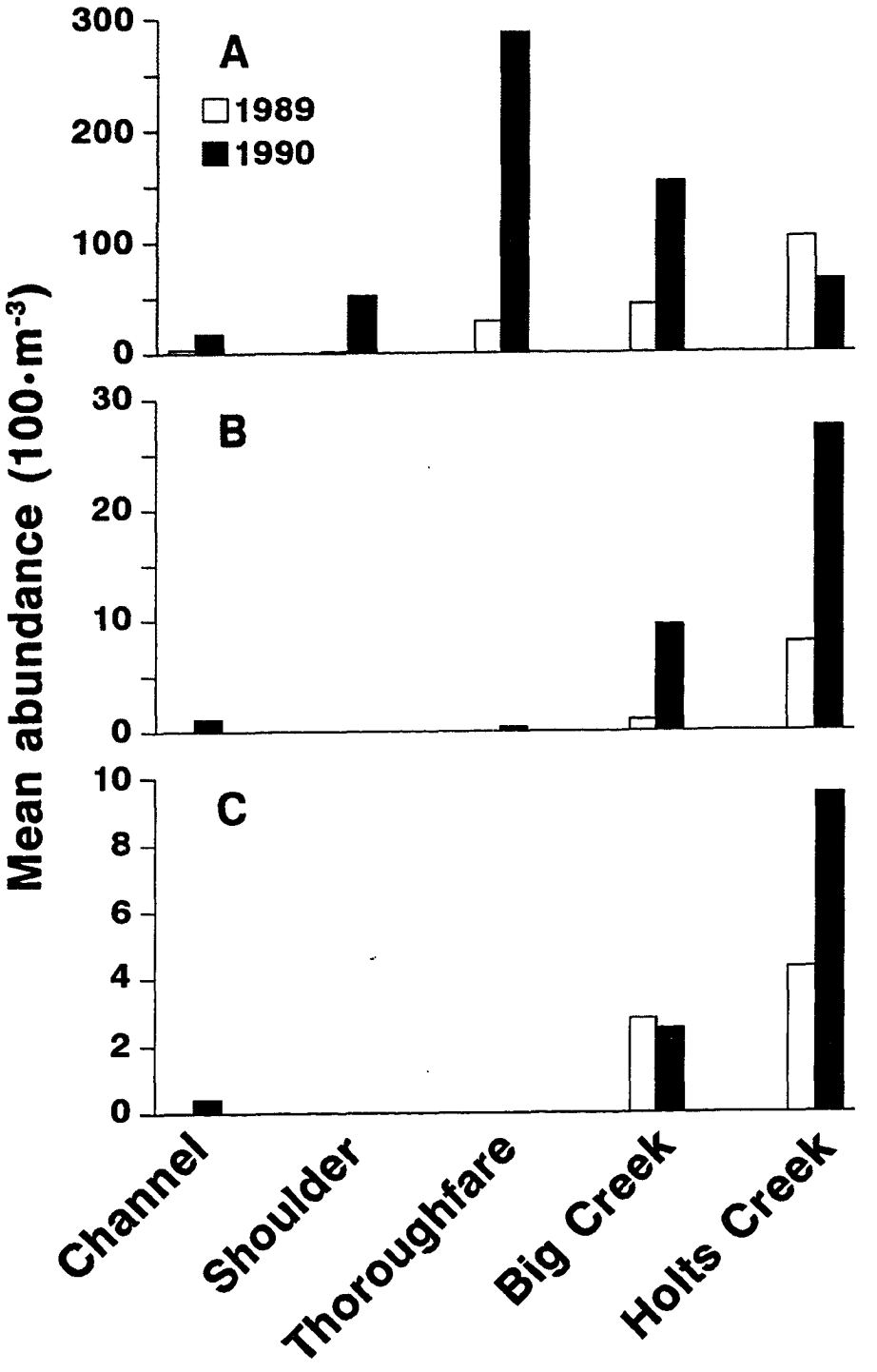


Figure 4-37. Total zooplankton abundances in potential tidal freshwater nursery habitats in 1989 (A) and 1990 (B).

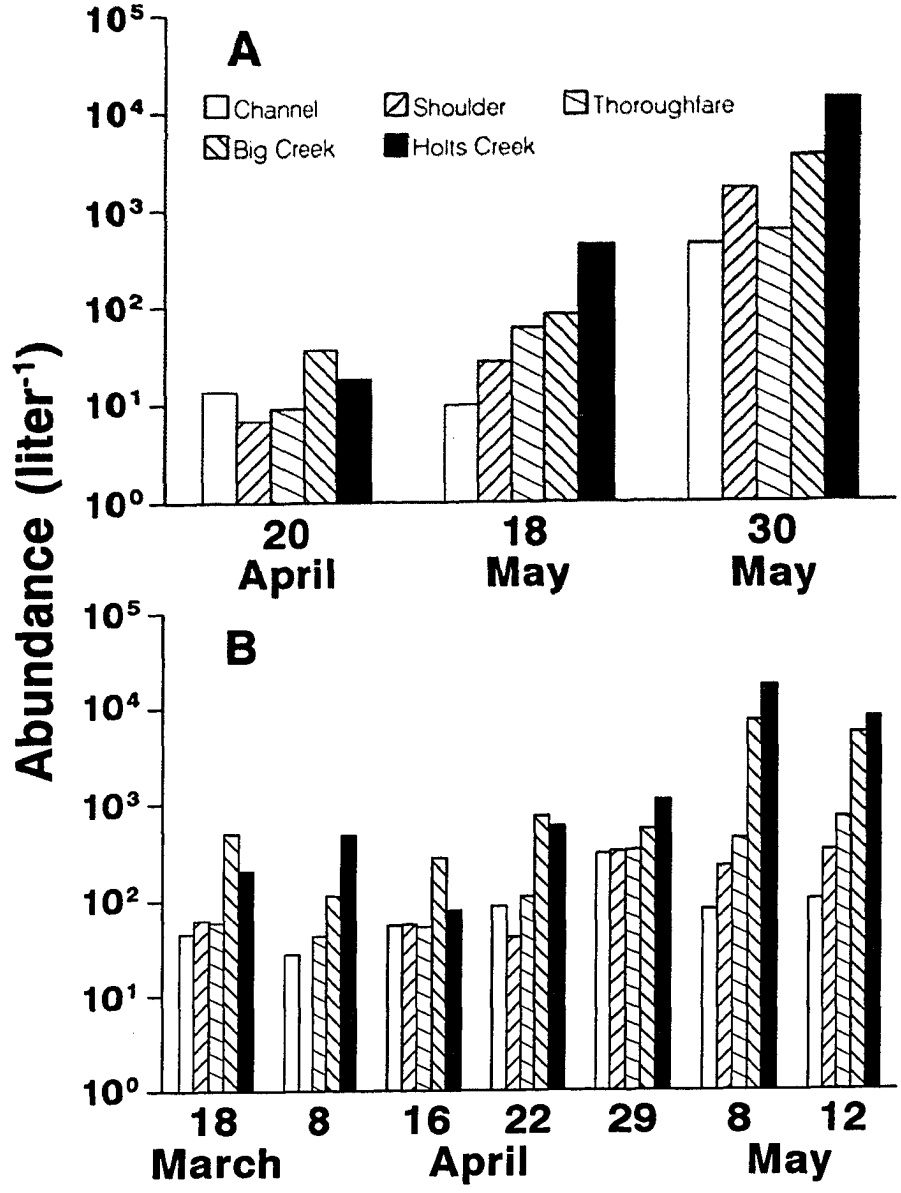


Figure 4-38. Abundances of rotifers, copepod nauplii and copepodites, and cladocerans in potential tidal freshwater nursery habitats in 1989: channel (A), shoulder (B), Cumberland Thoroughfare (C), Big Creek (D), and Holts Creek (E).

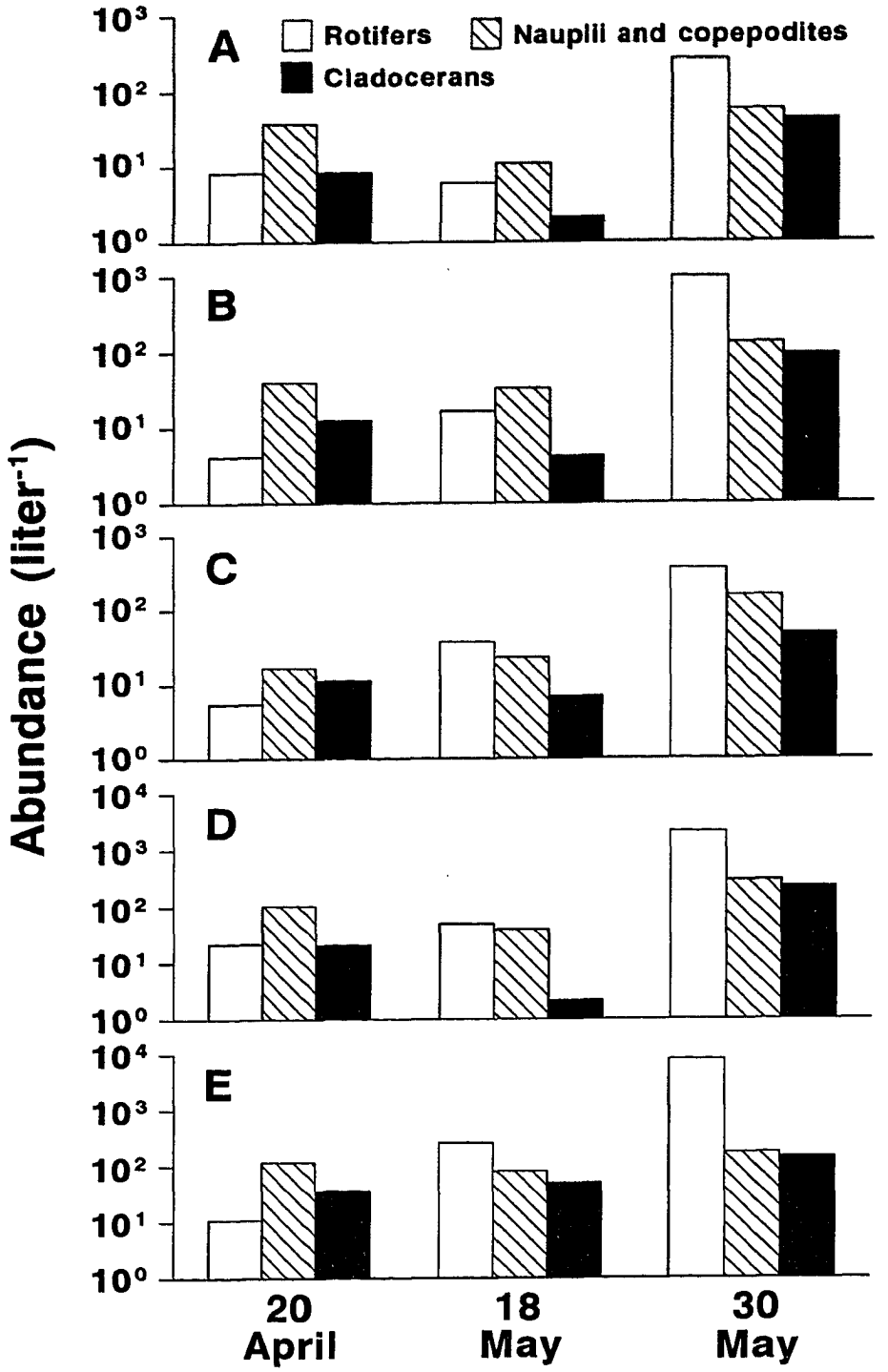


Figure 4-39. Abundances of rotifers, copepod nauplii and copepodites, and cladocerans in potential tidal freshwater nursery habitats in 1990: channel (A), shoulder (B), Cumberland Thoroughfare (C), Big Creek (D), and Holts Creek (E).

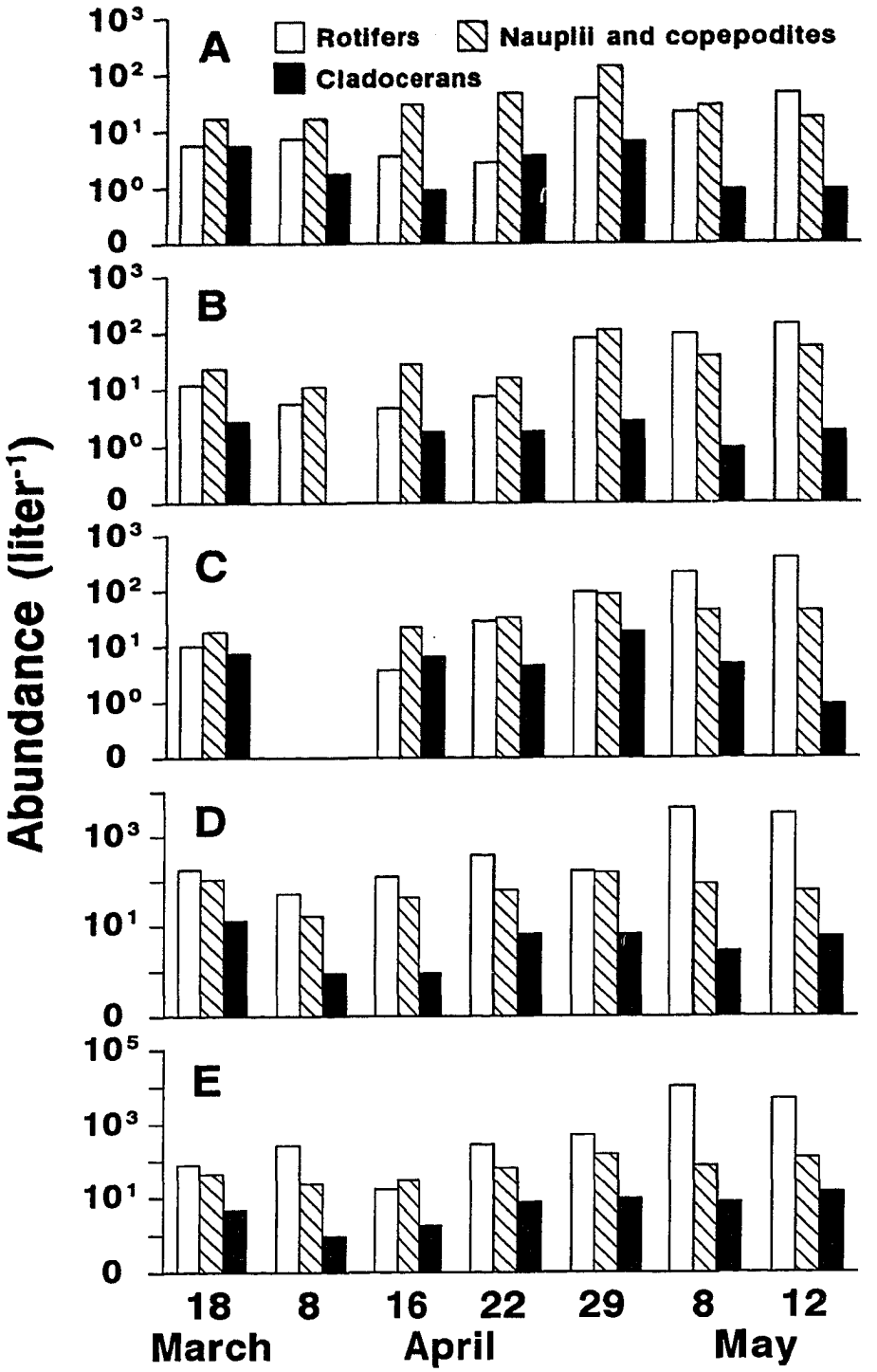


Figure 4-40. Mean observed abundance of rotifers (A), copepod nauplii and copepodites (B), cladocerans (C), and total zooplankton (D) between potential tidal freshwater nursery habitats during mid- to late April and early to mid-May time intervals.

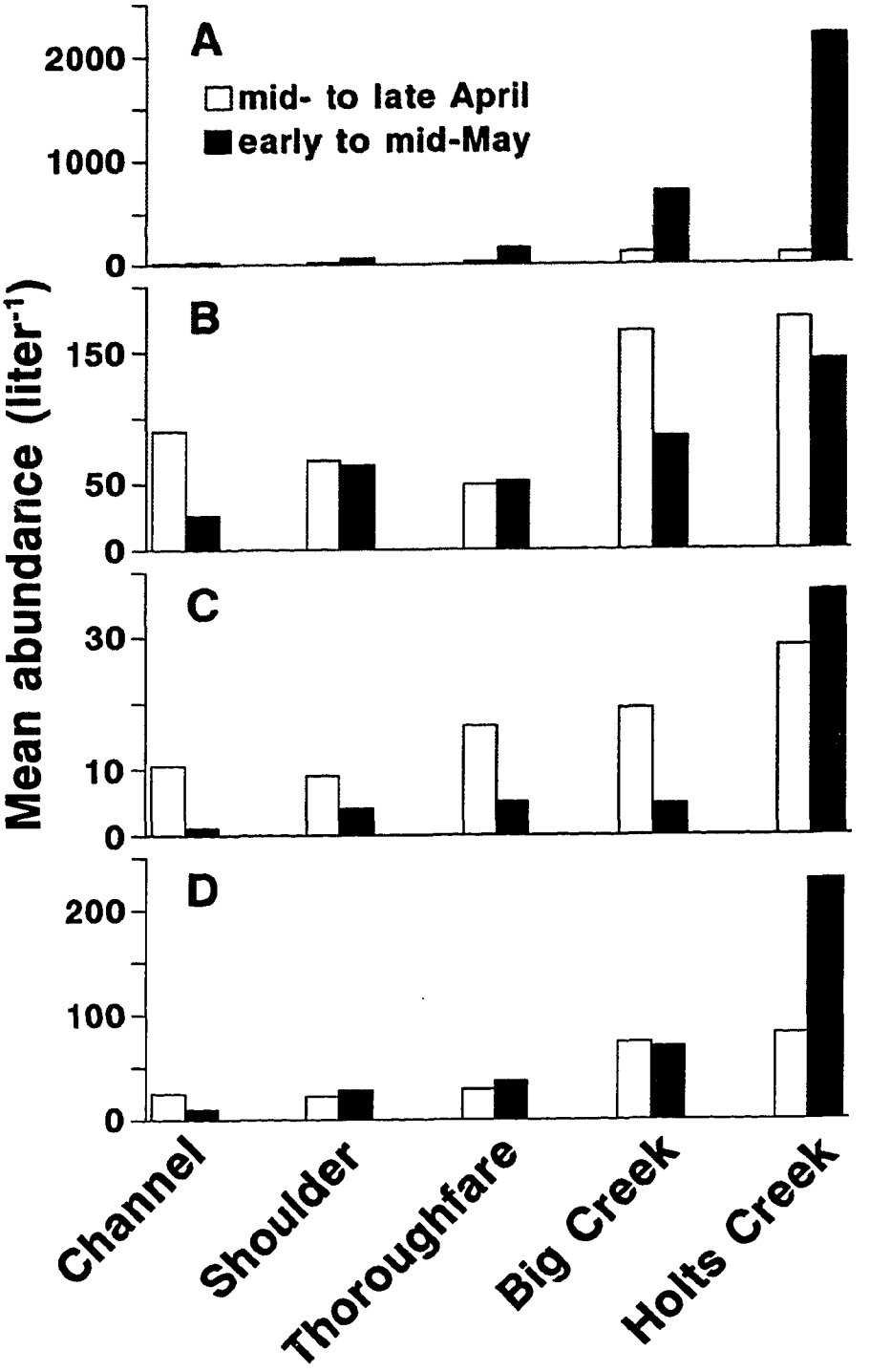


Figure 4-41. Mean observed abundance of rotifers (A), copepod nauplii and copepodites (B), cladocerans (C), and total zooplankton (D) between potential tidal freshwater nursery habitats in 1989 and 1990.

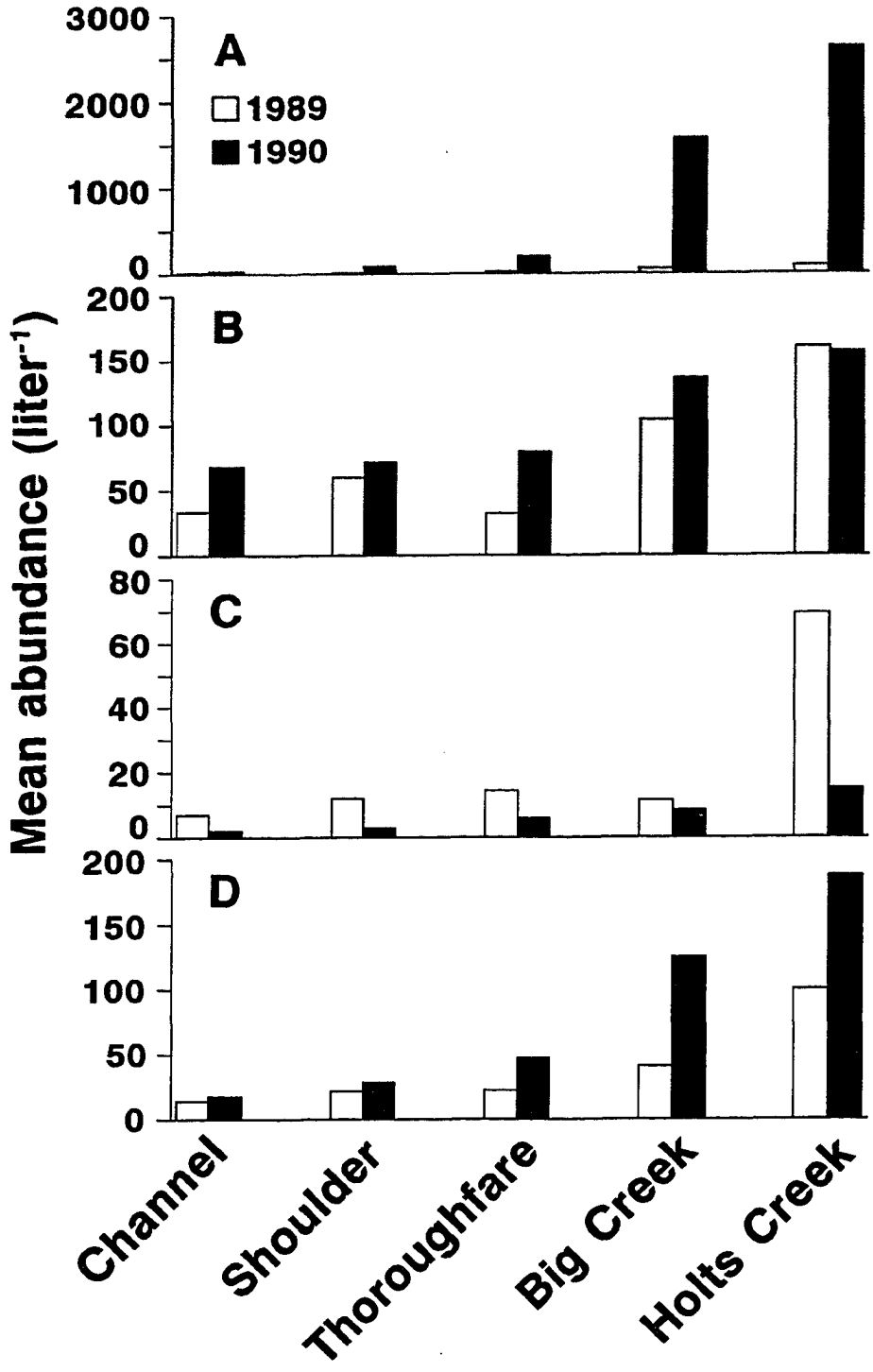


Figure 4-42. Hatch date frequency distributions for river herring larvae in 1989 (A) and 1990 (B).

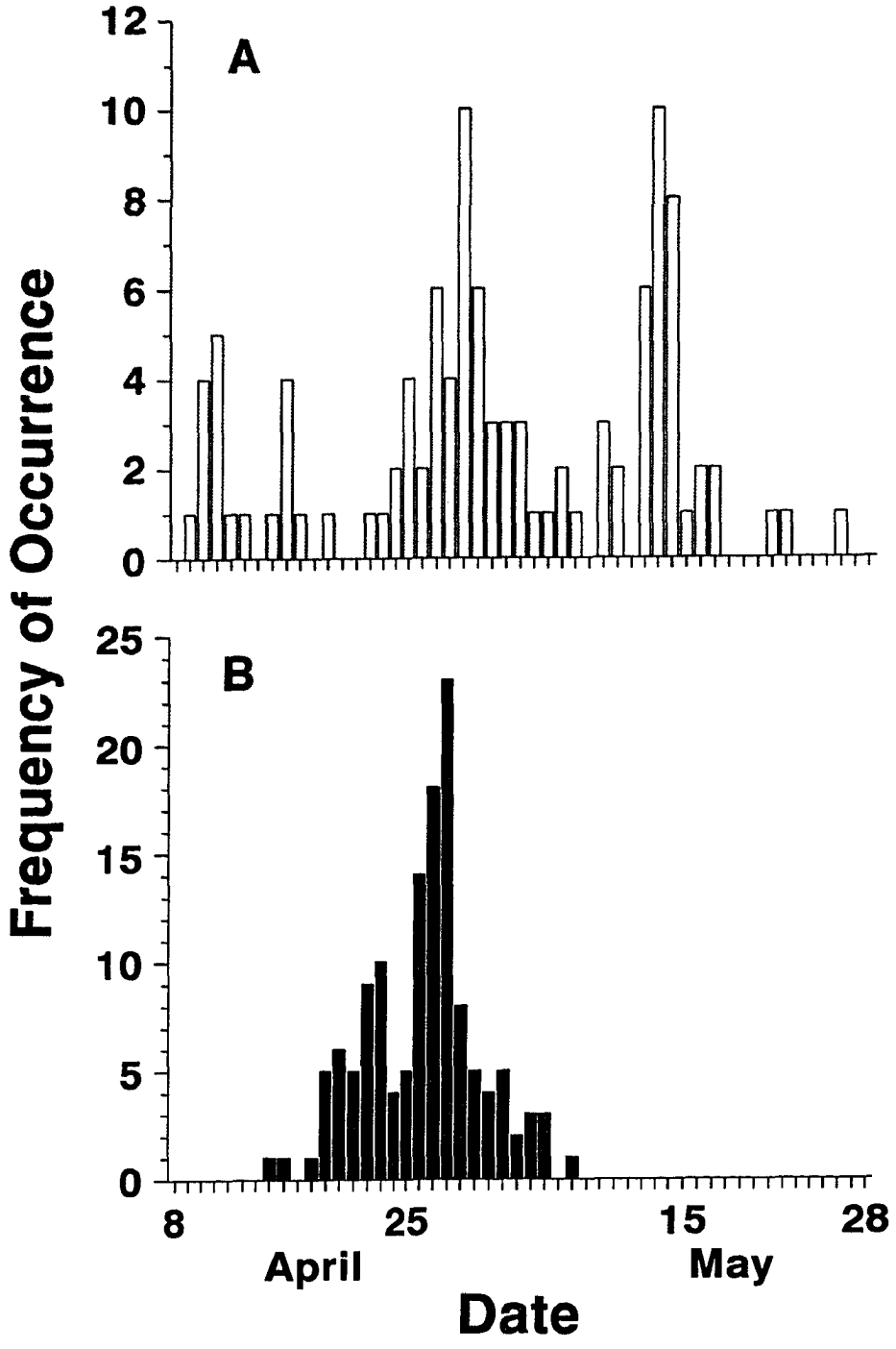


Figure 4-43. Larval river herring standard length (mm) to estimated age (days after hatching) relationship for the 1989 'early-spawn' cohort: A) standard length-at-age plot, B) studentized residuals scatterplot for ordinary least-squares regression, C) studentized residuals scatterplot for weighted least-squares regression.

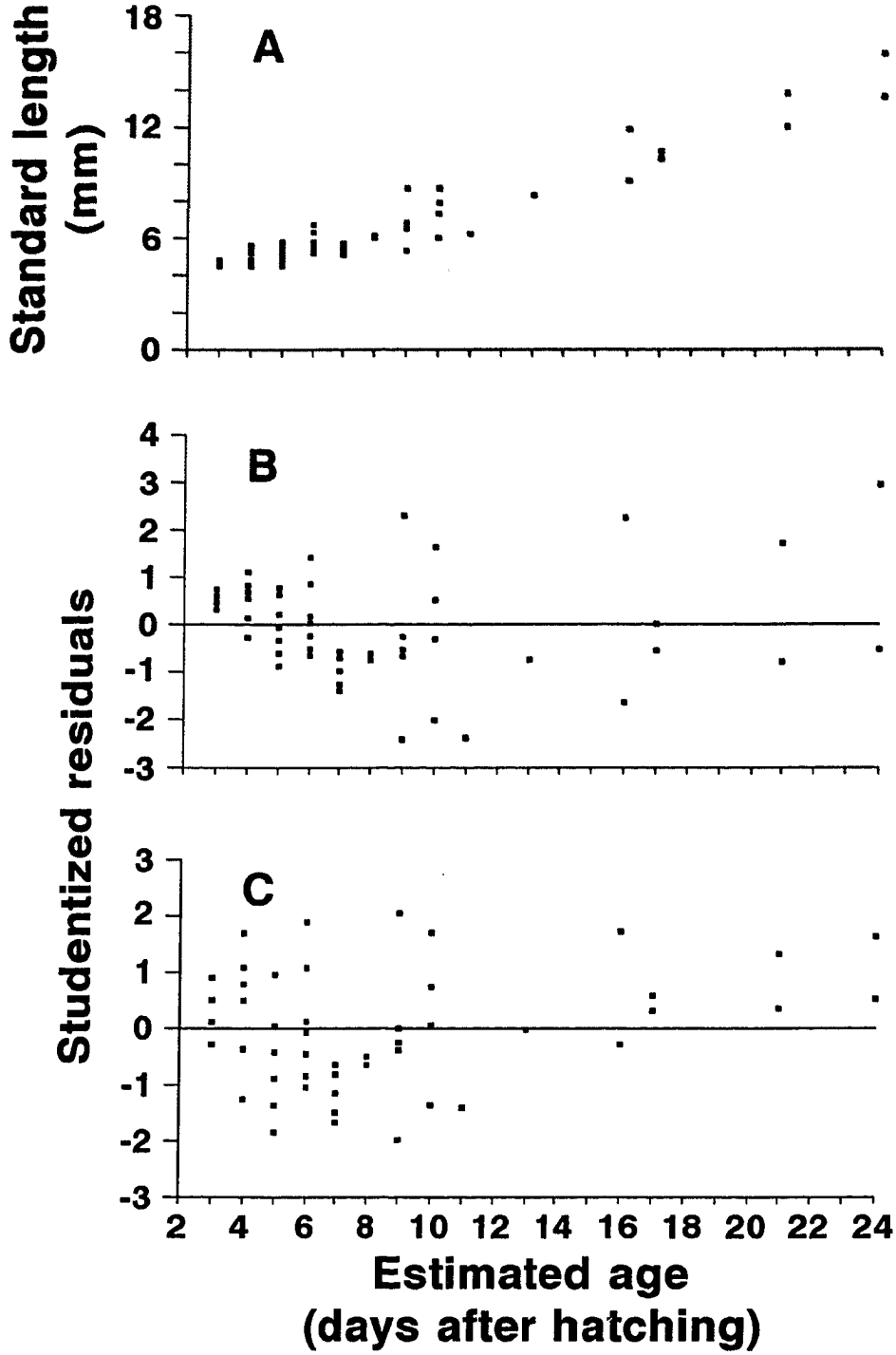


Figure 4-44. Larval river herring standard length (mm) to estimated age (days after hatching) relationship for the 1990 'early-spawn' cohort: A) standard length-at-age plot, B) studentized residuals scatterplot for ordinary least-squares regression, C) studentized residuals scatterplot for weighted least-squares regression.

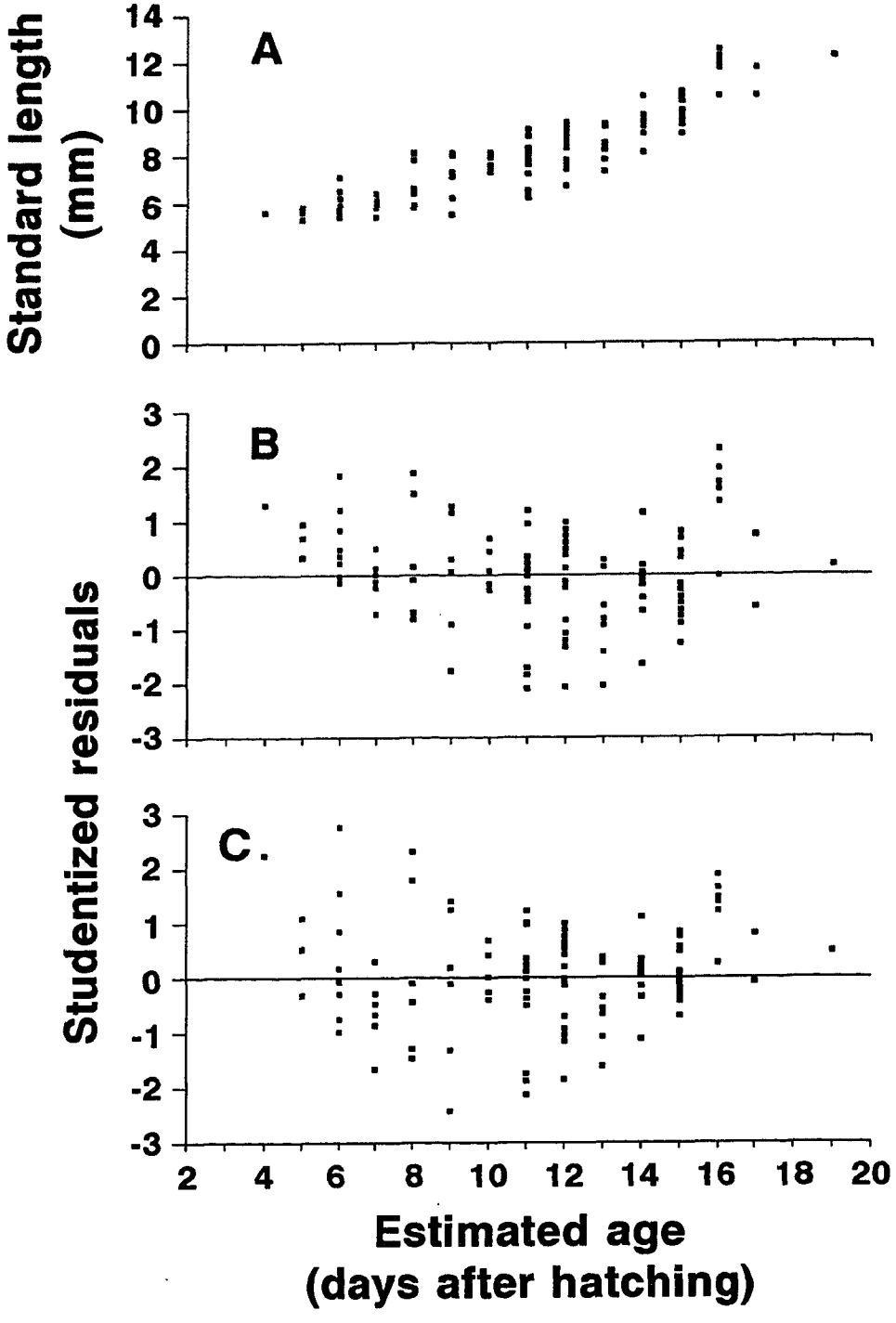


Figure 4-45. Studentized residuals for ordinary least-squares (A) and weighted least-squares (B) regression models relating standard length (mm) to age (days after hatching) for younger river herring larvae (<age 11 d) of the 1989 'early-spawn' cohort.

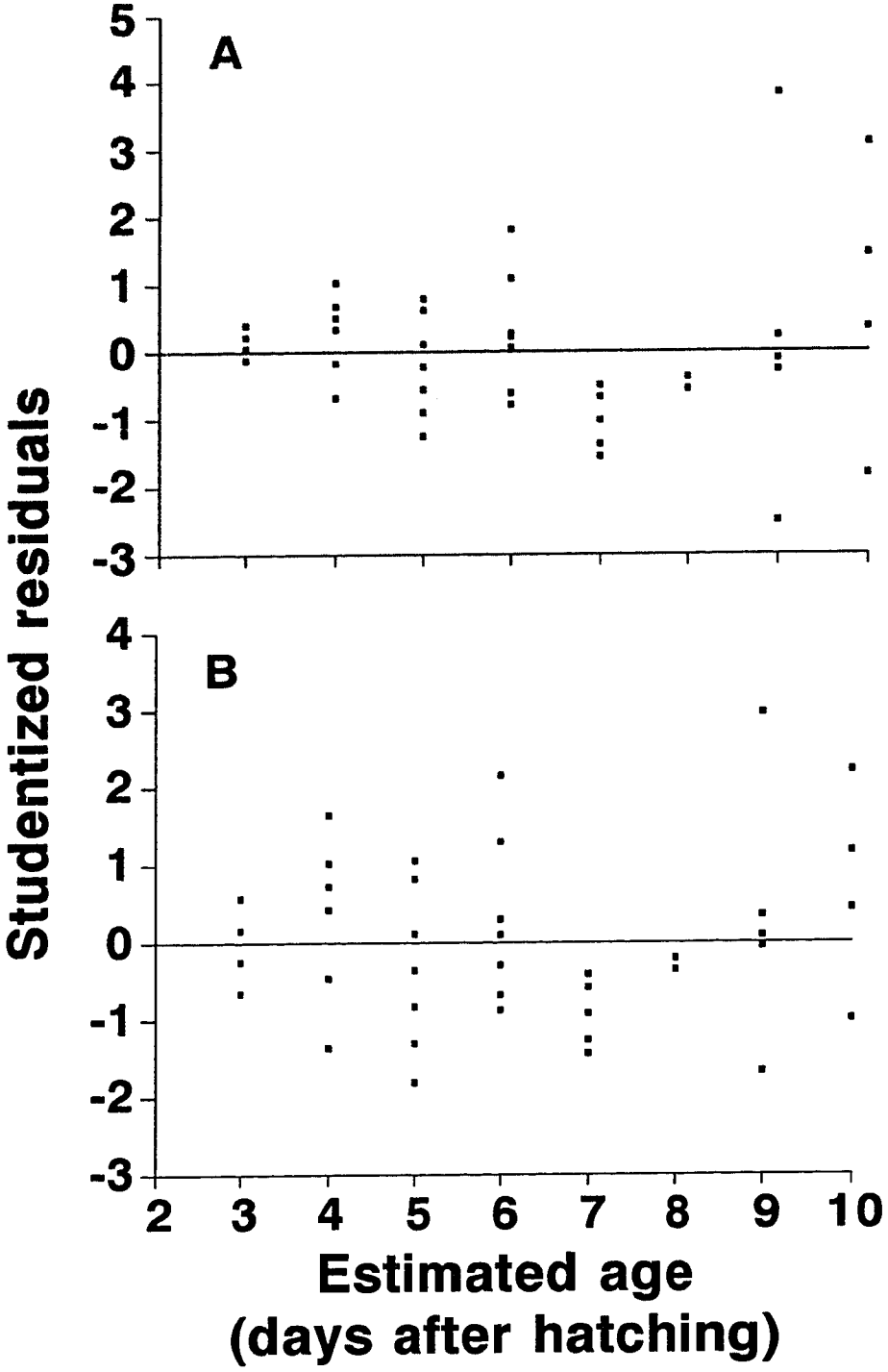


Figure 4-46. Studentized residuals for ordinary least-squares (A) and weighted least-squares (B) regression models relating standard length (mm) to age (days after hatching) for older river herring larvae (≥age 11 d) of the 1989 'early-spawn' cohort.

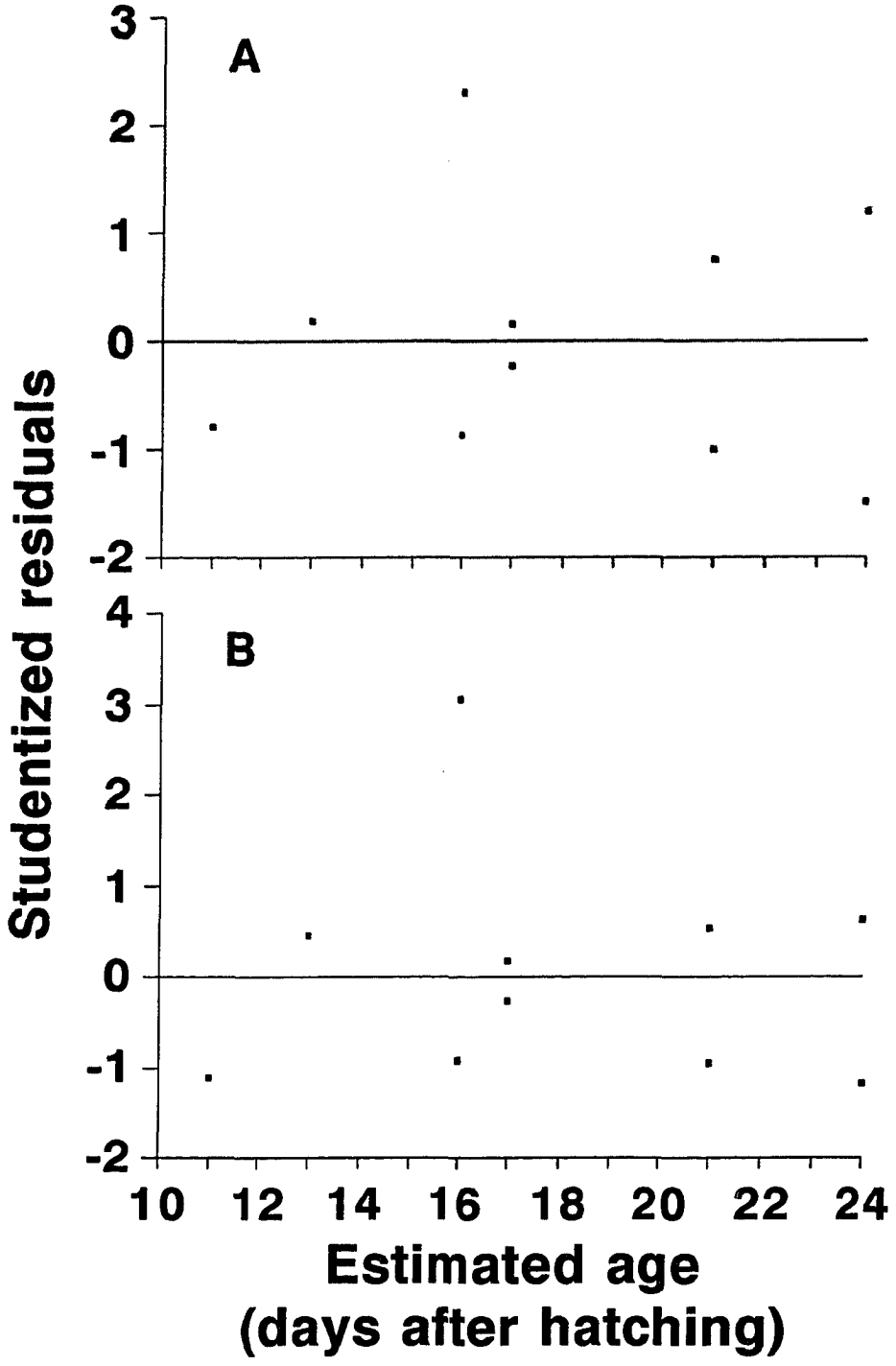


Figure 4-47. Studentized residuals for ordinary least-squares (A) and weighted least-squares (B) regression models relating standard length (mm) to age (days after hatching) for younger river herring larvae (< age 11 d) of the 1990 'early-spawn' cohort.

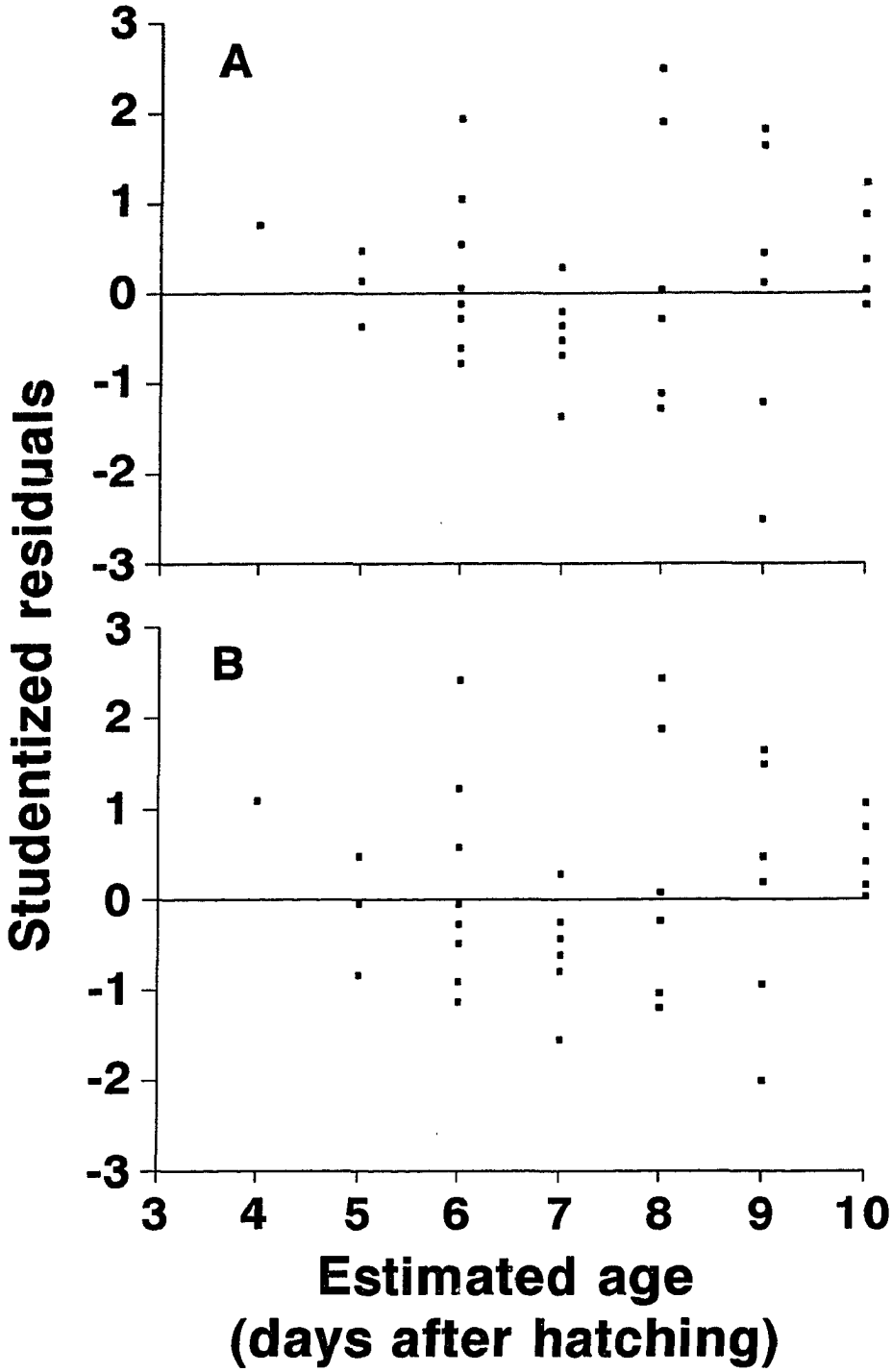


Figure 4-48. Studentized residuals for ordinary least-squares (A) and weighted least-squares (B) regression models relating standard length (mm) to age (days after hatching) for older river herring larvae (≥age 11 d) of the 1990 'early-spawn' cohort.

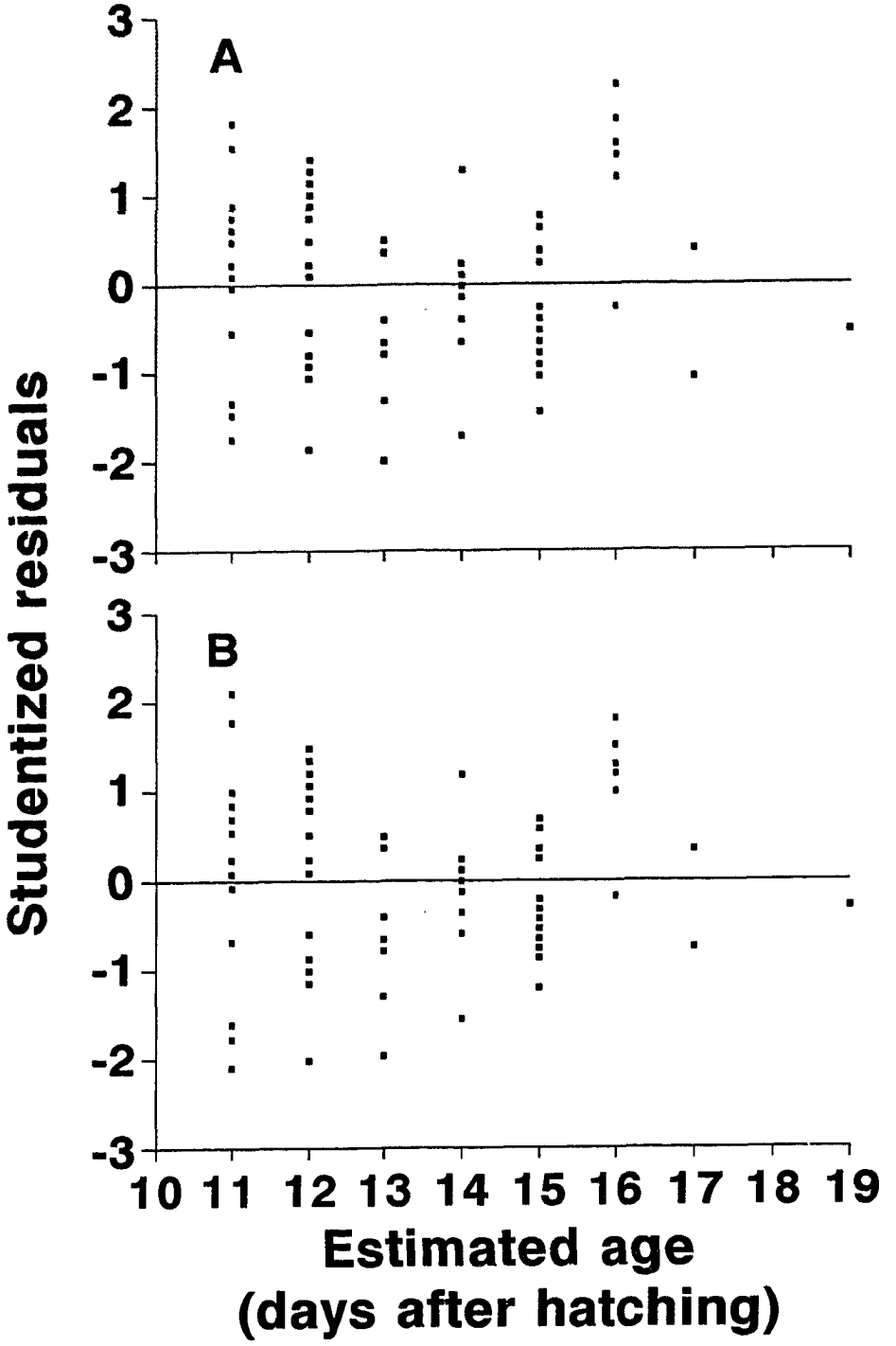


Figure 4-49. Larval river herring standard length (mm) to estimated age (days after hatching) relationship for the mainstem river in 1989 and 1990: A) standard length-at-age plot, B) studentized residuals scatterplot for ordinary least-squares regression, C) studentized residuals scatterplot for weighted least-squares regression.

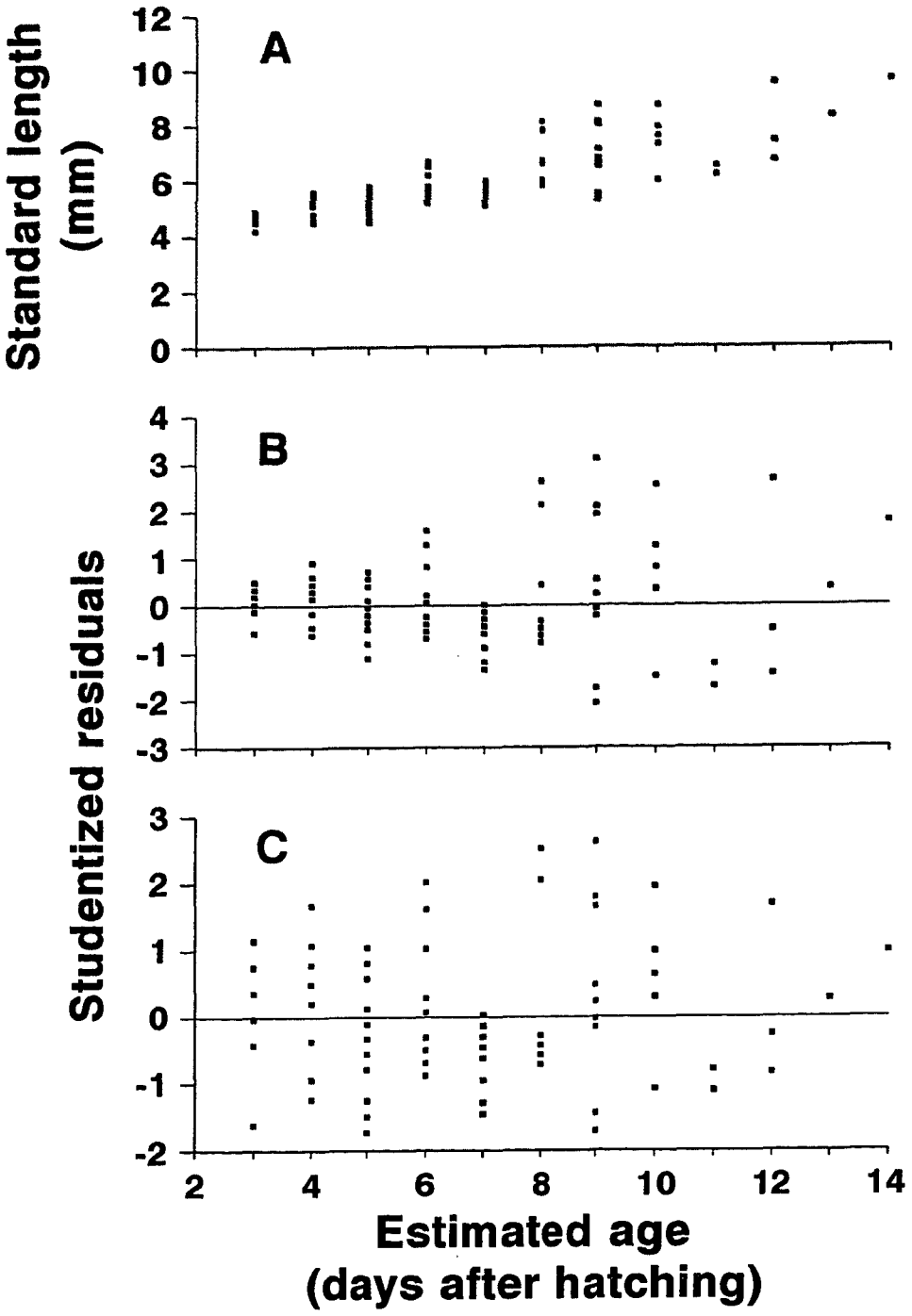


Figure 4-50. Larval river herring standard length (mm) to estimated age (days after hatching) relationship for the tidal creeks in 1989 and 1990: A) standard length-at-age plot, B) studentized residuals scatterplot for ordinary least-squares regression, C) studentized residuals scatterplot for weighted least-squares regression.

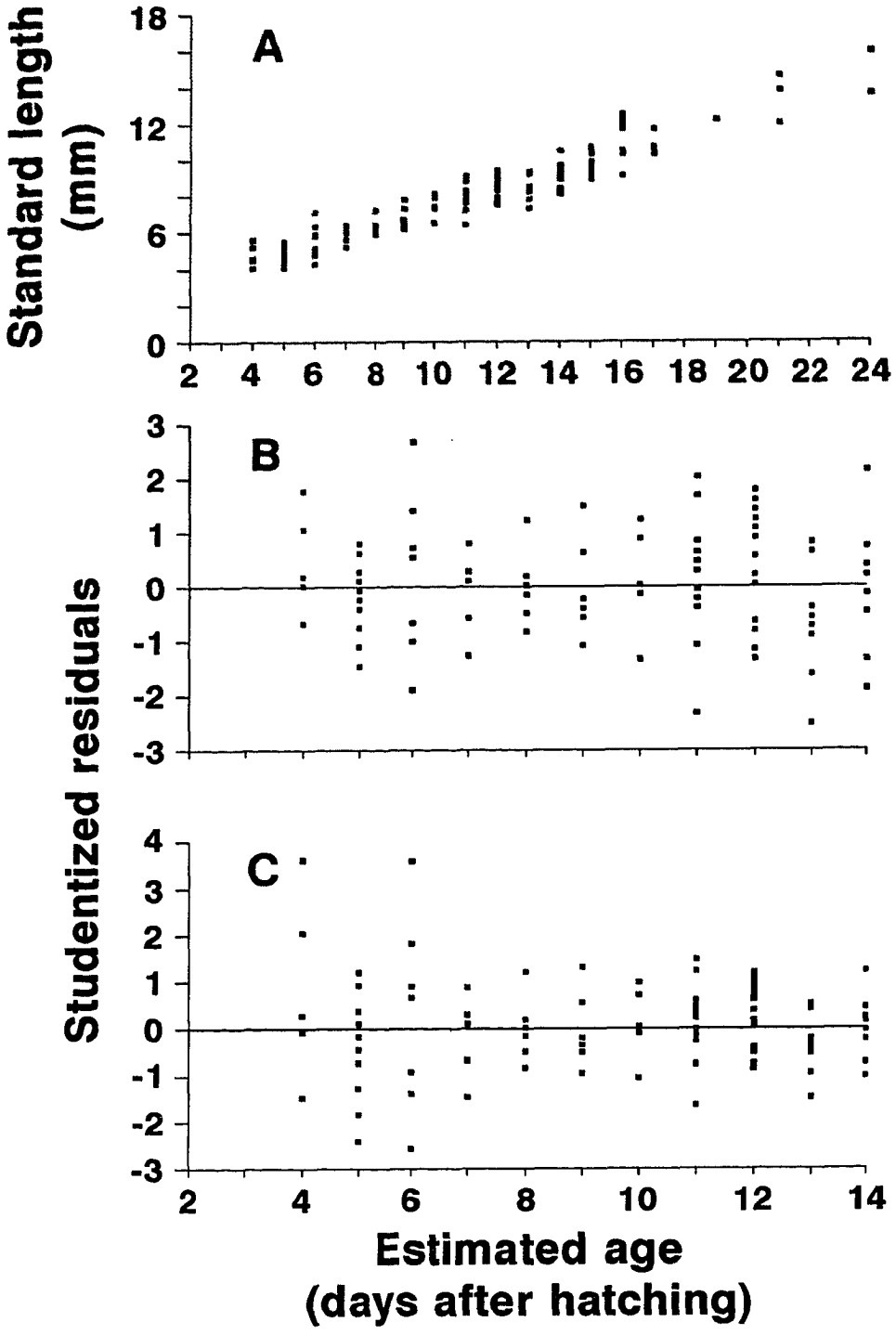


Figure 4-51. Estimated numbers of river herring larvae surviving to transform to the juvenile stage given an initial abundance of 10^6 larvae at the initiation of exogenous feeding over instantaneous daily mortality rates ranging from 0 to 0.5. The estimated larval river herring stage duration was 44 days in the mainstem river and 32 days in the tidal creeks.

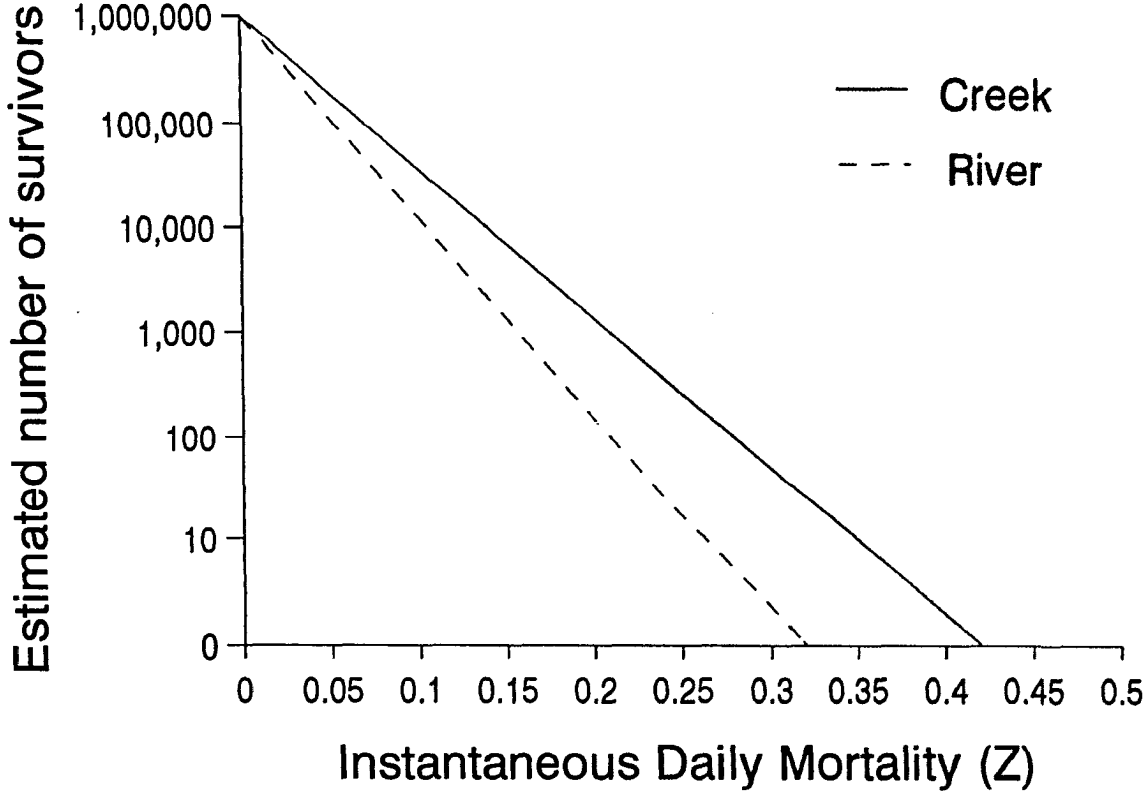


Figure 4-52. Larval river herring mean otolith daily growth-increment width (μm) to estimated age (days after hatching) relationship for the mainstem river (A) and tidal creeks (B) in 1989 and 1990. The 95% confidence intervals (dashed) and the 95% prediction intervals (solid) are shown in A and B. Comparison of fitted regression lines and 95% confidence and prediction intervals (C) show that slopes for the two regression relationships differed. Nearly complete overlap of 95% prediction intervals indicates that growth increment-width could not be used as a potential indicator of the habitat in which larvae reside.

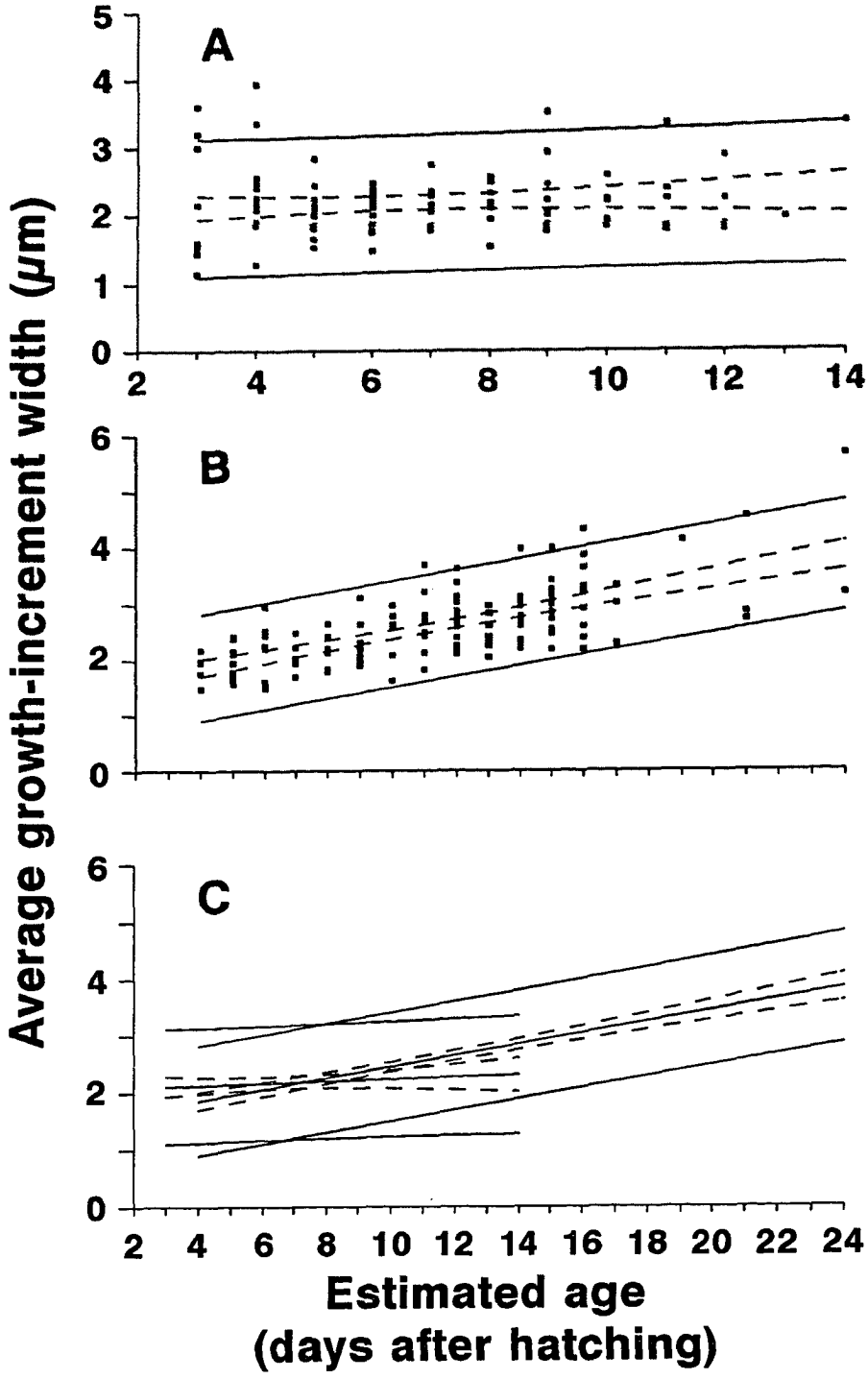


Figure 4-53. Hatch date frequency distributions of river herring larvae from the mainstem river (A) and tidal creeks (B). Abundances of yolk-sac and early preflexion larvae from the mainstem river (C, mean daily abundance) and in Cumberland Thoroughfare (D, observed abundance) and abundances of rotifers, copepod nauplii and copepodites, and cladocerans in the mainstem river (E) are shown to emphasize relationships between hatch dates of larvae and the timing of maximal larva and zooplankton abundances.

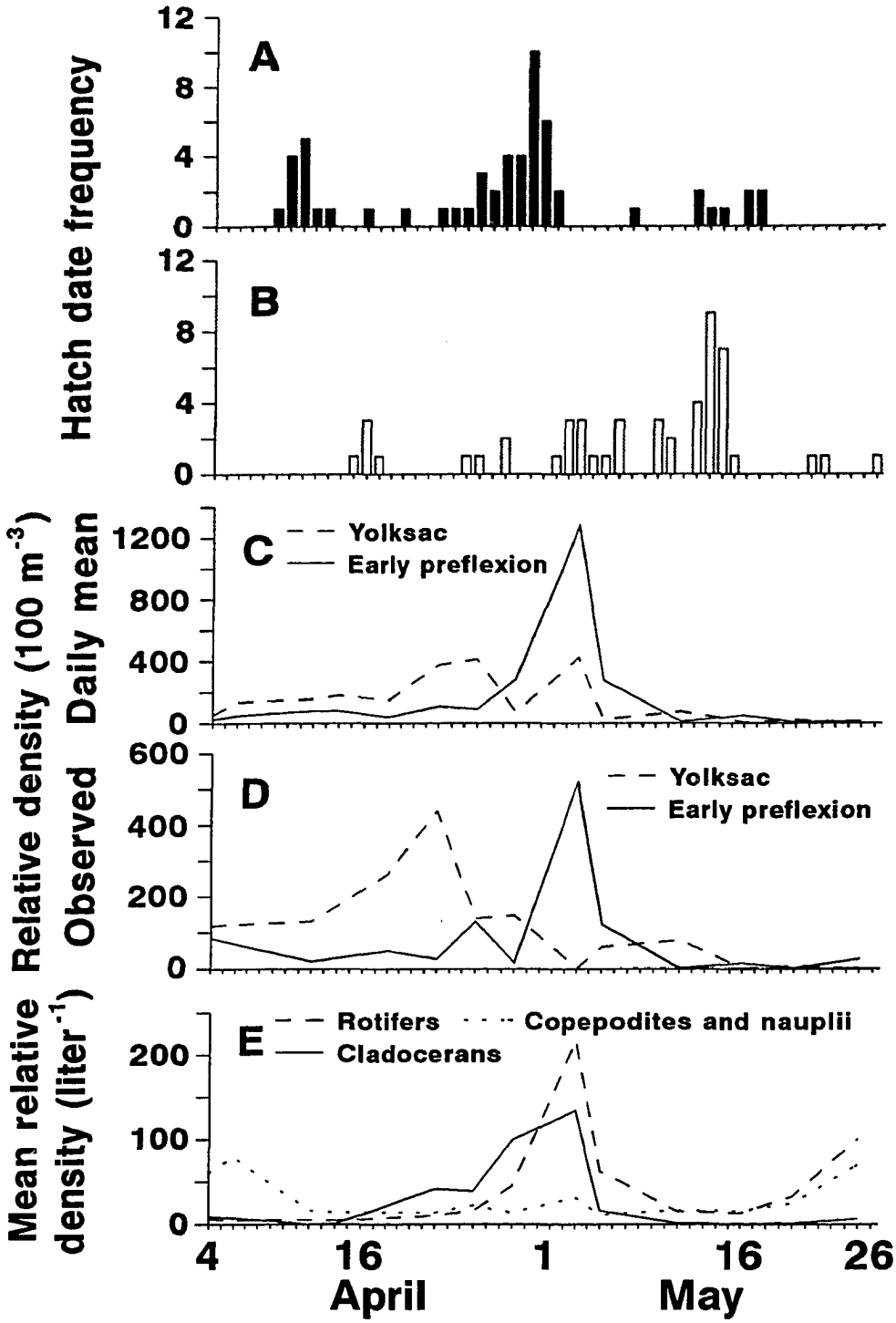


Figure 4-54. Mean abundances of rotifers, copepod nauplii and copepodites, and cladocerans in tidal creeks and the mainstem river on 20 April and 18 May, 1989.

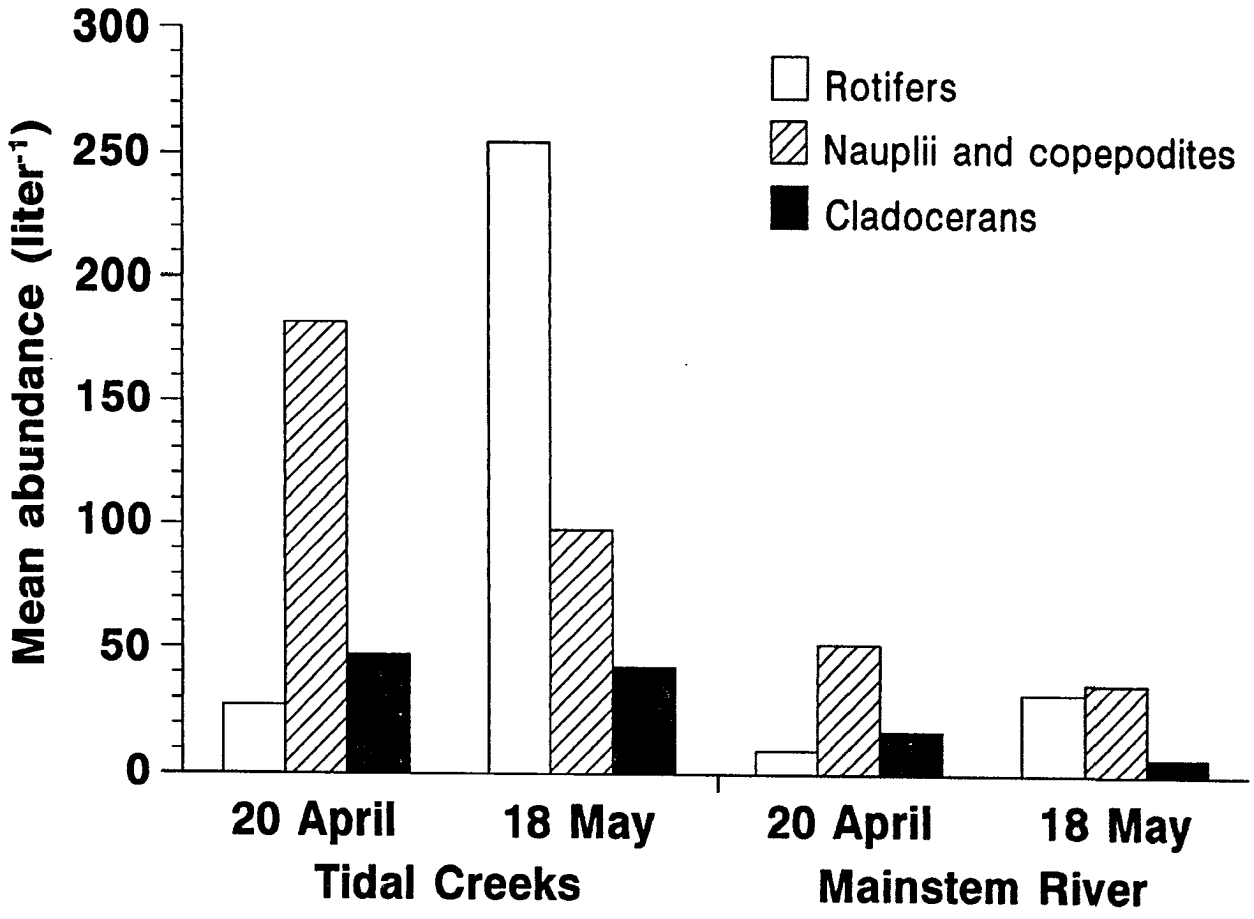


Figure 4-55. Hatch date frequency distributions of river herring larvae captured in Big Creek (A), the mainstem river (B-D) and in Holts Creek (E) in 1990. Hatch dates are shown in relation to early preflexion larval river herring abundance in the potential tidal freshwater nursery habitat: Big Creek (A), channel (B), thoroughfare (C), shoulder (D), and Holts Creek (E). Abundances are redrawn from Fig. 4-31 to show the shift in the distribution of larvae between habitats.

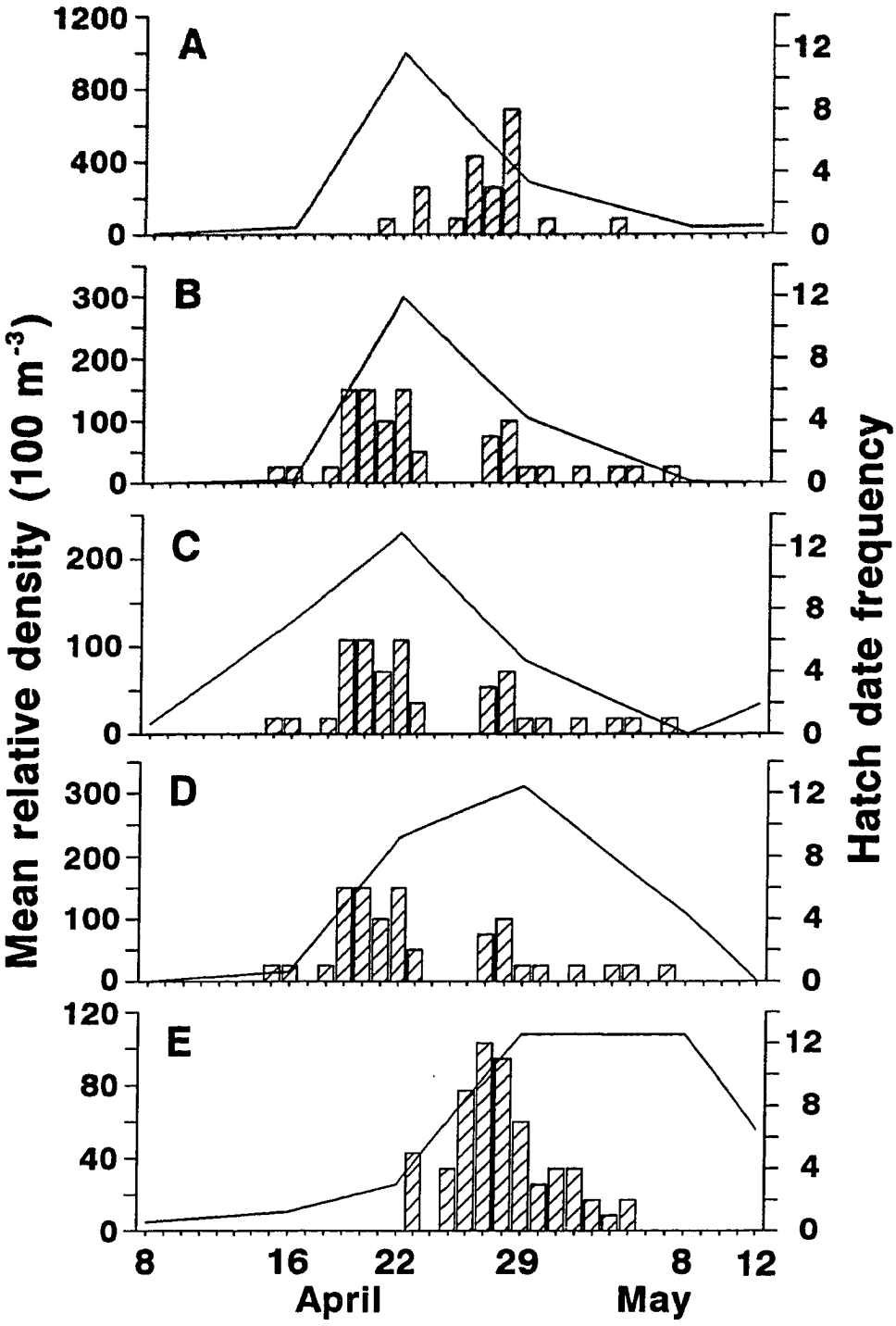


Figure 4-56. Simplified conceptual model of larval herring ecology in the tidal freshwater-oligohaline reach of southern Chesapeake Bay tributaries. Open arrows indicate trophodynamic relationships and closed arrows show potential intraspecific (1) and interspecific (2) larva-larva interactions.

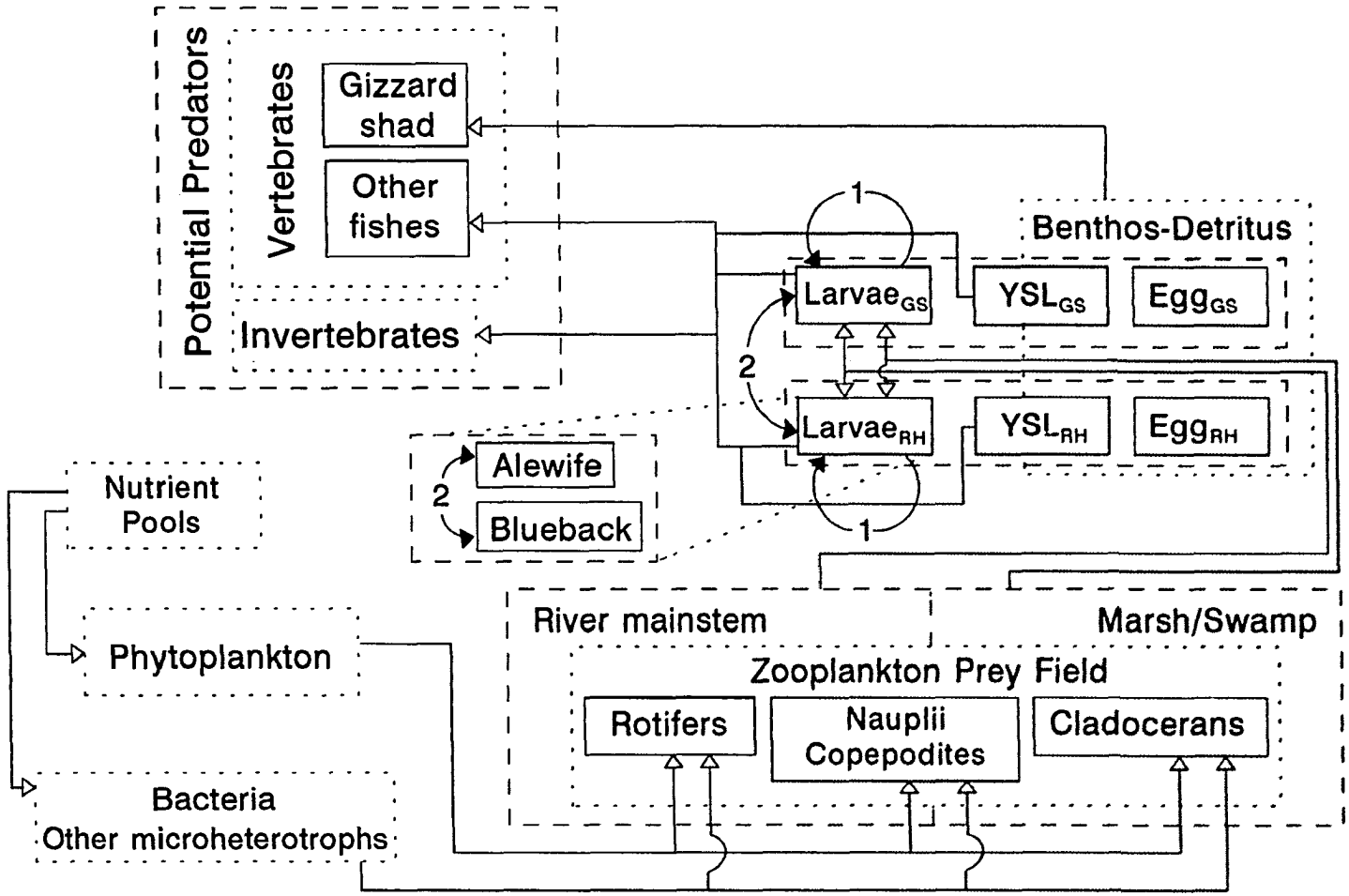
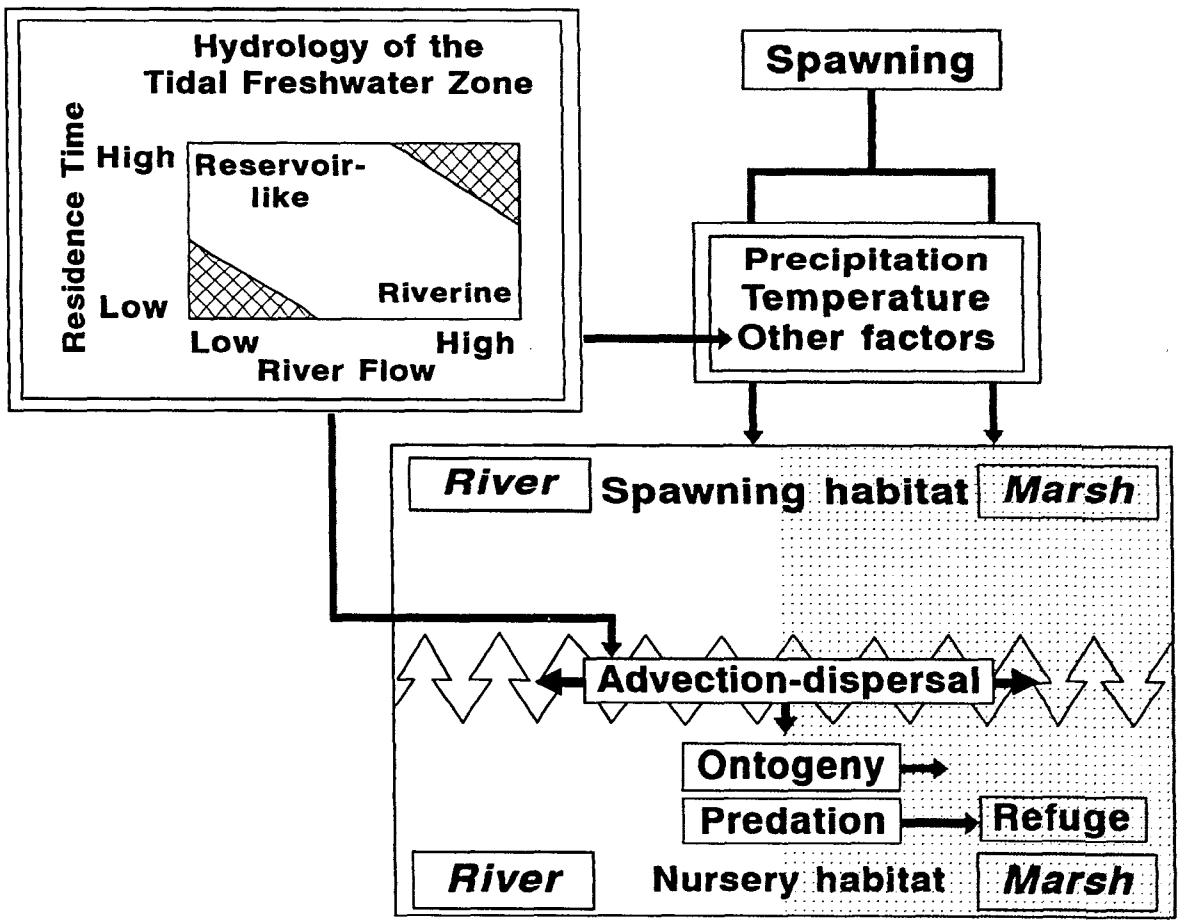


Figure 4-57. Potential determinants of larval herring distribution in the tidal freshwater-oligohaline reach of southern Chesapeake Bay tributaries.



Appendix 4-A. Summary of collection dates and locations in 1989 and 1990 along the mainstem river channel.

Date	Stratum	Location (km)	Location (nm)	Notes
22 March 1989	1	83.4	45	
	2	92.7	50	
	3	98.2	53	
	4	100.1	54	
	5	107.5	58	
	6	113.0	61	
	7	Thoroughfare		
28 March 1989	1	83.4	45	
	2	92.7	50	
	3	96.4	52	
	4	101.9	55	
	5	109.3	59	
	6	111.2	60	
	7	Thoroughfare		
4 April 1989	1	85.3	46	
	2	89.0	48	
	3	98.2	53	
	4	103.8	56	
	5	109.3	59	
	6	114.9	62	
	7	Thoroughfare		
6 April 1989	1	83.4	45	
	2	92.7	50	
	3	94.55	51	
	4	103.8	56	
	5	105.6	57	
	6	113.0	61	
	7	Thoroughfare		Not made

Appendix 4-A (continued).

Date	Stratum	Location (km)	Location (nm)	Notes
12 April 1989	1	87.1	47	
	2	90.8	49	
	3	94.5	51	
	4	100.1	54	
	5	105.6	57	
	6	111.2	60	
	7	Thoroughfare		
14 April 1989	1	87.1	47	
	2	92.7	50	
	3	98.2	53	
	4	101.9	55	
	5	109.3	59	
	6	114.9	62	Not made
	7	Thoroughfare		
18 April 1989	1	85.3	46	No zooplankton
	2	90.8	49	No zooplankton
	3	98.2	53	No zooplankton
	4	101.9	55	No zooplankton
	5	107.5	58	No zooplankton
	6	113.0	61	No zooplankton
	7	Thoroughfare		No zooplankton
22 April 1989	1	85.3	46	
	2	90.8	49	
	3	98.2	53	
	4	100.1	54	
	5	105.6	57	
	6	114.9	62	
	7	Thoroughfare		

Appendix 4-A (continued).

Date	Stratum	Location (km)	Location (nm)	Notes
25 April 1989	1	87.1	47	
	2	92.7	50	
	3	98.2	53	
	4	100.1	54	
	5	109.3	59	
	6	113.0	61	
	7	Thoroughfare		
28 April 1989	1	83.4	45	
	2	90.8	49	
	3	96.4	52	
	4	100.1	54	
	5	109.3	59	
	6	113.0	61	
	7	Thoroughfare		
3 May 1989	1	87.1	47	
	2	89.0	48	
	3	94.5	51	
	4	103.8	56	
	5	107.5	58	
	6	113.0	61	
	7	Thoroughfare		
5 May 1989	1	87.1	47	
	2	89.0	48	
	3	98.2	53	
	4	103.8	56	
	5	105.6	57	
	6	113.0	61	
	7	Thoroughfare		

Appendix 4-A (continued).

Date	Stratum	Location (km)	Location (nm)	Notes
11 May 1989	1	83.4	45	
	2	90.8	49	
	3	98.2	53	
	4	100.1	54	
	5	107.5	58	
	6	111.2	60	
	7	Thoroughfare		
16 May 1989	1	85.3	46	
	2	92.7	50	
	3	96.4	52	
	4	101.9	55	
	5	105.6	57	
	6	114.9	62	
	7	Thoroughfare		
20 May 1989	1	83.4	45	
	2	92.7	50	
	3	96.4	52	
	4	101.9	55	
	5	109.3	59	
	6	113.0	61	
	7	Thoroughfare		
25 May 1989	1	85.3	46	
	2	89.0	48	
	3	94.5	51	
	4	103.8	56	
	5	107.5	58	
	6	111.2	60	
	7	Thoroughfare		

Appendix 4-A (continued).

Date	Stratum	Location (km)	Location (nm)	Notes
21 March 1990	1	85.3	46	
	2	90.8	49	
	3	98.2	53	
	4	100.1	54	
	5	107.5	58	
	6	109.3	61	
	7	Thoroughfare		
10 April 1990	1	87.1	47	
	2	90.8	49	
	3	98.2	53	
	4	101.9	55	
	5	109.3	59	
	6	114.9	62	
	7	Thoroughfare		
27 April 1990	1	87.1	47	
	2	92.7	50	
	3	98.2	53	
	4	103.8	56	
	5	109.3	59	
	6	114.9	62	
	7	Thoroughfare		
9 May 1990	1	83.4	45	
	2	90.8	49	
	3	94.5	51	
	4	100.1	54	
	5	107.5	58	
	6	113.0	61	
	7	Thoroughfare		

Appendix 4-B. Collection dates for potential nursery habitats in the Pamunkey River tidal freshwater reach in 1989 and 1990.

2 April 1989 (not completed successfully)
20 April 1989
18 May 1989
30 May 1989
18 March 1990
8 April 1990
16 April 1990
22 April 1990
29 April 1990
8 May 1990
12 May 1990

Appendix 4-C1. Larval river herring abundances (100 m^{-3}) along the mainstem Pamunkey River channel in 1989 and 1990 by collection date, collection location, and size classes of larvae. Collection location is denoted by stratum number (see Appendix 4-A). Size classes are in standard length (mm).

Date	Location	Size class (mm SL)								
		4	5	6	7	8	9	10	11	12
4 April 1989	CT		42.2	42.2						
4 April 1989	1		13.9	16.8						
4 April 1989	2		24.6	9.9						
4 April 1989	3			21.9						
4 April 1989	4			38.0	18.1					
4 April 1989	5			17.6						
6 April 1989	1		12.1	12.1						
6 April 1989	2		16.1	176.7	32.1					
6 April 1989	3			16.7						
6 April 1989	4		9.7	9.7						
6 April 1989	5			29.3						
12 April 1989	CT		18.5							
12 April 1989	1		141.7	85.0		28.3				
12 April 1989	2		131.6	68.8	17.2					
12 April 1989	3		49.4	9.9						
14 April 1989	2		164.0	69.0		8.6			8.6	
14 April 1989	3		105.0	10.50	10.5					
14 April 1989	4		18.4	36.7						
18 April 1989	CT		34.9	14.0						

Appendix 4-C1. (Continued).

Date	Location	Size class (mm SL)								
		4	5	6	7	8	9	10	11	12
18 April 1989	1		17.5							
18 April 1989	2		196.6							
18 April 1989	3		12.5	15.0	0.7					
18 April 1989	4		20.1							
22 April 1989	CT		19.4	6.5						
22 April 1989	1		12.0	60						
22 April 1989	2		24.6	49.1						
22 April 1989	3		23.9			12.0				
22 April 1989	4		86.1	125.5	26.6	8.5		8.5	13.3	
22 April 1989	5	9.0	72.0	144.0	18.0					9.0
22 April 1989	6		13.3	13.3						
25 April 1989	CT		114.3	14.3						
25 April 1989	1		77.6	15.5						
25 April 1989	2		58.9	54.1	6.8					
25 April 1989	3		15.6	93.8						
25 April 1989	4		75.1	137.6						
25 April 1989	6		10.3	10.3						
28 April 1989	CT			16.3						
28 April 1989	1		22.5	44.9	7.5					
28 April 1989	2		64.3	479.2	35.8					

Appendix 4-C1. (Continued).

Date	Location	Size class (mm SL)								
		4	5	6	7	8	9	10	11	12
28 April 1989	3		12.4	24.7				12.4		
28 April 1989	4		29.2	175.4	14.7					
28 April 1989	5		117.5	386.1						
28 April 1989	6		77.2	205.8						
3 May 1989	CT		301.2	219.1						
3 May 1989	1		219.4	57.7						
3 May 1989	2		600.6	540.5						
3 May 1989	3		181.5	340.4	45.4	22.7				
3 May 1989	4		2942.6	619.5	154.9					
3 May 1989	5		738.2	218.0	78.6					
3 May 1989	6		794.8	159.0						
5 May 1989	CT		45.2	75.4						
5 May 1989	1	7.5	81.9	81.9						
5 May 1989	2	7.9	39.2	31.4		7.9				
5 May 1989	3		679.9	360.1						
5 May 1989	4		205.1	60.3						
5 May 1989	5		63.3	26.1	13.4					
11 May 1989	2	15.8	58.7							
16 May 1989	CT		13.5							

Appendix 4-C1. (Continued).

Date	Location	Size class (mm SL)								
		4	5	6	7	8	9	10	11	12
16 May 1989	1		39.0							
16 May 1989	2		123.2							
16 May 1989	4		68.5							
16 May 1989	5		30.8	15.4						
16 May 1989	6		13.4							
20 May 1989	1		10.8							
20 May 1989	2		4.1							
20 May 1989	4			7.8						
20 May 1989	5		23.9							
25 May 1989	CT		26.2							
25 May 1989	3		3.7							
25 May 1989	4		23.0							
25 May 1989	5		21.0							
25 May 1989	6		72.2	7.2						
21 March 1990	CT		16.4	21.8						
21 March 1990	1			7.5						
10 April 1990	CT		20.2	20.2						
10 April 1990	1		29.2							
10 April 1990	2		26.0							

Appendix 4-C1. (Continued).

Date	Location	Size class (mm SL)								
		4	5	6	7	8	9	10	11	12
10 April 1990	3		35.5							
10 April 1990	4			18.2						
27 April 1990	CT		82.4	68.6						
27 April 1990	1	4.9	19.5	43.8	4.9					
27 April 1990	2		13.3	26.6		4.4				
27 April 1990	3		26.8	92.6						
27 April 1990	4	5.8	58.4	58.4						
27 April 1990	5		506.3	961.9						
27 April 1990	6	12.1	325.9	77.2	20.5					
9 May 1990	CT		17.4							
9 May 1990	4		22.7	11.4						
9 May 1990	5	16.5	70.6	16.5						
9 May 1990	6	12.3	49.0							

Appendix 4-C2. Larval gizzard shad abundance (100 m^{-3}) along the mainstem Pamunkey River channel in 1989 and 1990 by collection date, collection location and size classes of larvae. Location is denoted by stratum number (see Appendix 4-A). Size classes are in standard length (mm).

Date	Location	Size class (mm SL)					
		4	5	6	7	8	9
12 April 1989	1		46.4				
14 April 1989	2					8.3	
14 April 1989	3		9.7				
18 April 1989	3		0.7				
22 April 1989	3		9.0				
22 April 1989	4			12.9			
25 April 1989	2		9.6	7.3			
25 April 1989	3		13.7				
25 April 1989	4		10.0				
28 April 1989	1		6.2	6.2			
28 April 1989	2		54.4	77.2			
28 April 1989	3		12.4	12.4			
28 April 1989	4		18.3	52.2			
28 April 1989	6		23.6				
3 May 1989	CT		190.8				
3 May 1989	1		32.6	10.9			
3 May 1989	2	38.0	342.3		38.0		
3 May 1989	3		78.7				
3 May 1989	4		743.4				
3 May 1989	5		33.2	28.4			
5 May 1989	CT		24.1				
	1	4.9	48.9	4.9			
	2		7.2				
	3		251.8				
	4		11.5				
11 May 1989	2		13.2				
25 May 1989	CT		13.1				
	3		2.3				
	4	2.3	13.8				
	5		18.9				
	6		30.2	7.6			

Appendix 4-C2. (Continued).

Date	Location	Size class (mm SL)					
		4	5	6	7	8	9
21 March 1990	1			3.7			
10 April 1990	1		7.3				
27 April 1990	3		9.1	12.1		4.5	12.1
27 April 1990	4		5.6				
27 April 1990	5			48.9			
27 April 1990	6		24.9				
9 May 1990	4		8.5				
9 May 1990	5	14.4					

Appendix 4-C3. Larval river herring abundance (100 m^{-3}) in potential tidal freshwater nursery habitats of the Pamunkey River in 1989 and 1990 by collection date, collection location of capture, developmental stage, and size classes of larvae. Location is denoted by stratum number (see Appendix 4-A). Developmental stages are denoted as: 1) early preflexion; 2) late preflexion; and, 3) postflexion. Size classes are in standard length (mm).

Date	Location	Stage	Size class (mm SL)											
			4	5	6	7	8	9	10	11	12	13	14	15
20 April 1989	Channel	1		11.5	11.6									
20 April 1989	Shoulder	1		5.9	5.6									
20 April 1989	Thoroughfare	1		17.4	18.9									
20 April 1989	Big Creek	1	6.6	19.4	55.7	9.8								
		2						6.3						
20 April 1989	Holts Creek	1		12.6	48.7	17.8								
18 May 1989	Thoroughfare	1		21.7										
18 May 1989	Big Creek	1		10.4	10.4									
		3										5.8	7.1	14.2
18 May 1989	Holts Creek	1	4.6	65.0	48.6	14.2	22.7	9.1	9.1					
		2				5.9	53.2	29.6	17.7					
		3								11.1	16.2	5.5		5.4
30 May 1989	Channel	1		18.3										
30 May 1989	Thoroughfare	1	6.6	6.6										
30 May 1989	Big Creek	1	6.3	8.5										
30 May 1989	Holts Creek	1	14.7	8.2										
18 March 1990	Channel	1		5.1	16.8									
18 March 1990	Shoulder	1		4.7	6.4									
18 March 1990	Thoroughfare	1		8.9	5.3									

Appendix 4-C3. (Continued).

Date	Location	Stage	Size class (mm SL)											
			4	5	6	7	8	9	10	11	12	13	14	15
18 March 1990	Big Creek	1			13.9									
8 April 1990	Thoroughfare	1		11.1	6.4									
8 April 1990	Big Creek	1			4.4		4.7							
8 April 1990	Holts Creek	1		4.4		5.2								
16 April 1990	Channel	1		4.9	4.9									
16 April 1990	Shoulder	1		7.7	23.2									
16 April 1990	Thoroughfare	1		46.1	74.3	15.9								
16 April 1990	Big Creek	1	7.3	31.9	8.4									
16 April 1990	Holts Creek	1		9.3	11.8									
22 April 1990	Channel	1	10.4	137.2	151.3	10.4								
22 April 1990	Shoulder	1		81.5	147.3									
22 April 1990	Thoroughfare	1		82.3	147.2									
22 April 1990	Big Creek	1		425.3	549.8	43.1								
22 April 1990	Holts Creek	1		11.4	20.2									
29 April 1990	Channel	1		63.3	26.6	30.2								
		2				6.5								
29 April 1990	Shoulder	1	32.5	211.2	55.7	27.9								
29 April 1990	Thoroughfare	1		21.6	46.7	15.6								
		2							5.8					

Appendix 4-C3. (Continued).

Date	Location	Stage	Size class (mm SL)											
			4	5	6	7	8	9	10	11	12	13	14	15
29 April 1990	Big Creek	1		21.7	137.0	126.2								
		2					6.7							
29 April 1990	Holts Creek	1		17.2	30.3	56.2	8.6							
8 May 1990	Channel	1			5.2									
8 May 1990	Shoulder	1	6.5	105.2										
		3							6.5					
8 May 1990	Big Creek	1		17.6	23.9									
		2			25.7	163.2	249.4	77.8						
		3						10.1	9.5	11.1	3.6			
8 May 1990	Holts Creek	1		35.9	58.2	27.3								
		2				185.4	753.9	620	127.7					
		3							22.3	33.9	8.4	5.5		
12 May 1990	Channel	2				7.1								
12 May 1990	Thoroughfare	1	4.8	31.8										
12 May 1990	Big Creek	1	8.3	73.9										
		2				8.9								
		3									8.9			
12 May 1990	Holts Creek	1		37.1	36.8									
		2			41.9	112.1	109.3	71.3	20.7					
		3						25.5	120.0	22.9	9.3			

Appendix 4-C4. Larval gizzard shad abundances (100 m^{-3}) in potential tidal freshwater nursery habitats of the Pamunkey River in 1989 and 1990 by collection date, collection location, developmental stage, and size classes of larvae. Location is denoted by stratum number (see Appendix 4-A). Developmental stages are denoted as: 1) early preflexion; 2) late preflexion; and, 3) postflexion. Size classes are in standard length (mm).

Date	Location	Stage	Size class (mm SL)								
			4	5	6	7	8	9	10	11	12
20 April 1989	Big Creek	1			5.6						
18 May 1989	Big Creek	1		13.6							
18 May 1989	Holts Creek	1		5.4	1.5			3.0	1.5		
		2						5.6			
		3								4.6	
30 May 1989	Channel	1	3.0	7.8	0.5						
30 May 1989	Thoroughfare	1	2.2	2.9	1.5						
30 May 1989	Big Creek	1	0.3	8.2	0.6						
30 May 1989	Holts Creek	1	0.8	5.4	0.8	0.2					
8 April 1990	Holts Creek	1	2.6								
22 April 1990	Channel	1		10.1							
22 April 1990	Thoroughfare	1		6.2	6.2						
29 April 1990	Channel	1		62.0		5.4					
		2				2.2	2.2				
29 April 1990	Shoulder	1		184.0	10.4						
29 April 1990	Thoroughfare	1	1.7	43.5	17.6	4.4					
29 April 1990	Big Creek	1		19.0	13.0	6.9					
29 April 1990	Holts Creek	1		45.8	8.6						

Appendix 4-C4. (Continued).

Date	Location	Stage	Size class (mm SL)								
			4	5	6	7	8	9	10	11	12
8 May 1990	Channel	1	1.3	1.3							
8 May 1990	Shoulder	1	9.7	42.6							
8 May 1990	Big Creek	1	1.9	24.3	5.7						
		2			10.4	399	10.4				
		3								2.8	1.4
8 May 1990	Holts Creek	1		16.9	17.0	3.4					
		2					119.2				
		3							4.7	4.8	4.9
12 May 1990	Thoroughfare	1	8.8	8.8							
12 May 1990	Big Creek	1		14.3							
12 May 1990	Holts Creek	1		15.8	4.0						
		2			35.8	5.1	20.5				

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