



## Themed Issue on Atlantic Striped Bass Population: Past, Present, and Future Challenges

# Influence of feeding on zooplankton on Striped Bass postlarval mortality, growth, and year-class success in the Choptank River, Maryland, during the 1980s and 2023–2024

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### ABSTRACT

**Objective:** We examined first-feeding Striped Bass *Morone saxatilis* postlarvae (larvae that had absorbed their yolk sacs) in the Choptank River, Maryland, during 2023–2024 to address whether their feeding success on zooplankton could be a major factor behind a series of poor year-classes during 2019–2024.

**Methods:** We estimated Choptank River Striped Bass postlarval feeding incidences on primary zooplankton prey and their associations with daily instantaneous growth and mortality rates of postlarvae from seven 1980s surveys (low and high mortality and poor to strong year-classes) to establish criteria with which to evaluate feeding during 2023–2024. Distributions of larvae by water temperature and conductivity during 1980s surveys were used to direct 2023–2024 postlarval collections for feeding analysis.

**Results:** Feeding incidences of first-feeding Striped Bass postlarvae on copepods in the Choptank River during 2023–2024 were high; feeding incidence on cladocerans was also high in 2024. Estimates of a proxy index for postlarval daily instantaneous mortality during 2023 and 2024 were low. However, year-class success was dismal during 2023 and low in 2024.

**Conclusions:** This feeding investigation did not encompass the entire 2019–2024 drought in year-class success, but the 2023–2024 surveys did not indicate a consistent, prominent role for feeding success of postlarvae.

### LAY SUMMARY

High feeding incidence of first-feeding Striped Bass postlarvae on zooplankton and low mortality did not always translate to better year-class success during the 1980s and 2023–2024. A prominent role of poor larval feeding success on zooplankton was not suggested for continuous poor year-class success during 2019–2024.

**KEYWORDS:** Chesapeake Bay, cladocerans, copepods, feeding incidence, growth, mortality, postlarvae, Striped Bass, year-class success

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## INTRODUCTION

Production of strong year-classes of Striped Bass *Morone saxatilis* from Maryland's portion of Chesapeake Bay (hereafter, "Upper Bay") spawning areas is important for fisheries along the Atlantic coast (Maryland Sea Grant, 2009; Richards & Rago, 1999; Uphoff, 2023). Year-class success of Striped Bass in the Upper Bay, as measured by a juvenile index (JI; geometric mean catch per shore zone seine haul at fixed stations), has proven to be a reliable indicator of recruitment to Atlantic coast fisheries (Durell & Weedon, 2024; Goodyear, 1985; Hollis, 1967; Maryland Sea Grant, 2009; Richards & Rago, 1999; Schaefer, 1972). The Upper Bay JI has been poor during 2019–2024 (Figure 1; Durell & Weedon, 2024). This deterioration of year-class success followed a period of intermittent strong and moderate year-classes during 1993–2018 (Figure 1) and resembles the beginning of an extended nadir in recruitment that developed in the 1970s and continued through the 1980s (Richards & Rago, 1999; Uphoff, 2023). This recent decline in Upper Bay recruitment has become a major management concern for Atlantic coast Striped Bass fisheries (Atlantic States Marine Fisheries Commission, 2024).

Spawning and larval nursery habitats (both are basically the same) are in freshwater to low-salinity ( $\leq 0.5\text{‰}$ ) main-stem tidal reaches of larger Upper Bay tributaries, and the estuarine turbidity maximum is particularly important (Martino & Houde, 2010; Maryland Sea Grant, 2009; North & Houde, 2003). Striped Bass eggs are large (3–4 mm in diameter), with a large perivitelline space; they are semi-buoyant, becoming suspended in the water column due to turbulence (Setzler et al., 1980; Westin & Rogers, 1978). Larvae live in open waters, and early juveniles move inshore to stay through the first summer (Kernehan et al., 1981; Setzler et al., 1980; Uphoff, 1989). Spawning generally occurs during April–June and is triggered by noticeable increases in water temperature (Setzler et al., 1980; Westin & Rogers, 1978). Survival from eggs to first-feeding postlarvae ( $\sim 7$  d posthatch) is low (0.2–5.2%; Secor & Houde, 1998). Year-class success of Upper Bay Striped Bass is largely determined within the first 3 weeks of life in early spring and is mainly a product of environmentally influenced, highly variable survival of eggs and larvae (Houde, 1996; Maryland Sea Grant, 2009; Rutherford et al., 1997; Ulanowicz & Polgar, 1980; Uphoff, 1989, 1992, 1993, 2023).

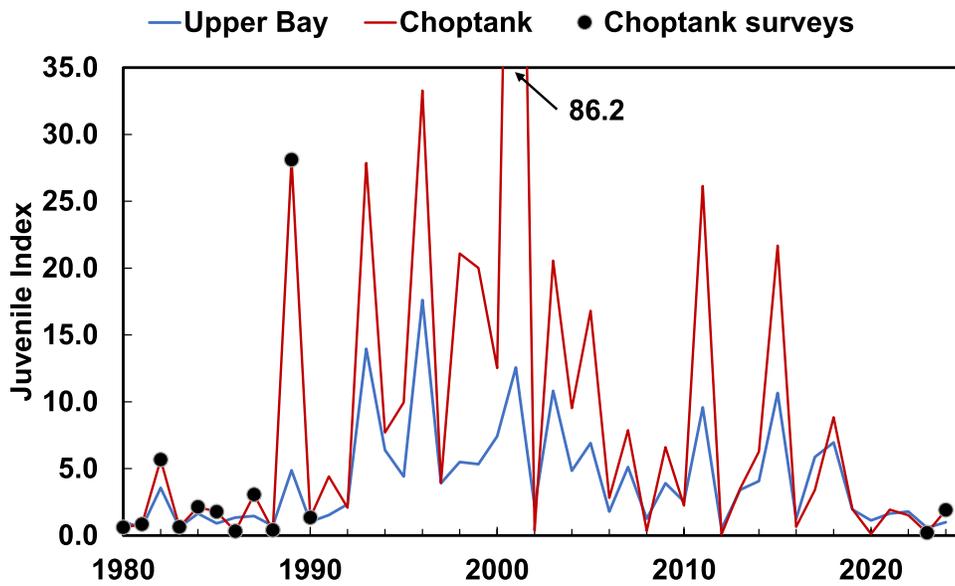
Water temperature and flow are important environmental influences on year-class success of Striped Bass (Maryland Sea Grant, 2009). Survival of eggs and prolarvae is negatively affected by low ( $\leq 11\text{--}12^\circ\text{C}$ ) and high ( $\geq 21^\circ\text{C}$ ) water temperatures (Maryland Sea Grant, 2009; Rutherford et al., 1997; Secor & Houde, 1995; Setzler et al., 1980; Uphoff, 1989, 1992). A large portion of spawning may occur over a few days early in the season, starting at low—sometimes lethal—temperatures in a gamble that subsequent conditions will favor offspring survival (Maryland Sea Grant, 2009). Temperature may also indirectly influence survival via its effect on the timing of zooplankton blooms for first-feeding larvae (match–mismatch hypothesis), while flow has been associated with zooplankton dynamics, nursery volume, location of the nursery, advection from the nursery, water quality, and toxicity of contaminants (Martino & Houde, 2010; Maryland Sea Grant, 2009; Millette

et al., 2020; North & Houde, 2001, 2003; Secor et al., 2017; Shideler & Houde, 2014; Uphoff, 1989, 1992, 2023).

Availability of zooplankton prey is commonly accepted to affect larval Striped Bass nutritional condition, growth, size, survival, and recruitment in the Chesapeake Bay (Cowan et al., 1993; Houde, 2008; Martin et al., 1985; Martino & Houde, 2010; Maryland Sea Grant, 2009; North & Houde, 2001, 2003; Rutherford et al., 1997; Shideler & Houde, 2014). Cowan et al. (1993) identified the density of zooplankton prey during the larval stage as important in modeling variations in recruitment success in the Chesapeake Bay; large fluctuations in simulated recruitment resulted from small changes in the mortality rates of feeding larvae and younger stages (Cowan et al., 1993). Copepods (primarily *Eurytemora*) and cladocerans (primarily *Bosmina*) have been the main items encountered in Chesapeake Bay Striped Bass larval diet studies (Campfield & Houde, 2011; Martin et al., 1985; Martino & Houde, 2010; North & Houde, 2001, 2003; Rutherford et al., 1997; Shideler & Houde, 2014; Uphoff, 1989).

Successful or unsuccessful initial feeding of larvae is one of the foundational hypotheses explaining variations in year-class success of fishes, but a strong connection has not been universally supported by studies (J. T. Anderson, 1988; Hare, 2014; Hjort, 1914; Houde, 2008; Limburg et al., 1997; Nunn et al., 2012). Growth and mortality in larval fish may be linked processes connected to feeding success and expressed as variable sizes at age, stage durations, and stage-specific mortality and as highly variable year-class success (J. T. Anderson, 1988; Cowan et al., 1993; Houde, 2008; Nunn et al., 2012; Rutherford et al., 1997). The concept that larval feeding and size-specific growth and mortality rates positively interact predicts that survival of a cohort is directly related to feeding and growth rates during the prerecruit period (J. T. Anderson, 1988).

We collected Striped Bass postlarvae (larvae that had absorbed their yolk sacs) in the Choptank River during 2023–2024 to assess the extent to which poor success in feeding on zooplankton underlies the recent poor year-class success. We used the distributions of Choptank River larvae by water temperature and specific conductance (hereafter, "conductivity") during the 1980s to design 2023–2024 sampling. Seven years of feeding data from Choptank River surveys in the 1980s were used to develop metrics and criteria with which to judge feeding success of first-feeding Striped Bass postlarvae collected during 2023 and 2024. The 1980s were generally a period of poor year-class success and lower postlarval survival in the Choptank River, but several years of higher postlarval survival were present, as were a moderate year-class (1982) and a strong year-class (1989; Figure 1; Durell & Weedon, 2024; Uphoff, 1989, 1992, 1993). We included White Perch *Morone americana* postlarvae in the 2023–2024 feeding analysis because they shared larval habitat and diet with Striped Bass postlarvae and their year-class success was well correlated with that of Striped Bass (Campfield & Houde, 2011; Cowan et al., 1993; Limburg et al., 1997; North & Houde, 2001, 2003; Uphoff, 2023). White Perch feeding incidence (FI) offered an additional source of information on zooplankton availability, and the degree of contrast in White Perch and Striped Bass postlarval feeding success could provide insight on zooplankton abundance and larval feeding ability.



**Figure 1.** Striped Bass juvenile index (geometric mean) time series for Maryland's portion of the Chesapeake Bay (Upper Bay) and for the Choptank River during the study period. Black dots indicate years when ichthyoplankton surveys sampled postlarvae in the Choptank River.

## METHODS

### Study area

The Striped Bass JI for the Choptank River has undergone a decline in recent year-class success similar to the decline in the Upper Bay JI (Figure 1; Durell & Weedon, 2024). The Choptank River, located on the east side of the Chesapeake Bay, is the fourth largest (1,734 ha) of 12 spawning and larval nursery areas in the Upper Bay; together, these spawning areas comprise an estimated 57,448 ha (Hollis, 1967; Figure 2). Four additional Chesapeake Bay spawning areas are situated in Virginia (Olney et al., 1991). Year-class success of Striped Bass in four Upper Bay spawning and nursery areas (Head of Bay, Potomac River, Nanticoke River, and Choptank River) has been assessed by a shore zone seine survey of young of the year during summer since 1954 (Durell & Weedon, 2024). The Upper Bay JI is the geometric mean from seine samples collected at 22 fixed stations during summer in the four areas combined. The Choptank River has four of these stations (Durell & Weedon, 2024).

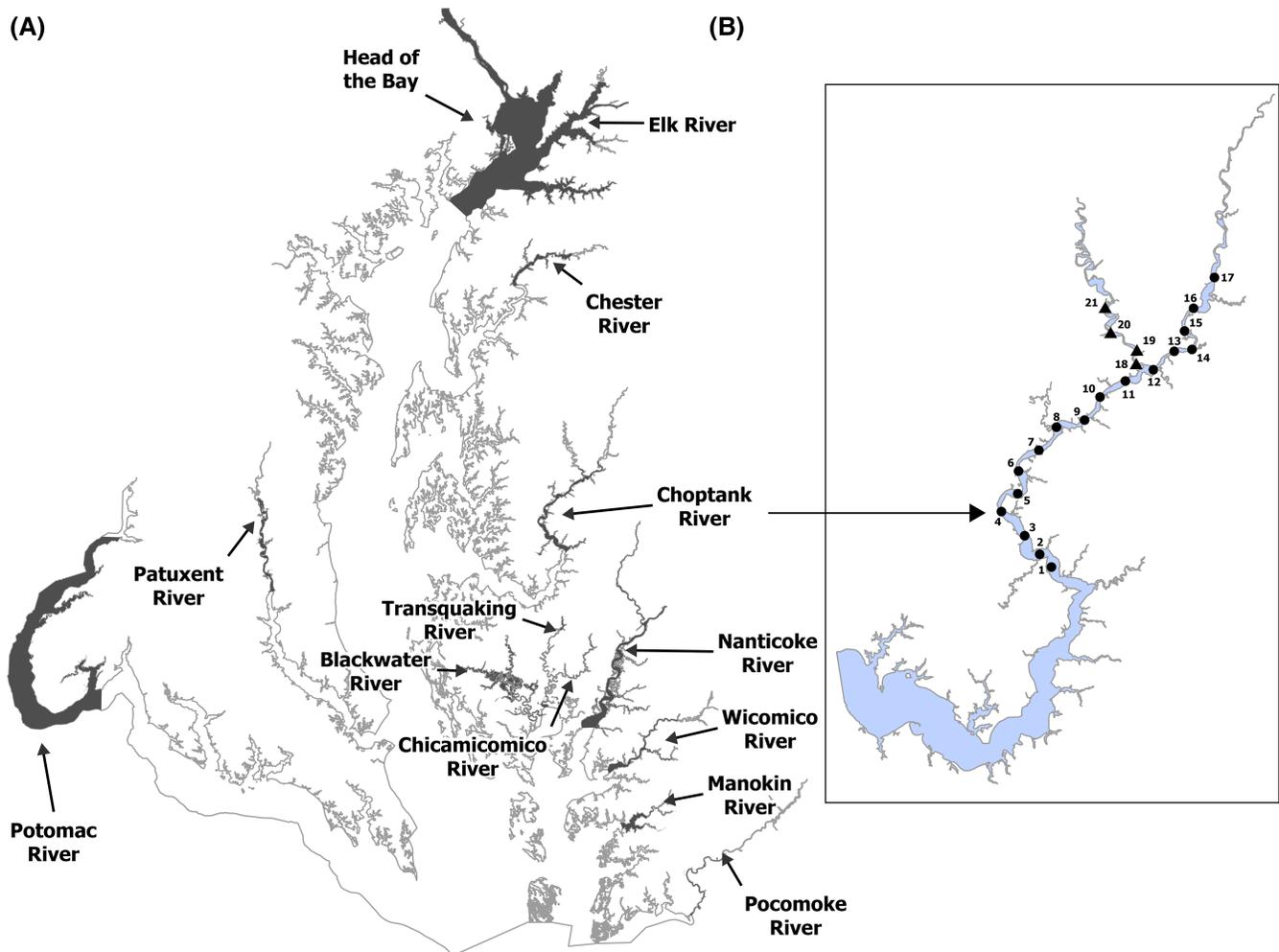
### 1980–1990 collections

Striped Bass eggs, larvae, and early juveniles were sampled from April to mid-June in 1980–1990 with midwater and bottom trawls that were fitted with 0.5-m-diameter, 0.5-mm-mesh plankton nets (8:1 length: opening ratio) as liners in their cod ends. Bottom channel and inshore bottom habitats were sampled with a 3.05-m box trawl made of 1.27-cm stretch-mesh knotless nylon. A 1.53- × 1.53-m midwater trawl was used to sample surface to middepth habitat in the channel; the mouth of the midwater trawl was made of 3.18-cm stretch-mesh nylon, and the remainder of the net was 1.27-cm stretch-mesh nylon. These nets were the same design used by Kernehan et al. (1981) to survey Striped Bass early life stages in the Head of Bay during 1973–1977. All trawls were towed at approximately 1.03 m/s for 2 min in the same

direction as the tidal current. Sampling was conducted during daylight hours, usually in the morning. In 1980–1986, four stations were sampled within the Choptank River Striped Bass spawning area (stations 1, 5, 10, and 16; Figure 2). One site per day was sampled, and all samples collected during a weekly sample interval were taken within 5 d of each other. Two bottom tows (5–8 m deep) and two midwater tows (0.5–1.5 m below the surface) were made in the channel at all four stations. Two inshore bottom trawl tows (1–2 m deep) were made per station except at station 16, where the shallows were not extensive enough. During 1987–1990, the Choptank River spawning area was divided into 21 stations that were 1.61 km apart (Figure 2). Stations were aggregated into four subareas: Tuckahoe Creek and three subareas covering the spawning area of the main stem. These subareas approximated the geographic coverage of the fixed stations in the main stem during 1980–1986 and incorporated an important tributary. The lower nursery area consisted of stations 1–5, the middle area comprised stations 6–11, the upper area encompassed stations 12–17, and Tuckahoe Creek consisted of stations 18–21 (Figure 2). Eight to 12 stations were visited randomly within a week. Each subarea had at least two sites selected randomly per week. A bottom trawl tow and a midwater trawl tow were made in the channel at each visit prior to the last week of May to sample eggs, prolarvae, and postlarvae. An additional inshore tow was made, where possible, from the last week of May through early to mid-June to sample early juveniles (Uphoff, 1989, 1992). Temperature (°C) and salinity (‰) were measured at each site during 1980–1990; conductivity (μS/cm), dissolved oxygen (mg/L), and pH measurements were added after 1986 (Uphoff, 1989, 1992).

### 2023–2024 collections

Sampling for feeding larvae during 2023–2024 was conducted in addition to an egg presence–absence survey that used the 1987–1990 stratified random design (Uphoff, 1993, 2023).



**Figure 2.** Locations of (A) Striped Bass spawning areas in the upper Chesapeake Bay (shaded areas) and (B) sites sampled in the Choptank River. During 1980–1986, sampling occurred at fixed stations 1, 5, 10, and 16. Main-stem sites (dots) and Tuckahoe Creek sites (triangles) were sampled with a stratified random design during 1987–1990.

Different gears were used for sampling eggs (0.5-mm-mesh, 0.5-m-diameter conical net; Uphoff, 2023) and postlarvae (the midwater trawl described for the 1980–1990 collections).

In 2023, Striped Bass postlarvae in the main-stem Choptank River were collected weekly via the same midwater trawl sampling procedures used in the 1980s. Sampling was increased to twice per week during 2024. Water temperature ( $^{\circ}\text{C}$ ), pH, dissolved oxygen (mg/L), conductivity ( $\mu\text{S}/\text{cm}$ ), and salinity ( $\text{‰}$ ) were recorded at each site. Larval feeding samples were placed in jars, preserved with 5–10% formalin, stained with rose bengal dye, and stored for laboratory sorting.

We developed a cumulative distribution of larval catches by  $1^{\circ}\text{C}$  temperature increments from pooled 1980s surveys to aid in (1) targeting when to sample feeding Striped Bass larvae during 2023–2024 and (2) interpreting how much of the postlarval period might have been covered. Uphoff (1989, 1992) estimated that a postlarval period in the Choptank River began 1 week after the midpoint of the peak spawning period (time span to collect 85% of counted eggs) and lasted for the time estimated for growth from 6 to 12 mm total length (TL; Uphoff, 1989, 1992). We were not conducting a full early life stage survey that would provide comparable growth information. Sample

sizes within temperature increments varied, but the trend was expected to be reasonably representative. Sampling for feeding postlarvae in 2023–2024 began a week after major spawning was detected during the egg presence–absence survey and targeted the temperatures at which most larvae were collected.

A similar analysis of the distribution of larvae by 200- $\mu\text{S}/\text{cm}$  conductivity increments was developed to refine where to sample. Measurements were available from the years 1987–1989. Spawning and larval nursery salinity boundaries in the Choptank River varied annually due to flow and precipitation and varied daily with tides. Conductivity potentially offered a fine-scale salinity indicator for locating larvae. Three conductivity increments representing upper, middle, and lower nursery regions were estimated for sampling. Once sampling for feeding larvae began, one site within each conductivity increment would be randomly selected during each sampling date (i.e., three sites per date) using the conductivity observed during the most recent egg survey visit.

#### Laboratory procedures

Organisms were identified to the lowest practical taxonomic level and life stage. The structural definitions of Rogers et al.

(1977) were used to differentiate prolarvae (larvae with yolk), postlarvae (larvae that had absorbed their yolks), and juveniles (postmetamorphic stages). Total lengths of Striped Bass and White Perch prolarvae, postlarvae, and juveniles were measured to the nearest millimeter during 1980–1986 and 2023–2024 and to the nearest tenth of a millimeter during 1987–1990. All Striped Bass and White Perch larvae and juveniles in a sample were measured if there were fewer than 30. Otherwise, a subsample of the first 30 larvae encountered in a Petri dish that had been mixed beforehand was selected. Measurements in tenths of a millimeter were rounded to the nearest millimeter when classifying them into length bins (for example, larvae in the 5-mm bin would consist of those between 4.6 and 5.5 mm). *Morone* individuals with lengths of 11–14 mm collected during 1980–1990 were cleared and stained to aid identification (Fritzsche & Johnson, 1980).

For each measured Striped Bass or White Perch postlarva, the gut was teased apart and the food item or items (cladocerans, copepods, and miscellaneous) in the gut were recorded; cladocerans were most likely to be *Bosmina longirostris* and copepods were most likely to be *Eurytemora carolleeae* based on other Chesapeake Bay studies (Campfield & Houde, 2011; Martin et al., 1985; Martino & Houde, 2010; Millette et al., 2020; North & Houde, 2003; Shideler & Houde, 2014). The copepod category included both adults and copepodites; these stages were not differentiated. The miscellaneous category included unidentifiable contents, debris, and other organisms. In the 1980s, each food type was assigned a score of 0–4 for relative fullness. If food was not present, the gut was assigned a score of 0. If up to one-fourth of the gut contained an item, it was assigned a score of 1. If one-fourth up to one-half of the gut contained an item, it was assigned a score of 2. If one-half up to three-fourths of the gut contained an item, it was assigned a score of 3. If the gut was filled by an item, a score of 4 was assigned. The sum of scores for all items in a gut could not exceed 4.

We re-examined 1980s feeding data for Striped Bass postlarvae that were 10 mm and smaller. This size range represented lengths prior to and once year-class success was set in the 1980s; most postlarval mortality would occur at these sizes (Uphoff, 1989, 1992). In the 1980s, relative abundances of Striped Bass larvae or early juveniles in 1-mm length increments between 10 and 20 mm were strongly correlated with the Choptank River Striped Bass JI, relative abundances of 8–9-mm larvae were moderately correlated with the JI, and relative abundances of 5–7-mm larvae were poorly correlated with the JI (Uphoff, 1989, 1992).

Striped Bass and White Perch larvae that were 10 mm and less in our 2023–2024 collections were identified based on external characteristics. White Perch are more developmentally advanced than Striped Bass until about 7–8 mm (Lippson & Moran, 1974). Striped Bass postlarvae were most often identified by the presence of an oil globule or oil droplets that would be absent in similarly sized White Perch postlarvae (J. H. Uphoff Jr., personal observation). In experiments testing temperature and delayed initial feeding, Striped Bass conserved their oil globules until they reached standard lengths greater than 8 mm (Rogers & Westin, 1981). Much less often, ventral pigment patterns just below the gills were considered when

the presence of oil was uncertain; White Perch often had well-defined, dark-pigment “dashes” that were either aligned (two dashes) or in a box pattern (four dashes), while Striped Bass had irregular pigment blotches in the same area (Uphoff, personal observation). If the two species could not be separated, they were classified as *Morone*.

### Data analysis

Striped Bass postlarvae collected during Choptank River ichthyoplankton surveys in 1981–1986 and 1989–1990 had been examined for feeding success. The only published analysis of 1980s Choptank River feeding data was a summary of Striped Bass postlarval FI on all items and the frequency of occurrence of copepods, cladocerans, or miscellaneous items during 1981–1985 (Uphoff, 1989). We re-examined Choptank River Striped Bass postlarval feeding data as well as growth and mortality estimates from the 1980s surveys (Uphoff, 1989, 1992, 1993) to establish baselines for comparison with the 2023–2024 collections.

Feeding data were re-entered from the original data sheets for re-analysis. Estimates of daily instantaneous mortality ( $Z$ ) and growth ( $G$ ) of postlarvae ( $G$  was based on length of larvae) during 1980–1989 were available from Uphoff (1993). Estimates of  $G$  and  $Z$  for 1990 were available from data summaries in printouts and notes saved from the early 1990s. Multiple Striped Bass postlarval feeding success metrics were estimated and compared with  $Z$  and  $G$  to form criteria for successful and unsuccessful feeding for comparisons with 2023 and 2024 data.

We classified 5–7-mm Striped Bass postlarvae as first-feeding larvae, matching the lengths used by Uphoff (1989). A second group of larger postlarvae (8–10 mm) was also created for comparisons of feeding metrics with first-feeding postlarvae. Uphoff (1989) classified approximately 18% of larvae at 5 mm as postlarvae (the remainder would be prolarvae); 42% of larvae at 6 mm, 89% of larvae at 7 mm, and 100% of 8–10-mm larvae were classified as postlarvae. We estimated the following summary feeding metrics based on food category scores for each size-group of Striped Bass postlarvae collected for feeding analysis during 1980–1990: mean scores of all food items, cladocerans, copepods, and miscellaneous items.

The feeding success scoring system used during 1980–1990 was amenable to estimating FI (proportion with food or a food item) as well because it had a zero category. We estimated FI on all items, cladocerans, copepods, and miscellaneous items. The FI on a given food item category  $x$  (where  $x$  could be all items, cladocerans, copepods, or miscellaneous) was estimated as

$$FI_x = N_x / N_{\text{total}},$$

where  $N_x$  is the number of examined postlarvae with food item  $x$  present and  $N_{\text{total}}$  is the total number of postlarvae examined. The SD of  $FI_x$  was estimated from the normal distribution approximation of the binomial distribution as follows (Ott 1977):

$$SD = \left\{ \left[ FI_x \times (1 - FI_x) \right] / N_{\text{total}} \right\}^{0.5}.$$

We reported the mean score and FI for miscellaneous items but did not include them in subsequent analyses because copepods and cladocerans have been identified in Chesapeake Bay Striped Bass larval studies as the main food items and because the “miscellaneous” category encompassed food and non-food items in unknown proportions. The “all-item” category included miscellaneous items.

Candidate feeding metrics (annual mean feeding score or FI) based on 1980s data for first-feeding postlarvae were compared with each other, estimates of Striped Bass postlarval  $Z$  and  $G$ , and comparable feeding metrics of 8–10-mm Striped Bass postlarvae and 5–7-mm White Perch postlarvae by using correlation analysis (all items, cladocerans, or copepods;  $N=7$  for each 1980s feeding comparison). If feeding scores and FIs on the same items in the 1980s were strongly correlated, then FI was chosen for comparisons of 1980s and 2023–2024 feeding success to eliminate redundancy. Our preference was to use FI because its use was widespread among Striped Bass larval feeding studies, interpretation was straightforward and robust (Baker et al., 2014), and CIs could easily be constructed. Bivariate plots were viewed to ensure that linear analyses would capture basic dynamics. In some cases, asymptotic curvilinear relationships were suspected and an inverse transformation of the  $x$ -axis variable was used to linearize the data (Neter et al., 1985; Sokal & Rohlf, 1981). We classified correlations as strong based on  $|r|$  greater than 0.80 (Ricker, 1975). Weak correlations were indicated by  $|r|$  less than 0.50, and moderate correlations fell in between. We considered strong and moderate correlations to be of interest. Levels of significance are reported, but the potential for biological significance took precedence over  $P$ -values less than 0.05 (D. R. Anderson et al., 2000; Smith, 2020).

We developed criteria for successful feeding of 5–7-mm Striped Bass postlarvae based on feeding levels that were reflected by high or low  $Z$  and  $G$ . Briefly,  $G$  was estimated from the increase in weekly mean lengths during each survey using the exponential growth equation, and the estimate of  $G$  was used to as a relative time scale (days) and applied to the survey abundance-at-length distribution for larvae between 6 and 12 mm to derive  $Z$ . The natural logarithm of abundance in the catch at each millimeter size-class was modeled against relative age for each year to estimate the annual  $Z$  of postlarvae (average for all cohorts within a year) and its SE. Methods used to estimate  $Z$  and  $G$  in the 1980s are presented in more detail in Appendix A and are described by Uphoff (1989, 1992, 1993).

Feeding success metrics for Striped Bass and White Perch postlarvae were of interest, and the same set of metrics that were moderately or strongly associated with  $G$  and  $Z$  for Striped Bass postlarvae was estimated for 5–7-mm White Perch postlarvae during 2023–2024. Contrast or similarity in feeding metrics of these two species could provide insight on zooplankton abundance and postlarval feeding dynamics. High contrast would be indicated by substantially higher feeding success of more advanced White Perch, indicating species-specific feeding capabilities, preferences, and/or competitive advantages. Similar feeding metrics between species (low contrast) would indicate that the zooplankton supply was the main influence on feeding.

The 2023–2024 sampling program was not designed to be a full early life history study; estimates of  $G$  and  $Z$  comparable to

those estimated in the 1980s could not be made. We tested the ratio of feeding sample sizes for the 5–7-mm ( $N_{5-7}$ ) and 8–10-mm ( $N_{8-10}$ ) Striped Bass during the 1980s as a proxy index of survival for 2023–2024 samples. The ratio was estimated as

$$N_{\text{ratio}} = N_{8-10}/N_{5-7}.$$

The  $N_{\text{ratio}}$  time series was compared to  $Z$  for years in common during the 1980s using correlation ( $N=7$ ) to judge whether it might be a reasonable proxy index to categorize  $Z$  as high or low in 2023–2024.

We also tested for associations of initial Striped Bass larval relative abundance with feeding metrics in the 1980s to explore density-dependent feeding success. Total larval catches in the annual length-frequency distributions peaked at 6 mm in the 1980s surveys (Uphoff, 1989, 1993). We  $\log_e$  transformed the catches of 6-mm larvae ( $\log_e N_6$ ) for our index of initial abundance of first-feeding larvae to linearize them, and we correlated them with feeding metrics that were best associated with  $Z$  and  $G$ . Total annual survey catches were adjusted for differences in sampling effort (total number of trawls) among surveys before  $\log_e$  transformation. Estimates of adjusted catches were available for 1980–1990 from retained notes. Ideally, we would have used 5–7-mm larval catches, but those estimates were not available and data could not be reanalyzed to produce new estimates (the data resided in an unsupported format that was no longer documented).

We also correlated  $\log_e N_6$  during 1980–1990 with a Choptank River index of Striped Bass spawning status based on spatial and temporal dispersion ( $Ep$ ; the proportion of plankton net samples with eggs; Uphoff, 1993, 1997, 2023). Uphoff (2023) used long-term baywide juvenile indices and  $Ep$  from Upper Bay spawning areas to address the hypothesis that the collapse of Chesapeake Bay Striped Bass recruitment that began in the 1970s and lasted into the 1980s was solely driven by recruitment overfishing. This hypothesis was not well supported for the whole period, but poorer than expected JIs—among the lowest of the time series—coincided with depleted baywide  $Ep$  during 1982–1988 (Uphoff, 2023). Estimated  $Ep$  in the Choptank River during 1980–1990 was depleted during 1982–1988 (as described above) but not in the remainder of the time series (Uphoff, 1993, 2023). The range in  $Ep$  provided an opportunity to examine the association of spawning status with the initial abundance of larvae entering or at the first-feeding stage.

Fisheries management responds to the strength of the year-class, so we correlated the feeding metrics that were most strongly associated with  $G$  and  $Z$  in the Choptank River with the Choptank River JI during the 1980s and 2023–2024 to examine the strength and direction of their associations with this indicator of year-class success.

## RESULTS

### 1980s feeding metrics

Feeding metrics could be estimated for 1981–1985 and 1989–1990; annual sample sizes were 104–390 for 5–7-mm Striped Bass postlarvae and 19–314 for 8–10-mm postlarvae (Table 1). Sample size of first-feeding larvae was very low in 1986 ( $N=10$ ), so that year was dropped from analysis.

**Table 1.** Choptank River Striped Bass postlarval feeding metrics and statistics, by size-class, during 1981–1985 and 1989–1990. Abbreviations are as follows: TL = total length, clad = cladoceran, mean = mean feeding score, FI = feeding incidence, cope = copepod, All = all items, Misc = miscellaneous items,  $N_{ratio}$  = ratio of  $N$  between the 8–10-mm and 5–7-mm length-classes,  $G$  = instantaneous daily growth rate of postlarvae, and  $Z$  = instantaneous daily mortality rate of postlarvae.

Size-class and metric	Year						
	1981	1982	1983	1984	1985	1989	1990
<b>5–7 mm TL</b>							
Clad mean	1.10	1.20	0.60	0.40	0.20	1.00	0.30
FI <sub>clad</sub>	0.55	0.63	0.31	0.33	0.12	0.57	0.22
FI <sub>clad</sub> SD	0.03	0.03	0.05	0.03	0.03	0.03	0.02
Cope mean	0.20	0.50	0.20	0.60	1.70	0.40	0.70
FI <sub>cope</sub>	0.09	0.26	0.11	0.24	0.70	0.22	0.38
FI <sub>cope</sub> SD	0.01	0.02	0.03	0.03	0.04	0.03	0.03
All mean	1.30	1.70	1.20	1.10	1.90	1.50	1.20
All FI	0.64	0.75	0.62	0.55	0.80	0.69	0.58
All FI SD	0.02	0.02	0.05	0.03	0.04	0.03	0.03
Misc mean	0.06	0.05	0.37	0.07	0.11	0.08	0.22
Misc FI	0.05	0.05	0.16	0.06	0.11	0.15	0.19
Misc FI SD	0.01	0.02	0.08	0.02	0.04	0.02	0.02
$N$	390	321	104	287	104	202	276
<b>8–10 mm TL</b>							
Clad mean	0.78	1.51	1.63	1.29	0.00	1.15	0.34
FI <sub>clad</sub>	0.42	0.71	0.74	0.61	0.00	0.64	0.27
FI <sub>clad</sub> SD	0.05	0.04	0.10	0.05		0.03	0.03
Cope mean	0.74	1.24	0.52	0.93	1.60	0.84	1.13
FI <sub>cope</sub>	0.40	0.62	0.16	0.46	0.75	0.46	0.58
FI <sub>cope</sub> SD	0.05	0.04	0.08	0.05	0.05	0.03	0.03
All mean	1.72	2.78	1.45	2.33	1.71	2.16	1.82
All FI	0.76	0.89	1.00	0.82	0.83	0.86	0.87
All FI SD	0.05	0.03	0.00	0.04	0.04	0.02	0.02
Misc mean	0.20	0.05	0.21	0.11	0.11	0.16	0.35
Misc FI	0.16	0.05	0.16	0.06	0.11	0.15	0.25
Misc FI SD	0.04	0.02	0.08	0.02	0.00	0.02	0.03
$N$	83	143	19	103	75	314	219
$N_{ratio}$	0.21	0.44	0.18	0.36	0.72	1.55	0.79
$G$	0.030	0.034	0.034	0.034	0.044	0.031	0.038
$Z$	0.199	0.096	0.160	0.196	0.055	0.065	0.044

Mean feeding scores of 5–7-mm Striped Bass postlarvae ranged from 1.10 to 1.90 for all items, from 0.20 to 1.20 for cladocerans, from 0.20 to 1.70 for copepods, and from 0.05 to 0.37 for miscellaneous items (Table 1). Feeding incidences ranged from 0.55 to 0.80 for all items (all-item FI), from 0.12 to 0.63 for cladocerans (FI<sub>clad</sub>), from 0.09 to 0.70 for copepods (FI<sub>cope</sub>), and from 0.05 to 0.19 for miscellaneous items (Table 1). Mean feeding scores and FIs were strongly correlated ( $r = 0.97$ – $0.99$ ,  $P \leq 0.0002$ ) for all items, cladocerans, and copepods. Based on this strong agreement and preference for FI metrics, we dropped feeding scores from further analysis.

Higher FI<sub>clad</sub> ( $>0.50$ ) occurred during 1981, 1982, and 1989, whereas FI<sub>clad</sub> values for the remaining years were lower ( $<0.35$ ). Higher FI<sub>cope</sub> ( $>0.35$ ) occurred during 1985 and 1990; mid-range FI<sub>cope</sub> (0.22–0.26) occurred in 1982, 1984, and 1989; and lower FI<sub>cope</sub> ( $<0.11$ ) occurred during the remaining years. Miscellaneous FI was low relative to the other two item-specific categories and only exceeded one of them (FI<sub>cope</sub>) in 1983; miscellaneous FI was close to FI<sub>clad</sub> in 1985 and 1990 (Table 1).

The all-item FI for 5–7-mm postlarvae was poorly correlated with FI<sub>clad</sub> ( $r = 0.07$ ,  $P = 0.87$ ) and modestly correlated with FI<sub>cope</sub> ( $r = 0.55$ ,  $P = 0.20$ ; Figure 3A). Inspection of the bivariate plot of FI<sub>clad</sub> and FI<sub>cope</sub> suggested a negative curvilinear association between them, and an inverse transformation of FI<sub>clad</sub> provided a strong fit ( $r = 0.90$ ,  $P = 0.005$ ; Figure 3B).

#### 1980s estimates of $G$ and $Z$

During 1980–1990, estimates of  $G$  ranged from 0.030 to 0.044, and the three highest estimates (1985, 1986, and 1990) were between 0.038 and 0.044. These highest estimates could be differentiated from five of the lower estimates (range = 0.030–0.034) based on 95% CI overlap (Figure 4). Three estimates of  $G$  (1984, 1987, and 1988) could not be differentiated as high or low (Table 1; Figure 4).

Estimates of  $G$  were weakly correlated with the all-item FI ( $r = 0.41$ ,  $P = 0.36$ ) and strongly correlated with item-specific estimates of FI. The correlation was negative for FI<sub>clad</sub> ( $r = -0.83$ ,  $P = 0.02$ ) and positive for FI<sub>cope</sub> ( $r = 0.94$ ,  $P = 0.002$ ; Figure 5). Lower growth rates ( $G \leq 0.034$ ) occurred when FI<sub>clad</sub> was greater than 0.32 and when FI<sub>cope</sub> was less than 0.38 (Table 1; Figure 5).

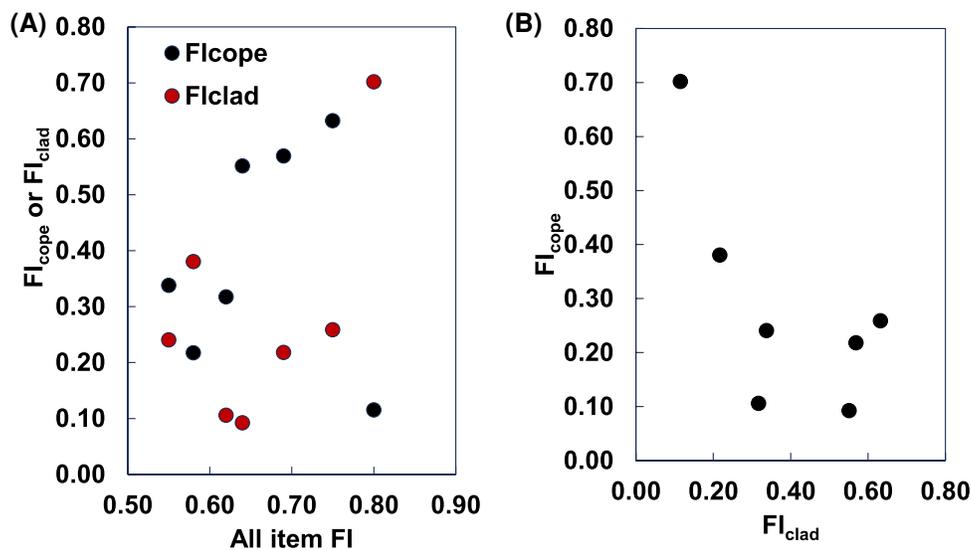
During 1980–1990, estimates of  $Z$  ranged from 0.04 to 0.22 (Table 1; Figure 6). There were four estimates of higher  $Z$  (0.16–0.22) and seven estimates of lower  $Z$  (0.04–0.11). Four of the lower estimates could be separated from the higher estimates based on 95% CI overlap. Two estimates (1986 and 1988) could not be separated from high or low estimates. There were three high estimates of  $Z$  (1981, 1983, and 1984) within the years with FI estimates, and the available lower estimates did not overlap the high estimates (Table 1; Figure 6).

The correlation of  $G$  with  $Z$  was modest and positive during 1980–1990 in the Choptank River ( $r = 0.57$ ,  $P = 0.066$ ). Estimates of  $Z$  were modestly and negatively correlated with the all-item FI ( $r = -0.50$ ,  $P = 0.250$ ). Inspection of the plot of  $Z$  and FI<sub>cope</sub> suggested a negative curvilinear relationship, and an inverse transformation of FI<sub>cope</sub> provided a moderate fit ( $r = 0.74$ ,  $P = 0.058$ ; Figure 7B). Points representing higher  $Z$  occurred exclusively when FI<sub>cope</sub> was 0.11 or less. When FI<sub>cope</sub> was between 0.22 and 0.24, there was one estimate of higher  $Z$  and two estimates of lower  $Z$ . Lower estimates of  $Z$  occurred exclusively when FI<sub>cope</sub> was 0.38 or more. The correlation of FI<sub>clad</sub> with  $Z$  was weak ( $r = 0.27$ ,  $P = 0.56$ ; Figure 7A).

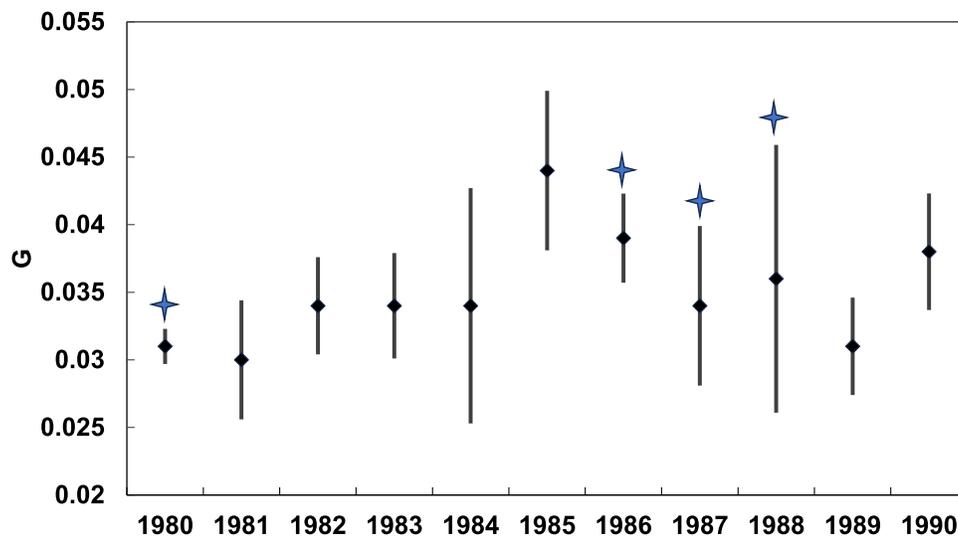
The plot of the  $N_{ratio}$  and  $Z$  during 1980–1990 suggested a negative curvilinear association, and an inverse transformation provided a strong fit ( $r = 0.81$ ,  $P = 0.028$ ; Figure 8). We used  $1/N_{ratio}$  as a proxy index for  $Z$  to compare 2023–2024 estimates with 1980s estimates. Low estimates of  $Z$  (0.04–0.10) fell between  $1/N_{ratio}$  estimates of 0.64 and 2.25, and high estimates of  $Z$  (0.16–0.24) fell between  $1/N_{ratio}$  estimates of 2.78 and 5.46 (Figure 8).

#### 1980s correlations of feeding incidences among size-classes and between *Morone* species

The all-item FI for 5–7-mm Striped Bass postlarvae was poorly correlated with the all-item FI for 8–10-mm postlarvae ( $r = -0.03$ ,  $P = 0.95$ ). On an item-specific basis, the FIs of first-feeding and more advanced Striped Bass postlarvae were moderately associated for cladocerans ( $r = 0.68$ ,  $P = 0.092$ )



**Figure 3.** (A) Plot of feeding incidence (FI) on all items (All item FI) against FI on cladocerans ( $FI_{\text{clad}}$ ) or copepods ( $FI_{\text{cope}}$ ) for 5–7-mm-total length Striped Bass postlarvae during 1981–1985 and 1989–1990 in the Choptank River and (B) plot of  $FI_{\text{cope}}$  against  $FI_{\text{clad}}$  for 5–7-mm-total length Striped Bass postlarvae during 1981–1985 and 1989–1990 in the Choptank River.



**Figure 4.** Annual estimates of the daily instantaneous growth rate ( $G$ ; diamonds) of 6–12-mm-total length Striped Bass postlarvae and their 95% CIs (lines) during 1980–1990. A star indicates that feeding incidence was not estimated for that year.

and strongly associated for copepods ( $r=0.83$ ,  $P=0.022$ ; Figure 9). Two years (1981 and 1985) exhibited lower  $FI_{\text{clad}}$  as length-group progressed from smaller to larger, but the remaining years exhibited an increase in  $FI_{\text{clad}}$  (Table 1). Estimates of  $FI_{\text{cope}}$  always increased as the Striped Bass postlarval size-class increased (Table 1). Differences in item-specific FIs between size-classes ( $[FI_x \text{ for } 5\text{--}7\text{-mm postlarvae}] - [FI_x \text{ for } 8\text{--}10\text{-mm postlarvae}]$ ) were  $-0.42$  to  $0.12$  for cladocerans and  $-0.36$  to  $-0.05$  for copepods.

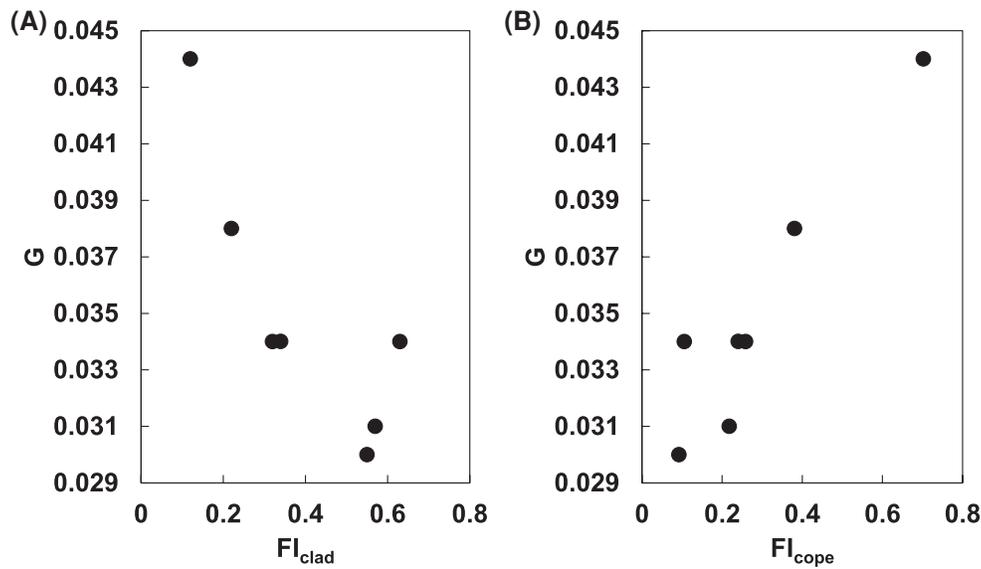
Annual sample sizes for 5–7-mm White Perch postlarvae were 130–753 during the 1980s (Table 2). Analyses for White Perch were confined to FIs on cladocerans ( $WPF_{\text{clad}}$ ) and copepods ( $WPF_{\text{cope}}$ ) since these were the 5–7-mm Striped Bass metrics that were best associated with  $G$  and  $Z$ . Feeding

incidence of 5–7-mm White Perch ranged from 0.04 to 0.75 for  $WPF_{\text{clad}}$  and from 0.10 to 0.71 for  $WPF_{\text{cope}}$  (Table 2).

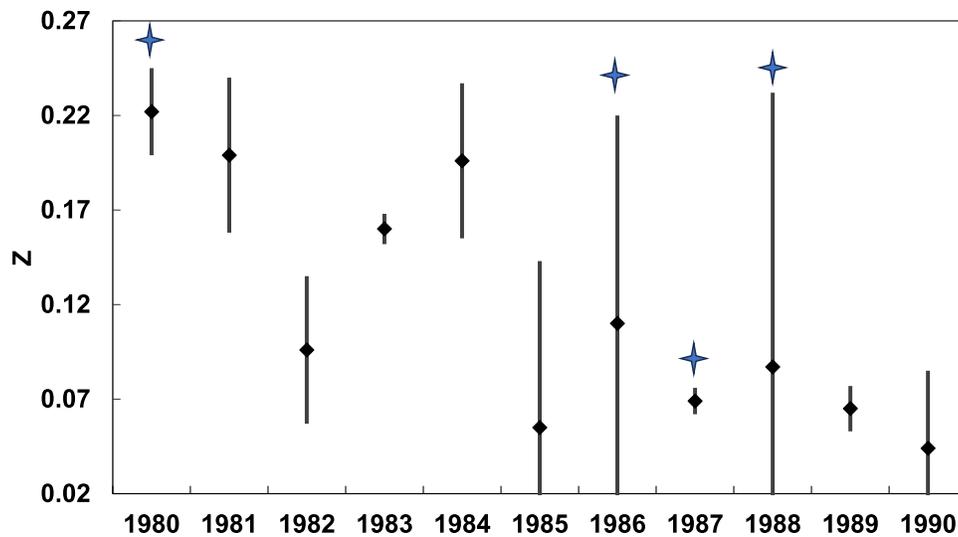
Positive and strong correlations were found between  $WPF_{\text{clad}}$  and Striped Bass  $FI_{\text{clad}}$  ( $r=0.85$ ,  $P=0.0146$ ) and between  $WPF_{\text{cope}}$  and Striped Bass  $FI_{\text{cope}}$  ( $r=0.96$ ,  $P=0.0006$ ) for 5–7-mm postlarvae (Figure 10). Both correlations indicated that trends in FI on these items would likely be similar between 5–7-mm postlarvae of these species. Differences in item-specific FIs ( $[Striped \text{ Bass } FI_x] - [WPF_{\text{clad}}]$ ) were  $-0.20$  to  $0.13$  for cladocerans and  $-0.17$  to  $-0.01$  for copepods.

#### 1980s feeding criteria

Criteria for judging  $FI_{\text{cope}}$  and  $FI_{\text{clad}}$  of first-feeding Striped Bass postlarvae in 2023–2024 as high or low were developed



**Figure 5.** Feeding incidences on (A) cladocerans ( $FI_{clad}$ ) and (B) copepods ( $FI_{cope}$ ) for 5–7-mm-total length Striped Bass postlarvae plotted against the daily instantaneous growth rate ( $G$ ) for postlarvae during 1981–1985 and 1989–1990.

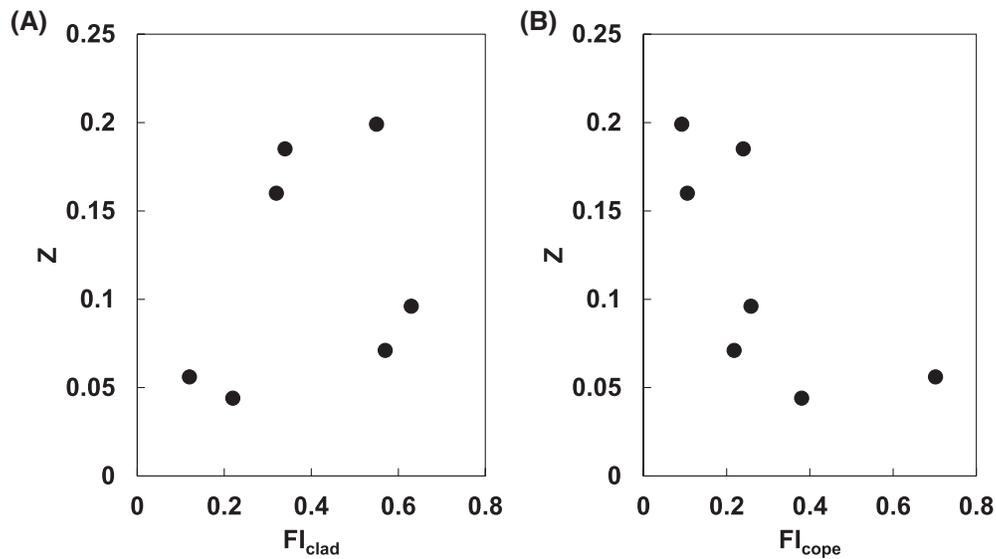


**Figure 6.** Annual estimates of the daily instantaneous mortality rate ( $Z$ ; diamonds) of 6–12-mm-total length Striped Bass postlarvae and their 95% CIs (lines) during 1980–1990. A star indicates that feeding incidence was not estimated for that year.

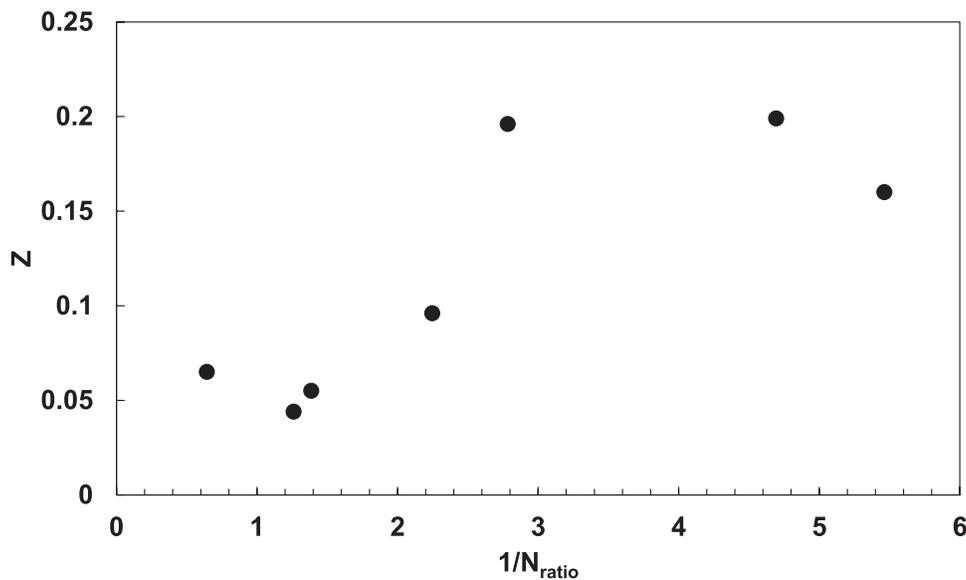
from the feeding studies conducted during the 1980s. Lower growth rates ( $G \leq 0.034$ ) occurred when  $FI_{cope}$  was less than 0.38 (Table 3). High  $Z$  occurred exclusively when  $FI_{cope}$  was 0.11 or less;  $FI_{cope}$  between 0.22 and 0.24 exhibited one estimate of high  $Z$  and two estimates of low  $Z$ ; and low estimates of  $Z$  occurred when  $FI_{cope}$  was 0.38 or more. However, 2 of 4 years exhibiting low  $Z$  (1982 and 1989) in the Choptank River displayed a combination of moderate  $FI_{cope}$  (0.26 and 0.22, respectively) and high  $FI_{clad}$  ( $\geq 0.57$ ). High  $Z$  in 1984 occurred under moderate  $FI_{cope}$  (0.24) coupled with the third-lowest estimate of  $FI_{clad}$  (0.34). High  $Z$  occurred when  $FI_{clad}$  was between 0.31 and 0.55, coupled with low  $FI_{cope}$  between 0.09 and 0.24 (Table 3).

#### 1980s first-feeding larval relative abundance and feeding incidence

During 1980–1990, the effort-adjusted  $\log_e$  transformed catches of 6-mm Striped Bass larvae ( $\log_e N_6$ ) ranged from 4.16 (64 larvae in 1983) to 8.06 (3,176 larvae in 1989; Table 4). Estimates of  $FI_{cope}$  were poorly correlated with  $\log_e N_6$  ( $r = 0.33$ ,  $P = 0.47$ ), but  $FI_{clad}$  estimates were positively and moderately correlated with  $\log_e N_6$  ( $r = 0.72$ ,  $P = 0.07$ ; Figure 11). Estimates of  $Ep$  in the Choptank River during 1980–1990 ranged from 0.36 to 0.77 (Table 4). Estimates of  $\log_e N_6$  were moderately correlated with  $Ep$  ( $r = 0.74$ ,  $P = 0.009$ ), indicating that the initial abundance of feeding larvae could have reflected spawning status during 1980–1990.



**Figure 7.** Feeding incidences on (A) cladocerans ( $FI_{clad}$ ) and (B) copepods ( $FI_{cope}$ ) for 5–7-mm-total length Striped Bass postlarvae plotted against the daily instantaneous mortality rate ( $Z$ ) for postlarvae during 1981–1985 and 1989–1990.



**Figure 8.** Estimates of  $1/N_{ratio}$  plotted against the daily instantaneous mortality rate ( $Z$ ) of postlarval Striped Bass, where  $N_{ratio} = (\text{number of 8–10-mm-total length postlarvae examined for gut contents}) \div (\text{number of 5–7-mm-total length postlarvae examined for gut contents})$ , during 1981–1985 and 1989–1990.

#### 1980s distribution of larvae by water temperature and conductivity

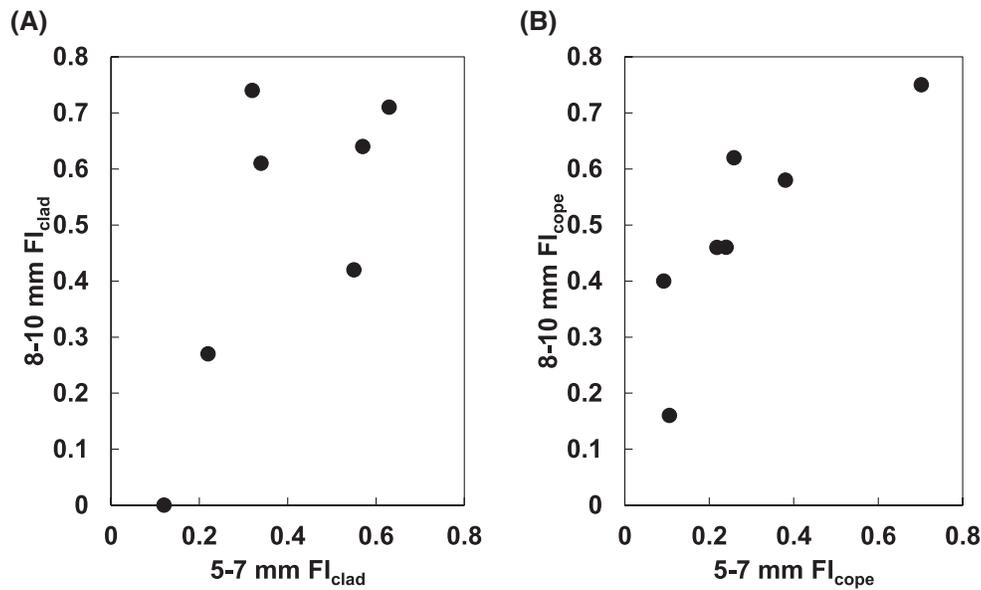
Cumulative counts of Striped Bass larvae in the Choptank River during 1980–1989 (42,562 larvae) exhibited their greatest increase between 15°C and 17°C, then exhibited a lesser but steady increase through 20°C (Figure 12A). A total of 2,054 samples were taken, and 612 contained larvae. Sampling for feeding postlarvae in 2023–2024 was (1) targeted to begin when temperatures were near or greater than 15°C after a major spawn was detected during the egg survey and (2) targeted to end when temperatures were around 20°C.

Striped Bass larvae were collected at conductivities between 98 and 8,270  $\mu\text{S}/\text{cm}$  during 1987–1989 (26,727 larvae and 503

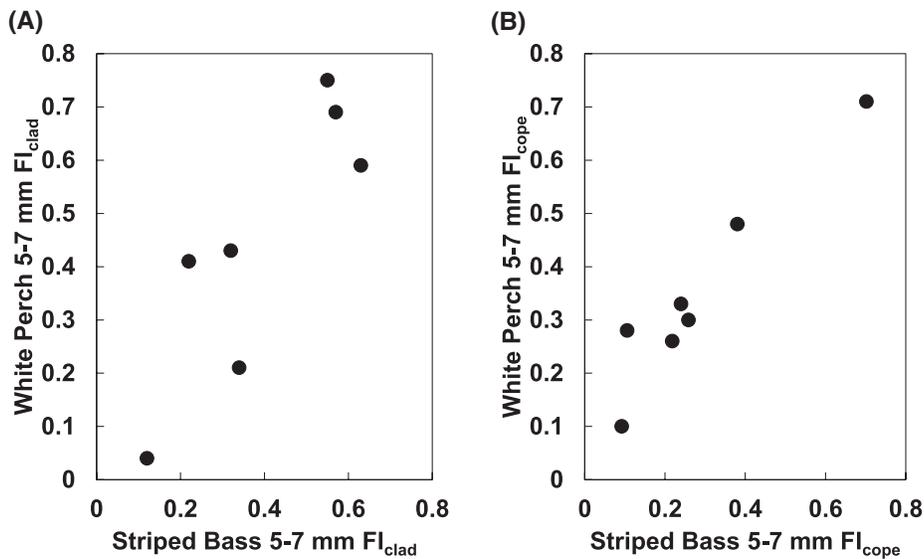
samples). Most larvae (96%) were collected when conductivities were at or less than 2,000  $\mu\text{S}/\text{cm}$  (25,732 larvae and 383 samples); therefore, we based sampling during 2023–2024 on a cumulative distribution truncated at 2,000  $\mu\text{S}/\text{cm}$  (Figure 12B). The cumulative distribution rose rapidly between 200 and 1,000  $\mu\text{S}/\text{cm}$ , and we planned 2023–2024 sampling to target this range (Figure 12B).

#### 2023–2024 Striped Bass and White Perch postlarval collections

We collected nine samples from the Choptank River across three dates in 2023 (April 13, 19, and 25). Water temperatures ranged between 19.5°C and 20.0°C. Thirty-one 5–7-mm-TL



**Figure 9.** Feeding incidences on (A) cladocerans (FI<sub>clad</sub>) and (B) copepods (FI<sub>cope</sub>) for 5–7-mm-total length Striped Bass postlarvae plotted against the corresponding values for 8–10-mm-total length postlarvae during 1981–1985 and 1989.



**Figure 10.** Feeding incidences on (A) cladocerans (FI<sub>clad</sub>) and (B) copepods (FI<sub>cope</sub>) for 5–7-mm-total length Striped Bass postlarvae plotted against the corresponding values for 5–7-mm-total length White Perch postlarvae during 1981–1985 and 1989–1990.

Striped Bass postlarvae and thirty-two 5–7-mm prolarvae were collected, as were thirty-nine 8–10-mm-TL Striped Bass postlarvae and sixty-seven 5–7-mm White Perch postlarvae (Table 5). First-feeding postlarvae (5–7 mm) were present in six of the nine samples. Striped Bass with lengths of 8–10 mm were present in three of the nine samples, and all were postlarvae; 5–7-mm White Perch postlarvae were present in all but one sample.

We collected 18 samples from the Choptank River across six dates in 2024 (April 18, 22, 25, and 29; May 2 and 6). Water temperatures ranged between 17.2°C and 22.0°C. A total of 1,215 5–7-mm Striped Bass postlarvae were collected, and 414 were examined for gut contents; an additional 531 prolarvae were collected in this length range. We collected 629 8–10-mm Striped Bass postlarvae, and 201 were examined for gut

contents; prolarvae were not present in this size-group. There were 1,024 5–7-mm White Perch postlarvae collected, and 348 were examined for gut contents (Table 5).

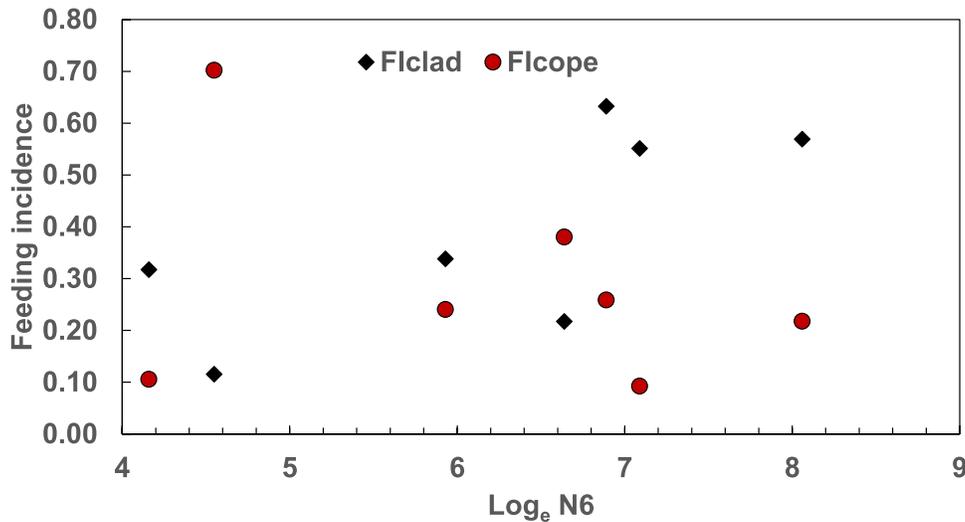
Dry conditions in 2023 resulted in higher than anticipated conductivity, and sampling deviated from the target conductivity range because a high conductivity gradient provided limited spacing of samples; average river discharge at the U.S. Geological Survey’s Choptank River gauge at Greensboro, Maryland (station 01491000), was 66% of the 1957–2020 average for March–April (Uphoff et al., 2024). Seventeen 5–7-mm Striped Bass postlarvae were collected within the 200–1,000-μS/cm target conductivity range (stations 13–16); 13 were collected at conductivities between 1,000 and 2,000 μS/cm (stations 9–11); and 1 was collected at 2,580 μS/cm (station 11).

**Table 2.** Choptank River 5–7-mm-total length White Perch postlarval feeding metrics and statistics during 1981–1985 and 1989–1990. Abbreviations are as follows: WPFI = White Perch feeding incidence, clad = cladoceran, and cope = copepod.

Metric	Year						
	1981	1982	1983	1984	1985	1989	1990
WPFI <sub>clad</sub>	0.75	0.59	0.43	0.21	0.04	0.69	0.42
WPFI <sub>clad</sub> SD	0.02	0.02	0.02	0.02	0.02	0.02	0.04
WPFI <sub>cope</sub>	0.10	0.30	0.28	0.33	0.71	0.26	0.48
WPFI <sub>cope</sub> SD	0.02	0.02	0.02	0.02	0.04	0.02	0.04
N	373	405	435	753	130	363	176

**Table 3.** Classification of daily instantaneous growth (G) and mortality (Z) rates based on copepod feeding incidence (FI) or the combination of copepod FI and cladoceran FI derived from 1981–1985 and 1989–1990 surveys.

Rate or FI	G and Z classification	
	Low	High
G		
Copepod FI	≤0.38	>0.38
Z		
Copepod FI	≥0.38	≤0.11
Copepod FI and cladoceran FI	0.22–0.26	0.24
	≥0.57	<0.34



**Figure 11.** Feeding incidence on copepods (FI<sub>cope</sub>) or cladocerans (FI<sub>clad</sub>) for first-feeding Striped Bass plotted against the log<sub>e</sub> transformed survey abundance of 6-mm-total length Striped Bass larvae (log<sub>e</sub>N<sub>6</sub>) during the 1980s.

Twenty-six 8–10-mm Striped Bass postlarvae were collected within the target conductivity range and 13 were collected at conductivities between 1,000 and 2,000  $\mu\text{S}/\text{cm}$ .

Average river discharge at the Choptank River gauge during March–April 2024 was 183% of the 1957–2020 average, indicating wet conditions. First-feeding Striped Bass were present in all but one sample during 2024; 950 were collected within the target conductivity range in 11 tows (stations 2–11); 149 were collected in three tows at conductivities between 141 and 186  $\mu\text{S}/\text{cm}$  (stations 9 and 10); and 116 were collected in four tows at 1,194–1,480  $\mu\text{S}/\text{cm}$  (stations 2–7). Striped Bass with lengths of 8–10 mm were present in half of the tows; none were captured in conductivities between 141 and 186  $\mu\text{S}/\text{cm}$ , 578 were collected within the target conductivity range (nine tows), and 51 were collected at 1,194–1,480  $\mu\text{S}/\text{cm}$  (four tows). White Perch with lengths of 5–7 mm were present in all but one tow; 399 were collected at conductivities between 141 and 186  $\mu\text{S}/\text{cm}$ , 588 were caught in the target conductivity range, and 38 were captured between 1,194 and 1,480  $\mu\text{S}/\text{cm}$ .

### 2023–2024 feeding incidences and Striped Bass postlarval mortality

Based on criteria developed from Choptank River surveys during the 1980s, FI<sub>cope</sub> of 5–7-mm Striped Bass postlarvae was well above the successful copepod feeding criteria for Z and G in 2023

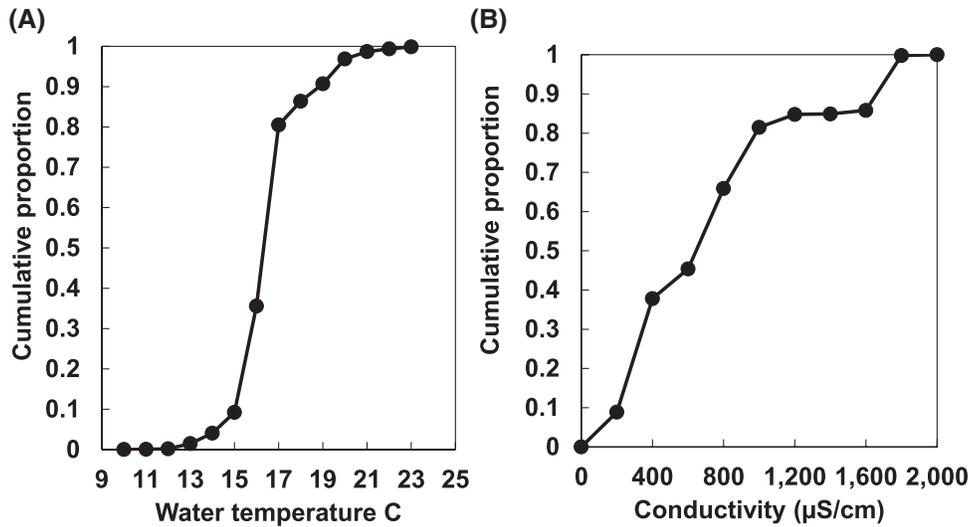
and FI<sub>clad</sub> was below the poor feeding criterion for Z (Table 5). In 2024, FI<sub>cope</sub> of 5–7-mm Striped Bass postlarvae was slightly above the successful copepod feeding criterion for Z and G and FI<sub>clad</sub> was well above the successful feeding criterion for Z (Table 5).

During 2023–2024, FI<sub>cope</sub> and FI<sub>clad</sub> for 8–10-mm Striped Bass postlarvae were well above those for 5–7-mm postlarvae (Table 5). In 2023, 5–7-mm White Perch postlarvae were over twice as successful at feeding on cladocerans and slightly more successful at feeding on copepods than were 5–7-mm Striped Bass postlarvae. Estimates of WPFI<sub>clad</sub> and WPFI<sub>cope</sub> were similar to Striped Bass FI<sub>clad</sub> and FI<sub>cope</sub> during 2024 (Table 5).

Estimates of FI<sub>cope</sub> for 5–7-mm Striped Bass postlarvae in 2023 and 2024 were the second and third highest of the full time series, respectively (1980s and 2023–2024,  $N=9$ ; Figure 13). The estimate of FI<sub>clad</sub> was low in 2023, but the 2024 estimate was the second highest of the time series (Figure 13).

The FI<sub>cope</sub> of 8–10-mm Striped Bass postlarvae in 2023 was tied for highest in the full time series, and FI<sub>cope</sub> in 2024 was the second highest (Figure 14). The estimate of FI<sub>clad</sub> in 2023 was the third lowest, and FI<sub>clad</sub> in 2024 was the highest (Figure 14).

The value of  $1/N_{\text{ratio}}$  in 2023 was 0.79, which was below the criterion ( $\leq 2.25$ ) that indicated low Striped Bass postlarval Z and was the second lowest observed among the years available (Figure 15). The  $1/N_{\text{ratio}}$  in 2024 was 2.08, which was near but below the criterion that indicated low Z (Figure 15).



**Figure 12.** Cumulative proportion of Striped Bass larvae (prolarvae and postlarvae), based on counts, collected in Choptank River ichthyoplankton surveys by (A) 1°C temperature increments during 1980–1989 and (B) 200-µS/cm conductivity increments during 1987–1989.

**Table 4.** Number of trawls (*N*), adjustment factor (proportion = [*N* in year *t*]/[*N* in the year with the lowest effort]), log<sub>e</sub> transformed adjusted abundance of 6-mm Striped Bass larvae in year *t* (log<sub>e</sub>*N*<sub>6</sub>) during 1980–1990, and the proportion of samples with eggs (*Ep*).

Year	<i>N</i>	Adjustment	Log <sub>e</sub> <i>N</i> <sub>6</sub>	<i>Ep</i>
1980	151	0.87	7.24	0.65
1981	161	0.82	7.09	0.66
1982	132	1.00	6.89	0.52
1983	132	1.00	4.16	0.36
1984	154	0.86	5.93	0.36
1985	154	0.86	4.55	0.49
1986	194	0.68	2.48	0.43
1987	186	0.71	5.6	0.56
1988	201	0.66	4.47	0.45
1989	180	0.73	8.06	0.77
1990	194	0.68	6.64	0.76

Estimates of WPF<sub>clad</sub> in 2023–2024 were in the mid-range of the full time series for White Perch (Figure 16). Both estimates of WPF<sub>cope</sub> were very close to the highest of the time series (Figure 16).

**Striped Bass juvenile indices and first-feeding success**

The Choptank River JI was poorly correlated with FI<sub>cope</sub> (*r* = -0.22, *P* = 0.607) and was modestly correlated with FI<sub>clad</sub> (*r* = 0.50, *P* = 0.202) of first-feeding Striped Bass postlarvae during 1981–1985, 1989–1990, and 2023–2024. Years of high FI for first-feeding larvae and low postlarval *Z* (or its proxy index, 1/*N*<sub>ratio</sub>) did not always translate to better year-class success.

**DISCUSSION**

**Striped Bass postlarval feeding incidence, growth, mortality, and year-class success**

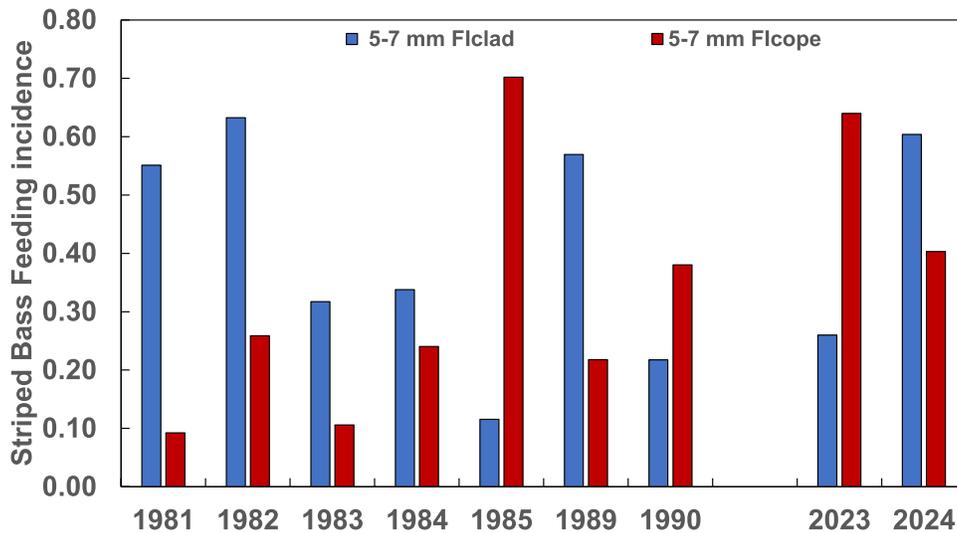
Feeding incidence of first-feeding Striped Bass postlarvae on copepods in the Choptank River during 2023 was high and

**Table 5.** Choptank River Striped Bass and White Perch postlarval feeding metrics and statistical characteristics, by size-class, during 2023–2024. Bold italic values indicate that successful feeding incidence (FI) criteria for daily instantaneous growth and mortality rates were met for first-feeding Striped Bass postlarvae. Criteria are presented in Table 3. Abbreviations are as follows: TL = total length, clad = cladoceran, cope = copepod, and *N* = number of guts examined.

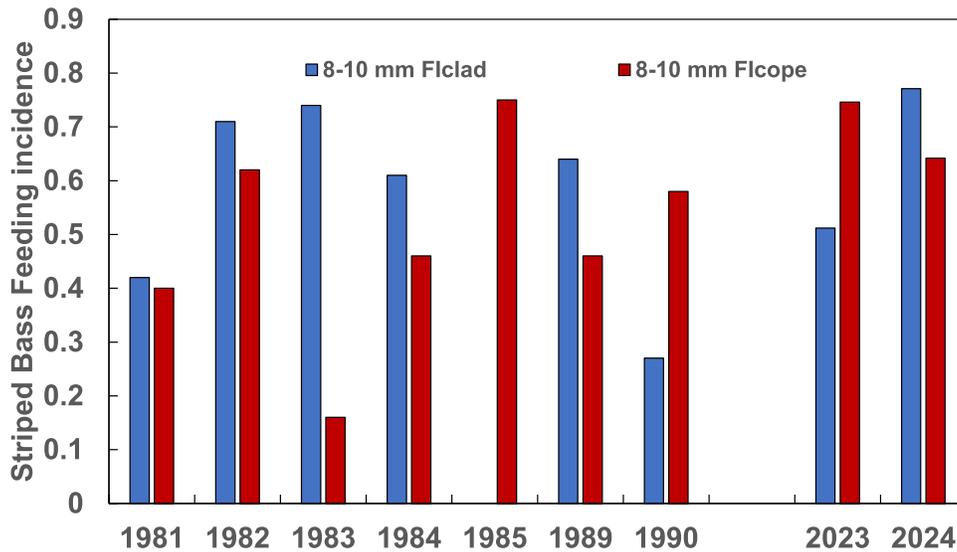
Metric	Striped Bass, 5–7 mm TL		Striped Bass, 8–10 mm TL		White Perch, 5–7 mm TL	
	2023	2024	2023	2024	2023	2024
FI <sub>clad</sub>	0.26	<b>0.60</b>	0.51	0.77	0.55	0.69
FI <sub>clad</sub> SD	0.08	0.02	0.08	0.03	0.06	0.02
FI <sub>cope</sub>	<b>0.64</b>	<b>0.40</b>	0.74	0.64	0.70	0.48
FI <sub>cope</sub> SD	0.09	0.02	0.07	0.03	0.06	0.03
<i>N</i>	31	414	39	201	67	348

within the boundaries associated with low *Z* during the 1980s. Feeding incidences on cladocerans and copepods during 2024 were classified as high and were within the range associated with low *Z* as well. Estimates of 1/*N*<sub>ratio</sub>, used as a proxy index for *Z* during 2023 and 2024, indicated low postlarval *Z*. However, Striped Bass year-class success was dismal in the Choptank River during 2023 and was poor in 2024 (JIs = 0.20 and 1.90, respectively; Durell & Weedon, 2024).

Estimates of FI<sub>clad</sub> and FI<sub>cope</sub> from the 1980s surveys were used to develop criteria by which to judge the feeding success of first-feeding Striped Bass postlarvae in samples collected during 2023 and 2024. Estimates of FI<sub>clad</sub>, FI<sub>cope</sub>, *G*, and *Z* in the Choptank River exhibited considerable variation during the 1980s that provided contrast for analyses. The highest FI<sub>clad</sub> was 5.5 times greater than the lowest value, and there was a 7.6 times difference for FI<sub>cope</sub>. Estimates of *G* and *Z* could be classified as high or low. Estimates of FI<sub>cope</sub> were positively associated with *G* and negatively associated with *Z* in the 1980s. Estimates of FI<sub>clad</sub> were modestly and



**Figure 13.** Feeding incidences on cladocerans ( $FI_{clad}$ ) and copepods ( $FI_{cope}$ ) for 5–7-mm-total length Striped Bass postlarvae in the Choptank River during 1981–1985, 1989–1990, and 2023–2024.



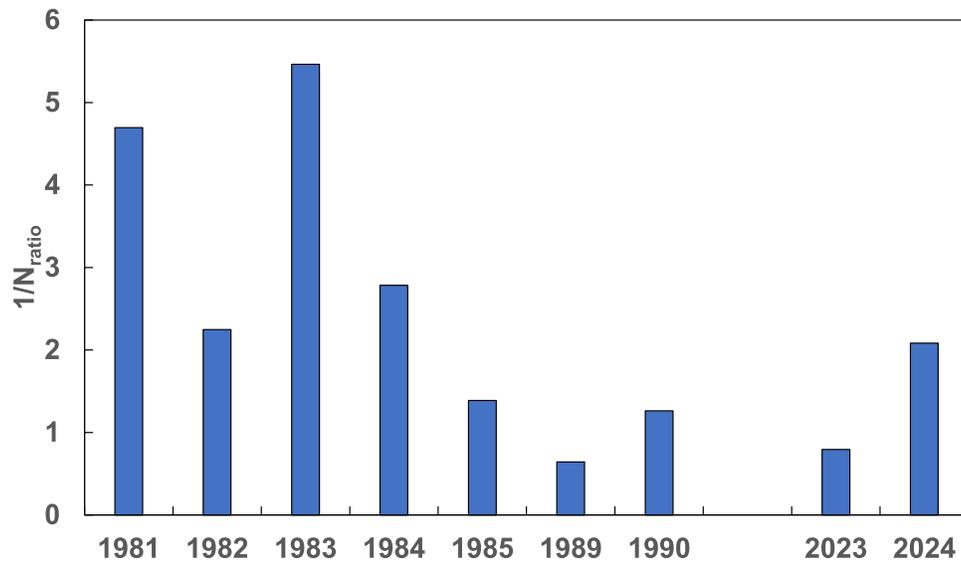
**Figure 14.** Feeding incidences on cladocerans ( $FI_{clad}$ ) and copepods ( $FI_{cope}$ ) for 8–10-mm-total length Striped Bass in the Choptank River during 1981–1985, 1989–1990, and 2023–2024.

negatively associated with  $G$ , and an association with  $Z$  was not apparent.

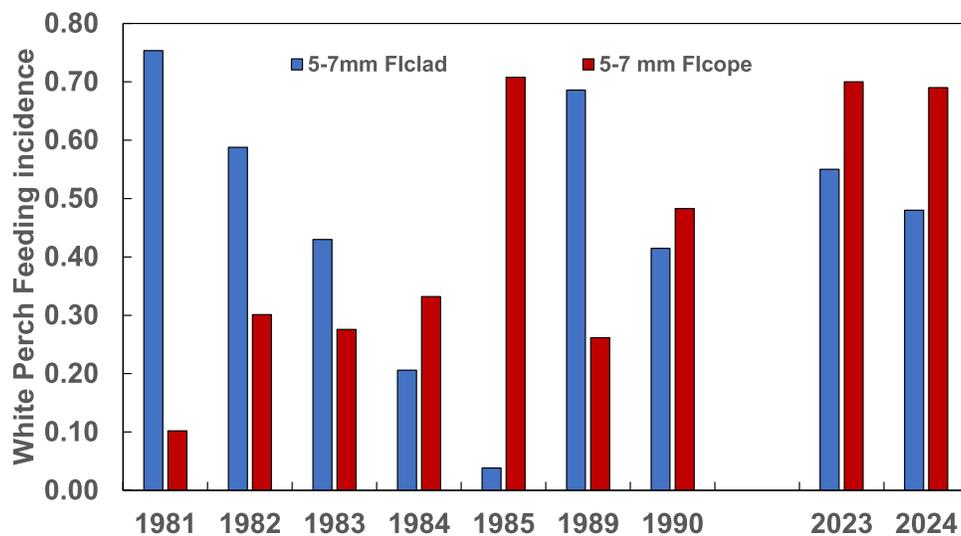
The Choptank River JI was not well correlated with  $FI_{cope}$  or  $FI_{clad}$ . Both  $G$  and  $Z$  were poorly correlated with the Choptank River JI during 1980–1990 ( $r = -0.33$  for  $G$  and  $r = -0.32$  for  $Z$ , with  $P = 0.33$  for both). The strongest year-class in the time series (1989; geometric mean = 28.10) was the product of high initial abundance of first-feeding larvae ( $\log_e N_6$ ), low  $G$  and  $Z$  of postlarvae, middling  $FI_{cope}$ , and high  $FI_{clad}$ . The second-highest year-class (1982; geometric mean = 5.68) had similar parameter estimates as the 1989 year-class except that the initial abundance of first-feeding larvae was less; lower  $\log_e N_6$  reflected the reduced  $Ep$  that was indicative of an overfished spawning stock (Uphoff, 1993, 1997, 2023). The poor 2024 year-class (JI = 1.90) was similar to 1982 and 1989 in  $FI_{cope}$ ,  $FI_{clad}$ , and  $Z$  (as indicated by its  $1/N_{total}$  proxy). Remaining year-classes with low  $Z$ , high

$FI_{cope}$ , and low  $FI_{clad}$  were poor. High  $FI_{clad}$  alone, as observed with the 1981 year-class, was reflected by high  $Z$  and low  $G$ .

Cladocerans appeared to be an important diet supplement in some years; first-feeding Striped Bass larval diets included more cladocerans when initial relative abundances of first-feeding larvae were higher. The mixed role of cladocerans likely reflected a trade-off for postlarvae between energy expended and obtained for search time, attack success, and handling (Limburg et al., 1997). Optimal foraging theory predicts that predators should select prey that maximize the energetic gains relative to the costs of capturing, ingesting, and digesting their prey (Nunn et al., 2012). Newly hatched individuals of many fish species prey mainly upon small zooplankters because of their inability to handle larger prey and their limited digestive capacity (Nunn et al., 2012). Larval fish do not have well-developed sight, and copepods could be easier for first-feeding



**Figure 15.** Trends in  $1/N_{\text{ratio}}$  (a proxy index for daily instantaneous mortality rate) for Striped Bass during the 1980s and 2023–2024, where  $N_{\text{ratio}} = (\text{number of 8–10-mm-total length postlarvae examined for gut contents}) \div (\text{number of 5–7-mm-total length postlarvae examined for gut contents})$ .



**Figure 16.** Feeding incidences on cladocerans ( $FI_{\text{clad}}$ ) and copepods ( $FI_{\text{cope}}$ ) for 5–7-mm-total length White Perch postlarvae in the Choptank River during 1981–1985, 1989–1990, and 2023–2024.

Striped Bass to see because of their larger size, greater pigmentation, or larger movement relative to *Bosmina* (Limburg et al., 1997). Cladocerans are common prey of larval fishes because they are easier to capture than copepods, even though the latter may be abundant and of greater caloric value (Limburg et al., 1997; Nunn et al., 2012). Limburg et al. (1997) estimated an energy value of 16,200 J per individual *Bosmina*, 29,100 J per adult copepod, and 8,570 J per copepod nauplius.

Copepods were an important diet item for larval Striped Bass in Head of Bay studies during 2001, 2003, 2007, and 2008 (Martino & Houde, 2010; Shideler & Houde, 2014). The role of cladocerans was more variable, and their inclusion in the diet supported growth and survival of larvae above the estuarine turbidity maximum and later in the spawning season

(Martino & Houde, 2010; Shideler & Houde, 2014). Striped Bass larvae may have selected for *Eurytemora* in the Head of Bay during 2007, but positive selection was not indicated during 2008 (Shideler & Houde, 2014). There was a negative preference for *Bosmina* in 2007, and selection was not evident in 2008 (Shideler & Houde, 2014). Striped Bass larvae positively selected for *Eurytemora* and negatively selected for *Bosmina* during 2001–2002 in the Patuxent River (Campfield & Houde, 2011). The lowest level of starvation of Striped Bass larvae in the Potomac River during 1981, as measured by morphometry, occurred when cladocerans were most abundant (Martin et al., 1985). Mean cladoceran and adult copepod densities during the last 2 weeks of May were positively correlated with abundances of late-stage Striped Bass larvae and with the JI values in the

Potomac River during 1976–1977, 1980–1982, and 1987–1989 (Rutherford et al., 1997). Limburg et al. (1997) found only partial support for the hypothesis that zooplankton blooms represented an energy advantage for co-occurring Striped Bass and White Perch postlarvae in the Hudson River during 1994. Copepods were highly selected except during the *Bosmina* bloom; larval cohorts coincident with the *Bosmina* bloom possessed an energetic advantage relative to early cohorts but not late cohorts (Limburg et al., 1997). In experiments, Striped Bass postlarvae were not unusually vulnerable to starvation during the transition to active feeding (Rogers & Westin, 1981).

First-feeding Striped Bass postlarvae maintained less-variable levels of the all-item FI (1.4 times) with mixes of copepods and cladocerans, but it was poorly associated with *G* and *Z* during the 1980s and 2023–2024. The range of our all-item FI estimates was 0.55–0.80, which was within estimates for the Head of Bay during 2001–2003 (>0.50 to ~0.90; Martino & Houde, 2010) and 2007–2008 (0.63 and 0.55, respectively; Shideler & Houde, 2014). Variation could have been different on a biomass or nutrition basis than indicated by FI due to size and energy differences between cladocerans and copepods.

Estimates of  $FI_{cope}$  always increased as the Striped Bass postlarval size-class increased from 5–7 mm to 8–10 mm over all years in the Choptank River, and  $FI_{clad}$  increased during most years. Feeding incidences for 5–7-mm White Perch postlarvae followed a similar pattern. Increased  $FI_{clad}$  and  $FI_{cope}$  for more developed 8–10-mm Striped Bass and 5–7-mm White Perch postlarvae could reflect combinations of larger gape, more developed eyesight and digestion, and greater feeding experience and swimming speed (Nunn et al., 2012).

### Caveats

Accuracy of estimated *Z* for Striped Bass in the 1980s assumed that using mean lengths to estimate *G* as a time scale for *Z* and size selectivity of the sampling gear did not badly bias these estimates (Uphoff, 1989, 1992). We judged that these estimates were sufficient for the purpose of categorizing *Z* as high or low to develop FI and  $1/N_{ratio}$  criteria for 2023–2024. Estimates of *G* in the Choptank River during the 1980s (0.030–0.044) fell within the range of estimates from other Chesapeake Bay spawning areas (nine estimates) or exceeded them (two estimates). Estimates of *G* based on larval otoliths of cohorts in the Patuxent River were 0.026–0.033 in 1991 (Secor & Houde, 1995), and estimates for the Nanticoke River were 0.030–0.035 in 1993 (Secor et al., 2017). Mean *G*-estimates based on changes in mean length at otolith age in the Upper Bay were 0.030 in 1989 (Rutherford et al., 1997), 0.024 in 2001, and 0.038 in 2003 (Martino, 2008).

We had concerns that low postlarval catches in 2023 were influenced by the sampling strategy employed, and we doubled the effort in 2024, anticipating low catches. However, catches were much better in 2024, and catches of 8–10-mm postlarvae per tow were similar to differences in year-class success for these 2 years. The ratio of 8–10-mm postlarvae per midwater tow for 2024 to 2023 was 8.1:1, and the ratio of Choptank River JIs for 2024 to 2023 was 10.3:1 as arithmetic means (Durell & Weedon, 2024), suggesting that year-class success had been set by the late postlarval stage. Correlations of postlarval relative abundance at length and the Choptank River JI during

1980–1988 strengthened rapidly after 7 mm TL, were moderate at 8–9 mm TL, and were strong by 10 mm TL (Uphoff, 1989, 1992). Year-class success was determined by 8 mm standard length in the Potomac River (Rutherford et al., 1997).

We used midwater trawls for 2023–2024 sampling in the Choptank River, while midwater and bottom trawls were used in the 1980s to sample Striped Bass early life stages (eggs to early juveniles) in the river (Uphoff, 1989, 1992, 1993). Midwater trawls offered cleaner samples (less detritus), were very unlikely to snag the bottom, and sampled postlarvae effectively (Uphoff, personal observation). Midwater and bottom channel trawls accounted for 49% and 44%, respectively, of the total catch of Striped Bass postlarvae during 1980–1985 when midwater channel, bottom channel, and inshore shoal habitats were sampled (Uphoff, 1989). Inshore catches of eggs and larvae were minor, and this habitat was dropped from egg and larval sampling but was retained for juvenile sampling during 1987–1990 (inshore accounted for 77% of early juvenile catch during 1980–1985; Uphoff, 1989).

Conductivity criteria for 2023–2024 sampling were intended to distribute samples spatially. The 200–1,000- $\mu\text{S}/\text{cm}$  target range proved too spatially narrow in practice under low-flow (2023) and high-flow (2024) conditions. Sites were sometimes grouped close spatially within the target range, and we had concerns about oversampling larvae from a limited area. We ended up expanding the range to 140–2,000  $\mu\text{S}/\text{cm}$  in the field to sample a broader spatial distribution.

During the 1980s, feeding samples were drawn from all sites where feeding larvae were encountered over a sampling season that covered eggs through early juveniles (from April to mid-June). In 2023–2024, sampling for feeding analysis began a week after a major spawn was detected during an egg presence–absence survey and continued until temperatures met or exceeded 20°C. The span of sampling for feeding Striped Bass larvae in our two size-groups was 14 d in 2023 and 18 d in 2024. During the 1980s, an estimated postlarval period for analyses began 1 week after peak spawning and lasted for the time estimated for larvae to grow from 6 to 12 mm (Uphoff, 1989, 1992). Estimated duration of the postlarval period was 14–21 d during 1980–1988 (Uphoff, 1992) and 17–21 d during 1989–1990 (Uphoff, unpublished data).

Analysis of Choptank River estimates from the 1980s indicated that  $1/N_{ratio}$  could serve as a proxy for *Z* to apply to 2023–2024. The 5–7-mm Striped Bass postlarvae were present in samples throughout the 2023–2024 surveys; 8–10-mm postlarvae were present in samples during the latter half of survey dates. Estimates of  $1/N_{ratio}$  in 2023–2024 could be positively biased if sampling of 8–10-mm postlarvae was incomplete; however, values of  $1/N_{ratio}$  for these 2 years still fell within the range of 1980s estimates indicating low *Z*.

### Earlier timing of the postlarval period

The period when postlarvae predominated in the Choptank River occurred earlier in 2023–2024 than during the 1980s. Postlarval collections began on April 13 in 2023 and on April 18 in 2024. Postlarval periods in the years 1980–1988 were estimated to begin as early April 22 and as late as May 18: Three began on April 22, one began on April 30, four began on May 1–8, and one began on May 18 (Uphoff, 1989, 1992).

Postlarval periods for 1989 and 1990 were estimated to have started on May 3 and May 1, respectively (Uphoff, unpublished data).

Temperatures rose very quickly in 2023–2024 during the 1-week interval from what we interpreted as peak spawn to when the sampling of feeding larvae started; subsequent sampling for feeding larvae did not occur at temperatures when the 1980s cumulative distribution of larvae increased rapidly (15–17°C). Temperatures encountered at peak spawn were 17.0–18.3°C on April 7, 2023 (they were 13.5–13.9°C on April 4). At initiation of sampling for feeding larvae (April 13, 2023), temperatures were 19.5–20.3°C. In 2024, temperatures were 18.0–18.9°C at the initiation of postlarval sampling (April 18) and were 13.7–14.2°C at the beginning of peak spawn on April 10 (they were 10.7–11.6°C on April 8). Temperatures at the end of postlarval sampling would have accounted for 97% (2023) and 91% (2024) of larvae in the 1980s cumulative distribution.

Analyses of temperatures in long-term spawning surveys of eggs or adult spawners have indicated a shortening of the spawning season since around 2000 (Giuliano, 2023; Uphoff et al., 2024). In general, spawning temperature milestones for the beginning and end of spawning in the Choptank River, Nanticoke River, Potomac River, and Head of Bay indicated that spawning was not starting much earlier, but it peaked and ended earlier (Giuliano, 2023; Uphoff et al., 2024). Shortening of the spawning season would be reflected by earlier postlarval periods.

Hinson et al. (2022) determined that warming in the Chesapeake Bay during 1985–2019 was occurring at a more rapid rate for May–October than for November–April; the split at April–May coincides with Striped Bass spawning and larval development in the Chesapeake Bay region. Projections of water temperatures under long-term climate warming indicated that earlier spawning would occur in Chesapeake Bay spawning areas in the future (Maryland Sea Grant, 2009; Peer & Miller, 2014). Higher temperatures during spring due to climate warming could have a negative effect on egg and larval survival due to a more rapid spring-to-summer transition that reduces the period in which temperatures are most favorable for survival (Maryland Sea Grant, 2009). Modeling of the effect of likely temperature increase scenarios under global warming on Striped Bass spawning in the Hudson River from 2010 to the 2090s indicated that spawning will occur earlier and will be of shorter duration (Nack et al., 2019).

### Conclusion

Our investigation of Striped Bass postlarval feeding success in 2023–2024 did not indicate that FIs on major zooplankton prey were too low, and our proxy indicator of Z did not indicate high postlarval mortality. Our feeding investigation did not encompass the entire recent 6-year drought in year-class success, but the findings for 2023–2024 did not indicate a consistent, prominent role for feeding success.

Hypotheses for investigating recent poor year-class success should not be limited to those of the past, but they are a place to start. Spawning status indicated by temporal and spatial dispersion (*Ep*), egg–prolarval mortality due to lethally low water temperature, and larval mortality associated with water quality were identified as independent influences on Striped

Bass year-class success in the Choptank River during the 1980s (Hall et al., 1993; Uphoff, 1989, 1992, 1993). A major assumption that might accompany the use of feeding information from the 1980s to judge the present is that food supply and larval feeding behavior—not underlying habitat conditions—affected zooplankton, feeding, *G*, and *Z*. Alkalinity and pH, factors that were implicated (along with toxic metals) in extended poor year-class success in the Choptank River during the 1980s, had improved during the early 1990s and seem to be no longer associated with excessive postlarval *Z* (Hall et al., 1993; Uphoff, 2023; Uphoff et al., 2024). Estimates of *Ep* through 2023 have not been low enough to explain poor recruitment (Uphoff, 2023; Uphoff et al., 2024). This leaves changes in temperature during spawning and early larval development as a hypothesis warranting investigative emphasis.

### DATA AVAILABILITY

Data will be made available on request.

### ETHICS STATEMENT

There were no specific ethical guidelines that were applicable to this study.

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### CONFLICTS OF INTEREST

There is no conflict of interest declared for this article.

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## APPENDIX A: ESTIMATING Z AND G FOR 1980S SURVEYS

Weekly length–abundance distributions were constructed by multiplying the proportion of fish in each 1-mm length interval

( $p_i$ ) of the length-frequency distribution by the weekly total catch ( $n_i$ ; Uphoff, 1989, 1992, 1993). Weekly catch totals of fish in each length interval ( $p_i \times n_i = N_i$ ) were then summed across the entire sampling season ( $\sum N_i$ ) to create a yearly length–abundance distribution that was adjusted to the lowest seasonal effort (132 trawls from the beginning of each survey to the first week of June). Each year’s instantaneous daily growth rate ( $G$ ) was estimated and applied as a time scale to the length–abundance distribution to estimate the daily instantaneous mortality rate ( $Z$ ; Uphoff, 1989, 1992, 1993).

Annual estimates of  $G$  were estimated by fitting the weekly mean lengths to the exponential growth model for  $G$  for each year during 1980–1990:

$$\log_e L_t = \log_e L_0 + G \cdot (X_t),$$

where  $L_t$  is the mean length of postlarvae during week  $t$ ;  $X_t$  is the number of days from the midpoint of the first week of sampling to the midpoint of week  $i$ ; and  $L_0$  is length at hatch. By using mean length to estimate  $G$ , we described the growth of individuals under average conditions but not growth variations that individual larvae might have exhibited under different conditions (Kaufmann, 1981).

The natural logarithm of abundance in the catch at each millimeter size-class was modeled against relative age for each year to estimate the annual  $Z$  of postlarvae (average for all cohorts within a year) and its SE. For convenience, 6–12-mm fish were categorized as postlarvae, although late prolarvae and early juveniles were also present in this length-group (Uphoff, 1989, 1993). Between 6 and 12 mm, each 1-mm length interval was assigned a relative age (in days) according to that year’s  $G$  by back-calculating the time needed to grow from 6 mm to a given length. Relative age was calculated as

$$X_t = (\log_e L_m - \log_e 6) / G,$$

where  $X_t$  is relative age or days past 6 mm,  $L_m$  is the 1-mm length interval from 6 to 12 mm, and  $G$  is the instantaneous growth rate.

Instantaneous mortality rates were calculated for each year as

$$\log_e N_{12} = \log_e N_6 - Z_t,$$

where  $Z$  is the instantaneous daily mortality rate for the entire length interval,  $N_{12}$  is the predicted number of 12-mm larvae at age  $t$ , and  $N_6$  is the number of 6-mm larvae at the beginning of the time interval.