

Title of Thesis: SPATIOTEMPORAL DISTRIBUTION OF  
CHESAPEAKE BAY MYSIDS IN THE  
CHOPTANK AND PATUXENT RIVERS,  
MARYLAND

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Thesis Directed By: Dr. Ryan Woodland, Marine Estuarine  
Environmental Sciences

#### ABSTRACT

Mysids are a critically understudied, but an ecologically important taxonomic group within Chesapeake Bay. The importance of these small, shrimp-like crustaceans to coastal food webs has been widely documented, but their complex diel movements and seasonal migrations have made thorough field studies of mysids difficult. This study examined patterns of mysid abundance differences between the Choptank and Patuxent rivers (including comparisons of sub-genera demographic abundances), abundance changes throughout the sampling season, within-population demographic dynamics, and co-occurring environmental conditions to determine whether mysid abundances are equal in the Choptank and Patuxent rivers. I hypothesized that mysid abundances in the study system will positively correlate with dissolved oxygen and that the Choptank River will display greater mysid abundances due to its historically

better water quality (particularly dissolved oxygen saturation) than the Patuxent River. Six primary stations in each river were sampled monthly from May to September of 2018. Numerical dominance of the mysid assemblage in both rivers shifted from *Neomysis americana* in the early summer to a mixed-species group belonging to the genus *Americamysis* (*Americamysis* spp.) between August and September. Total abundance across genera and abundance of *Neomysis* only were significantly greater in the Choptank River while *Americamysis* spp. abundances were significantly greater in the Patuxent River. The Patuxent River displayed overall lower dissolved oxygen saturation in the summer, which aligned with my hypothesis and may have influenced changes observed in mysid abundances. Understanding the intricacies of mysid population dynamics within nursery areas for ecologically and economically important predators should strengthen ecosystem-based management strategies.

*Key words: benthic-pelagic coupling; mysid; Neomysis; Americamysis; trophic dynamic; stable isotope; forage; Chesapeake Bay; Choptank River; Patuxent River; sonar imaging; ecosystem-based fisheries management.*



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THE CHOPTANK AND PATUXENT RIVERS, MARYLAND

by

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## Dedication

This work is dedicated to John Leonard Quill, Jr, the best man to ever live. 

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## List of Abbreviations

UMCES	University of Maryland Center for Environmental Science
CBL	Chesapeake Biological Laboratory
HPL	Horn Point Laboratory
NOAA	National Oceanic and Atmospheric Administration
EBFM	Ecosystem-Based Fishery Management
NMFS	National Marine Fisheries Service
EOTB	Maryland Department of Natural Resources: Eyes on the Bay
USGS	United States Geological Survey

# Chapter 1: Spatiotemporal distribution of mysids in the Choptank and Patuxent rivers, two tributaries of Chesapeake Bay

## Abstract

The importance of mysids as trophic links in key Chesapeake Bay food webs has been well documented. However, their abundance, distribution, and demographics haven't been examined in Chesapeake Bay since 1930. The goal of this study was to examine patterns of mysid abundances and demographic dynamics between and within two key Chesapeake Bay tributaries (the Choptank and Patuxent rivers). I hypothesized that mysid abundances would be greater in the Choptank River due to its historically better water quality (particularly dissolved oxygen saturation) than the Patuxent River. Secondly, I hypothesized that *Neomysis americana* (hereafter, *Neomysis*) would be the most abundant mysid species in both the Choptank and Patuxent rivers. Six stations in each river were sampled monthly from May to September of 2018. Numerical dominance of the mysid assemblage in both rivers shifted from *Neomysis* in the early summer to a mixed-species group belonging to the genus *Americamysis* (*Americamysis* spp.) between August and September. Total abundance across genera and abundance of *Neomysis* were significantly greater in the Choptank River in early summer, then did not differ from *Americamysis* spp. abundance thereafter. *Neomysis* abundance was greater than *Americamysis* spp. from



May through June, did not differ from *Americamysis* spp. abundance in July, and was less abundant than *Americamysis* spp. from August through September in the Patuxent River. The Patuxent River displayed overall lower dissolved oxygen saturation in the summer, which correlated with lower mysid abundances, providing support for my hypothesis. Understanding the intricacies of mysid population dynamics within nursery areas for ecologically and economically important predators should strengthen ecosystem-based management strategies for those areas.

### Introduction

#### Overview of Mysids

Mysids (Malacostraca: Peracarida: Mysida) are small, shrimp-like animals characterized by the presence of a statocyst and a marsupium which is comprised of modified oostegites on sexually mature females (Verslycke et al., 2004; Wortham-Neal & Price, 2002). They inhabit waters all over the globe ranging from freshwater to marine systems (Jumars, 2007; Mauchline, 1980; E. Mayor et al., 2017; Tattersall, 1951; Wittmann, 2012). Within their respective habitats, mysids occupy an important niche in their local food webs, occupying and contributing (as predators, primary consumers, and prey) to both benthic and pelagic habitats (Buchheister & Latour, 2015; Friedland et al., 1988; Torre & Targett, 2017; Walter et al., 2003; Woodland & Secor, 2013). A fundamental behavior of many mysid species that influences their trophic niche is diel vertical migration (Bouchard & Winkler, 2018; Herman, 1963; Hulburt, 1957; Sato & Jumars, 2008) although some mysids also

display horizontal migration behaviors (Lough & Aretxabaleta, 2014; Morgan & Threlkeld, 1982). By occupying epibenthic or demersal habitats during the day and expanding into pelagic habitats at night, vertically migrating mysids can link benthic and pelagic food webs.

Within the coastal mid-Atlantic region of the United States, a wide variety of predators rely on mysids as prey. Economically and ecologically important species such as weakfish (*Cynoscion regalis*), silver perch (*Bairdiella chrysoura*), Atlantic moonfish (*Selene setapinnis*), summer flounder (*Paralichthys dentatus*), banded drum (*Larimus fasciatus*), striped sea robin (*Prionotus carolinus*), lookdown (*Selene vomer*), and spotted hake (*Urophycis regia*) have shown strong reliance on mysids as forage (28–94% of diet by mass) in the Chesapeake Bay (Buchheister & Latour, 2015). Other known mysid predators of ecological, economical, and cultural import include bluefish (*Pomatomus saltatrix*), alewife (*Alosa pseudoharengus*), American shad (*A. sapidissima*), and striped bass (*Morone saxatilis*) (Buchheister & Latour, 2015; Friedland et al., 1988; Torre & Targett, 2017; Walter et al., 2003; Woodland & Secor, 2013). Mysid predation also has top down effects on their habitats, particularly on copepod community structure (Fulton, 1982). Mysid gut content analysis revealed that mysids capitalize on detrital macrophyte material when preferred food sources are scarce (Zagursky & Feller, 1985). Other studies suggest levels of detrital contributions to mysid diet are tied to feeding position based on diel vertical migration (Rudstam et al., 1989; 1985). Whatever the etiology for their varied food sources, the fact that mysids consume both benthic and pelagic foods (and are

consumed by predators in both habitats) makes them effective couplers of different habitats and trophic pathways (Jumars, 2007).

Aside from their ecological value as prey for fish in coastal food webs, mysids are useful as environmental indicators (another helpful result of their habitat-coupling capabilities). For example, mysids have the ability to fragment microplastics, which leads to increased bioaccumulation at higher trophic levels (Hasegawa & Nakaoka, 2021). They are frequently used as indicators of toxic material presence (McKenney & Matthews, 1990; Roast et al., 2000; Rose et al., 2015) and can be potentially used to signal endocrine disruption in co-occurring species (Verslycke et al., 2004). The presence of toxic material in mysids rather than other taxa may be a more reliable indicator of toxin presence in a given ecosystem due to the extensive inshore-offshore and vertical migrations that mysids undertake regularly. Because mysids are exposed to conditions and consume prey in multiple habitats, they are likely to encounter a study contaminant through environmental exposure or through trophic transfer.

Mysids are colloquially referred to as opossum shrimp. This name is derived from the pouch-like structure formed by oostegites pairs of mature females (Roast et al., 1998). The oostegites are located on the posterior thoracopods and are where ovigerous females carry their embryos (Grzeszczyk-Kowalska et al., 2014; Meland et al., 2015; Roast et al., 1998; San Vicente et al., 2014). Mysids exhibit multiple reproductive life history strategies, even within species. Mature females are able to produce multiple broods per year depending on temperature, which strongly influences maturation rates, life span, and population dynamics (Hopkins, 1965; Mauchline, 1980; Mayor et al., 2017; Mayor & Chigbu, 2018; Pezzack & Corey,

1978; Richards & Riley, 1967; Viñas et al., 2005; Wigley, 1971). Anticipated number of cohorts produced annually can be estimated by temperature ranges over time. For example, colder temperatures are prohibitive with respect to growth; at temperatures < 4°C, gonadal development may cease, and the optimal temperature for maximum growth, in *Neomysis americana* (S.I. Smith, 1873) specifically, is 25°C for a north Atlantic population (Pezzack & Corey, 1978).

#### Knowledge Gaps in Mysid Ecology

Despite their importance in local food webs, there are surprisingly few data available describing their abundance and distribution in the Chesapeake Bay, although recent work has described seasonal aspects of mysid abundance and growth in Maryland's Coastal Bays (E. Mayor et al., 2017). Throughout their range, abundance data are often lacking or incomplete for mysids (i.e., “chronically under-sampled”, sensu Jumars 2007). The disparity in site fidelity between mysids (low) and most researchers (high) has been posited as a potential explanation for the absence of a strong understanding of local mysid dynamics in some locations (Jumars, 2007). Another hurdle in mysid studies is their often complex display of onshore-offshore migrations (Bamber & Henderson, 1994) and diel vertical migrations (Jumars 2007). In some cases, mysid diel vertical migration correlates with sex and body size. O'Malley et al. (2018) observed a larger ratio of males occupying pelagic space during night sampling as well as mysids of larger body size occupying benthic space during night sampling. There is evidence to support that mysids migrate both vertically and horizontally as a response to drivers other than light intensity, such as redistributing based on food availability, water circulation patterns, flow rate

preferences, diet requirements by ontogenetic phase, and body size-determinant predator avoidance (Clutter, 1967; Jumars, 2007; Speirs et al., 2002; Webb & Wooldridge, 1990).

Location-dependent, within-species variation has been reported with respect to migration patterns. Historical studies report *N. americana* exhibiting diel vertical migrations in Chesapeake and Delaware Bays (Cowles, 1931; Hulburt, 1957), but not exhibiting this migratory pattern on Georges Bank (Whiteley, 1948). Herman (1963) observed a positive correlation between the diel vertical migration behavior of sexually mature *N. americana* with periods of mating. While sexually mature mysids exhibited diel vertical migrations that coincided with breeding periods, immature and juvenile mysids engaged in diel vertical migrations throughout the year (Herman, 1963).

Finally, Jumars (2007) attributes the general underrepresentation of mysids in food webs studies to the dispersed nature of mysid impacts on ecosystems. Their highly omnivorous diet and complex vertical and horizontal movements over daily, monthly, and seasonal cycles both within and across habitats can serve to dilute their apparent ecological effects. If the contributions of mysids were to include all trophic and habitat interactions within an ecosystem, in addition to their effects as habitat-coupling omnivores, the magnitude of their ecological impact could be more accurately estimated (Jumars, 2007).

#### Ecosystem-based Fisheries Management

Management strategies for fisheries in the United States began shifting toward more holistic approaches in the 1990s. The general consensus was that species-

specific management practices were able to achieve only short-term stability and in order to produce lasting solutions, whole ecosystems would need to be addressed (Christensen et al., 1996; Link, 2002; NMFS, 1999). In 1996, Congress instructed the National Marine Fisheries Service (NMFS) to create a panel for evaluating how effectively ecosystem management approaches are applied to fisheries management practices (NMFS, 1999). Aside from ecosystem-based fisheries management (EBFM) being more likely to succeed in achieving management goals, there is a federal mandate to pursue ecosystem-based approaches.

New information regarding understudied keystone species, such as Chesapeake Bay *N. americana* populations, could be directly applied to existing management frameworks for immediate enhancement. One such framework is already in place for the area investigated in this study. In 2006, the National Oceanic and Atmospheric Administration (NOAA) Chesapeake Bay office and the Chesapeake Fisheries Ecosystem Plan Technical Advisory Panel developed an ecosystem-based management plan (The Chesapeake Fisheries Ecosystem Plan Technical Advisory Panel, 2006). This plan addresses the management of a vast number of bay species including striped bass (*Morone saxatilis*), an economically important Bay species (Merriman, 1941). In order to apply an ecosystem-based management approach to a fishery like that of the striped bass, the ecological requirements of striped bass, including the prey that support Chesapeake Bay striped bass populations, need to be investigated. Mysids are among the least studied and most poorly understood component of striped bass diet in Chesapeake Bay (Jumars, 2007; Walter et al., 2003).

Until recently, the latest information on Chesapeake Bay-specific mysid ecology was derived from a coastal biodiversity survey in 1930 (Cowles, 1931), in which their abundance and distribution information were briefly described. Despite the lack of ecosystem-specific research, mysids seasonally account for more than half the diet of striped bass young-of-the-year (Boynton et al., 1980; Shears et al., 1991; Walter et al., 2003). Given the well-documented role of mysids as prey for many valuable regional fisheries species (Buchheister & Latour, 2015; Friedland et al., 1988; Torre & Targett, 2017; Walter et al., 2003), it is clear that addressing the existing knowledge gaps around the distribution, abundance, and population dynamics of this key forage group is imperative for successfully implementing the accurate food web models that are needed to inform EBFM in systems such as Chesapeake Bay.

Moving from species-oriented management to more EBFM-styled management promotes a more holistic view of an ecosystem. For example, inclusion of mysid spatiotemporal distribution and population demographics data into food web models could be used to determine what areas are likely to support managed populations of juvenile fish. Because studies show mysid species can be environmental indicators of toxic material in the environment (McKenney & Matthews, 1990; Roast et al., 1998, 2000) there is potential to utilize them as such in their natural environments. If mysid distributions can be mapped over time, changes to these mapped distributions might be able to be used as first-sign environmental indicators of environmental conditions and potentially hazardous contaminants (Modlin & Froelich, 1997).

## Study Area & Behavior- Based Sampling Scheme

The goals of my thesis are to identify patterns in mysid abundances and population demographics as they relate to environmental conditions within two Chesapeake Bay tributaries. The study location for this research is Chesapeake Bay, an estuary that supports highly productive spawning grounds and nursery habitats for a wide variety of fishes that are known to consume mysids. Within Chesapeake Bay, the Patuxent and Choptank rivers (Table 1) provide nursery habitat for environmentally and economically important mysid predators (Secor & Houde, 1995; Stence et al., 2013; Uphoff, 2008). I hypothesized that the Choptank River would exhibit greater mysid abundance compared to that of the Patuxent River and that *Neomysis* would be the most abundant mysid taxon in both rivers. Based on historical evidence and environmental tolerances of salinity and temperature of *N. americana* from the literature (Banse, 1964; Roast et al., 1998; Smith, 1873) a net-based sampling regime was designed and employed to survey the presence and abundance of mysid life stages, record water quality parameters, and to ultimately test my hypotheses. I deemed a comprehensive design that included sampling near the surface and in the midwater column at all sites was required to account for potential differences in mysid aggregations by species, sex, and developmental phases (Ohtsuka et al., 1995). Using mysid catch and population data, I evaluated mysid abundance differences between the two tributaries (including comparisons of sub-genera demographic abundances), abundance changes throughout the sampling

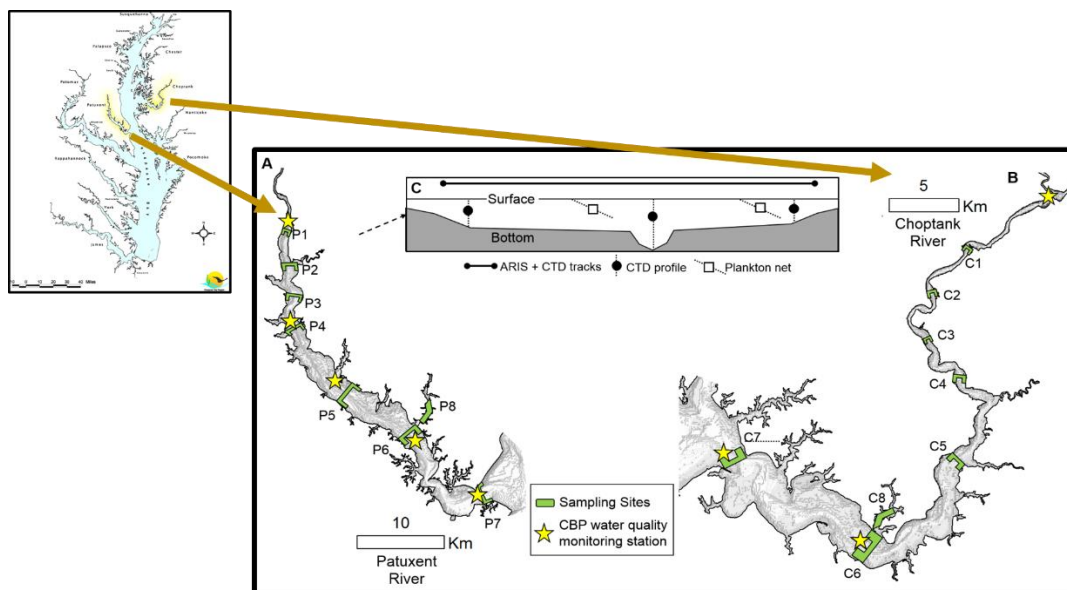


season, within-population demographic dynamics, and environmental parameter patterns.

### Materials & Methods

#### Sample Collection and Processing

One cruise was performed each month from May to September of 2018 on each of the two study rivers (Choptank and Patuxent). Fixed station locations ranged from upstream, oligohaline locations to downstream, mesohaline waters near the mouth of each river (Fig. 1). Station locations were verified prior to sampling during each cruise via handheld GPS. Sampling was constrained to begin one hour after sunset and conclude one hour before sunrise. Sampling for each river consisted of six stations, C1-C6 and P1-P6 for the Choptank and Patuxent rivers, respectively (Table 2). These stations were visited during each monthly cruise except when either the station was inaccessible due to the tidal stage or when there was insufficient time to visit the station at the end of the night. When possible, additional stations were also sampled, including an upstream station near the salt-front of each river (CU1, PU1), and lower stations closer to the confluence of each river with Chesapeake Bay (C7, C8, P7, P8).



**Figure 1.** Diagram of Chesapeake Bay showing locations of Patuxent and Choptank rivers (A-B) with station locations P1-P7 and C1-C7, respectively. Inset diagram (C) Cross-channel view of vertical water quality profile (CTD) and potential plankton net locations (ARIS+CTD tracks refer to additional project components not included in this thesis).

**Table 1.** Choptank and Patuxent River basin and watershed summaries from Fisher et al. (2006)

River Parameters	Units	Choptank	Patuxent
River length	km	68.0	62.0
Basin volume	10 <sup>6</sup> m <sup>3</sup>	1070.4	650.0
Surface Area	10 <sup>6</sup> m <sup>2</sup>	300.7	137.1
Mean depth	m	3.6	4.7
Agricultural land cover	%	61.5	20.3
Urban land cover	%	5.4	15.7

Zooplankton net samples were collected with circular 0.75-m diameter, 335- $\mu$ m mesh nets equipped with flow meters (Sea-Gear Corp ©, Melbourne, FL). Two zooplankton net tows were performed for each sampled station per cruise. Both tows were conducted along transects perpendicular to the channel for 3 minutes each, with an average vessel speed of ~1.85 kph. One tow was performed at the surface of the water with the rim of the net maintained just below the surface of the water

(“shallow”) and the second was a midwater tow conducted at approximately mid-water depth at a given station (“deep”). Target net depths during deep tows were approximated using an inclinometer while controlling the length of rope deployed from the winch. Upon net retrieval, flow meter readings were recorded and sample material was gently rinsed into the codend by spraying the outside of the net with a deck hose supplied with ambient water. Codend material was then sieved using a 250- $\mu\text{m}$  sieve and rinsed with 95%  $\text{CaCO}_3^-$  buffered ethanol (EtOH) before being stored in jars of EtOH.

**Table 2.** Dates of sampling cruises and stations sampled during each cruise.

<b>Cruise Date</b>	<b>River</b>	<b>Stations Sampled</b>
May 7, 2018	Choptank	C1-C6
May 10, 2018	Patuxent	P1-P6
June 4, 2018	Patuxent	P1-P7
June 6, 2018	Choptank	C1-C7
July 9, 2018	Patuxent	P1-P6
July 11, 2018	Choptank	C1-C7
August 6, 2018	Patuxent	P1-P6
August 9, 2018	Choptank	C1-C7
September 4, 2018	Choptank	C1-C8
September 6, 2018	Patuxent	P1-P7

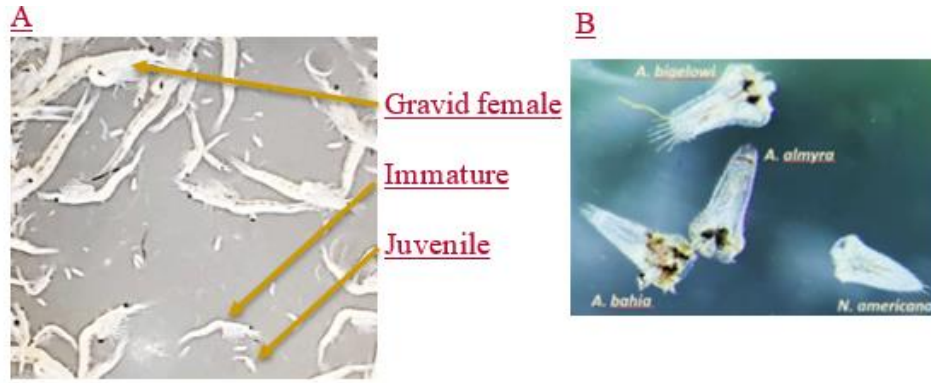
Vertical profiles of water temperature ( $^{\circ}\text{C}$ ), salinity (practical salinity unit scale), and dissolved oxygen (mg/L, % saturation) were collected at 3 locations along each station’s transect. Most data were collected using a MANTA II multiprobe sonde (Eureka© Water Probes, Austin, TX), but occasionally a YSI EXO multiprobe sonde (YSI, Yellow Springs, OH) was used when the MANTA II was unavailable. All multiprobe sondes were calibrated with laboratory standards prior to use. Profiles were collected on each flank of the river where water depths ranged between 3–4m and in the channel at the deepest point along each transect. Water quality

measurements were recorded at 0.5–1-m intervals from within 0.5m of the surface to within 0.5m of the bottom.

### Sample Processing

In the laboratory, mysids were removed from each sample jar, counted, and sorted into EtOH vials according to month sampled, tow depth category, size classification, taxonomic category, sex, and gravid state (Table 3). Mysids were identified as *Neomysis americana* (hereafter, *Neomysis* in the main text) or one of several species belonging to the genus *Americamysis* (i.e., *A. bahia*, *A. bigelowi*, *A. almyra*) (Heard, 2006), and then were separated into the following age-categories using the identifiers (Mauchline, 1980; Meland et al., 2015; Wortham-Neal & Price, 2002):

- Juvenile: late nauplius phase to juvenile form, under 10mm in length, sex determination not externally evident, and telson setation not developed (Herman, 1963; Wortham-Neal & Price, 2002)
- Immature: defined telson spiniform setae, secondary sexual characteristics not developed (Herman, 1963)
- Adult: defined telson spiniform setae (Fig. 2B) and secondary sexual characteristics fully developed (Herman, 1963)



**Figure 2.** Example of a gravid female, an immature, and a juvenile mysid (A) before separating into demographic categories and mysid telsons (B) showing distinct distal setation of common Chesapeake Bay species *Neomysis americana*, *Americamysis almyra*, *A. bigelowi*, and *A. bahia*.

Adults were separated by sex, and mature females further delineated as having an empty marsupium (not gravid) or having eggs in the marsupium (gravid) (Fig. 2A). Demographic category groups used for statistical comparisons include Total mysids, Total *Neomysis*, and Total *Americamysis* spp. (Tables 4, 5).

**Table 3.** Mysid demographic categories and classification table.

Age	Taxon	Sex	Gravid	Tow
Juvenile	<i>Neomysis americana</i>	male	yes	shallow
Immature	<i>Americamysis</i> spp.	female	no	deep
Adult				

Where samples were estimated to contain more than 200 individuals, a Folsom plankton splitter was used to serially split the sample until a given fraction was estimated to contain between 50–100 individuals. All individuals were identified under a dissecting microscope at 7–17 × magnification. If samples were split with the plankton splitter prior to sorting and counting, total sample counts of each mysid

group were determined by dividing the counted number of individuals by the ratio of the original sample represented by the split.

**Table 4.** Mysid demographic group abbreviations.

<b>Group</b>	<b>Abbreviation</b>
Juvenile (unspeciated)	Juv
Immature <i>Neomysis americana</i>	INeo
Adult <i>Neomysis americana</i> male	NeoM
Adult <i>Neomysis americana</i> non-gravid female	NeoNGF
Adult <i>Neomysis americana</i> gravid female	NeoGF
Immature <i>Americamysis</i> spp.	IAmer
Adult <i>Americamysis</i> spp. male	AmerM
Adult <i>Americamysis</i> spp. non-gravid female	AmerNGF
Adult <i>Americamysis</i> spp. gravid female	AmerGF

**Table 5.** Mysid demographic group components. See Table 4 for Group abbreviation definitions.

<b>Group:</b>	<b>Total mysids</b>	<b>Total <i>Neomysis americana</i></b>	<b>Total <i>Americamysis</i> spp.</b>
Juv	✓		
INeo	✓	✓	
NeoM	✓	✓	
NeoNGF	✓	✓	
NeoGF	✓	✓	
IAmer	✓		✓
AmerM	✓		✓
AmerNGF	✓		✓
AmerGF	✓		✓

#### Environmental Data Patching

Water quality profiles were aggregated and averaged to align with the location of net sampling in the water column. Values for each variable within 2m of each station's midwater depth were averaged for the deep tows and values measured between 0.5-m and 1-m depth were averaged for the shallow tows for each cruise. In several instances, I was unable to collect water quality profiles due to equipment

failure in the field. In these instances, values of each water quality variable were estimated using multiple linear regression model-based predictions (Tables 6 and 7) similar to Millette et al. (2020). Predictor variables used to estimate local water quality variable values included water temperature data from proximal monitoring stations PXT0455 (Maryland DNR Eyes on the Bay, 2021), 8577330 (NOAA Tides & Currents, 2021), Horn Point Laboratory Oyster Hatchery (UMCES Horn Point Laboratory, *Pers. Comm.*), Chesapeake Biological Lab Research Pier (UMCES Chesapeake Biological Laboratory, 2021) and river flow from USGS monitoring gauges 01594440 and 1491000 (USGS Water Data for the Nation, 2021), as well as station and year values (see Appendix, Table A1.). Year was included because additional monthly profile data that were not included in this thesis were available from all stations in 2019. All modeling was performed using R statistical software (R Core Team, 2015).

**Table 6.** Linear models used to patch missing environmental data using salinity and temperature data from Horn Point Laboratory Oyster Hatchery (HPL), temperature data from NOAA Tides & Currents (NOAA), temperature data from Maryland DNR Eyes on the Bay (EOTB), salinity data from Chesapeake Biological Laboratory (CBL), and stream flow data from USGS Water Data for the Nation (river flow).

<b>Parameter</b>	<b>Equation</b>	<b>Model</b>
Choptank Temperature	A	Temp = HPL temp + Chop river flow + station + year + station*year
Patuxent Temperature	B	Temp = NOAA temp + EOTB temp + station + year + station*year
Choptank Salinity	C	Sal = Chop river flow + HPL sal + station + year + station*year
Patuxent Salinity	D	Sal = Pax river flow + CBL sal + EOTB sal + station + year + station*year

**Table 7.** Linear model summaries for missing environmental data with parameter estimates (with standard errors, SE) and measure of model fit ( $R^2$ ). See Table 6 for a description of predictor variables.

River	Modelled Variable	R <sup>2</sup>	Predictor Variable	Estimate	SE	p
Choptank	Temperature	0.95	HPL Temperature	0.95	0.032	< 0.0001
			River Flow	-0.0022	0.00069	0.00
			Station	341	132.00	0.01
			Year	0.80	0.33	0.02
			Station*Year	-0.17	0.065	0.01
	Salinity	0.86	HPL Salinity	0.98	0.095	<0.0001
			River Flow	-0.003	0.001	0.02
			Station	85.30	283.00	0.76
			Year	0.45	0.69	0.52
			Station*Year	-0.042	0.14	0.77
Patuxent	Temperature	0.95	NOAA Temperature Upstream	0.73	0.045	< 0.0001
			Temperature	0.21	0.045	<0.0001
			Station	3.28	1.73	0.06
			Year	1.25	0.40	0.002
			Station*Year	-0.19	0.093	0.04
	Salinity	0.84	River Flow	-0.0003	0.0001	0.02
			CBL Salinity	0.94	0.17	<0.0001
			Upstream Salinity	-1.28	5.54	0.82
			Station	11.40	3.19	0.0006
			Year	1.25	0.75	0.10
			Station*Year	-0.54	0.17	0.003

## Statistical Analysis

### Environmental models

Once gaps in the water quality dataset were filled using the above models, water quality variables were modeled to test for differences between tributaries and among months during the study period. Potential predictors for each water quality variable included River, Month, the River\*Month interaction, station depth, and the



other water quality variables. For example, the starting model for water temperature was:

$$\text{Temperature} \sim \text{River} + \text{Month} + \text{River} * \text{Month} + \text{Salinity} + \% \text{DO}$$

Month was evaluated in each model as a continuous and categorical variable, and the version of Month included in the best performing model was used for each variable.

Initially, linear models were fitted to the data, however an examination of model residuals indicated violations of the parametric assumption of residual normality (Shapiro-Wilk normality test output below, also see Appendix Figures A1, A3, A5):

- temperature model:  $W = 0.92$ ,  $p\text{-value} < 0.0001$
- Salinity model:  $W = 0.93$ ,  $p\text{-value} < 0.0001$
- % DO model:  $W = 0.93$ ,  $p\text{-value} < 0.0001$

As an alternative, generalized additive models (GAM) of individual environmental variables were fitted using the same suite of potential predictor variables. GAMs were structured with an identity link assuming a normal error distribution and parameters were estimated using restricted maximum likelihood (Wood 2017). Final models were determined after stepwise adjustments based on AIC, dimension index significance level, adjusted  $R^2$ , and residual plot comparisons between models. Number of basis functions (k) per spline were adjusted to maximize fit without compromising predictive power. All analyses and plot generation were performed with R statistical software (R Core Team, 2023). GAM functions were supplied by the “*mgcv*” (Wood, 2023) and plotting graphics were supplied by “*ggplot*” (Wickham, 2016) packages.

Abundances of three groups, all mysids combined (Total mysids), only mysids belonging to the species *Neomysis*, and only mysids belonging to the genus *Americamysis* spp., were analyzed for spatial and temporal patterns within and among rivers. Juveniles were excluded from all but the “Total mysids” category as they were not identified to genus level. Differences in mean abundances between surface and deep net abundances were tested using paired Wilcoxon signed rank tests with continuity correction for each river. Tests were run separately for each river to determine if the effect of net location within the water column differed between the two rivers. Differences in abundance between rivers were tested for each taxonomic group by performing Kruskal-Wallis rank sum tests of month-station means. Differences in abundance between months within individual rivers was tested by performing a Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment. Parametric assumptions of residual normality and homogeneity of variance were evaluated and where assumptions were violated, a Wilcoxon signed-rank test with continuity correction was used to test differences in mysid abundance by genus for each month in each river.

Mysid demographic structure between rivers was analyzed using Kruskal-Wallis rank sum tests as non-normal distributions were detected for all demographic groups being examined. Differences between rivers in the ratios of three demographic groupings (*Neomysis* total: *Neomysis* female, *Neomysis* non-gravid female:*Neomysis* gravid female, and *Neomysis* total: *Neomysis* juveniles) were tested for median differences in distributions. The same ratios were compared across months without respect to river using Dunn (1964) Kruskal-Wallis multiple comparison test with

Holm's corrections (Knudson, 2009) of distribution medians. All tests were run using R statistical software (R Core Team, 2023). This analysis and plot generation was performed with R statistical software (R Core Team, 2023) using functions supplied by "ggplot" (Wickham, 2016), and "FSA" (Ogle et al., 2023) packages.

## Results

### Environmental Conditions

For all three water quality models, GAMs provided better or equal predictive power than linear models while better meeting the assumption of residual normality (Table 8; also see Appendix Figures A2, A4, A6). For water temperature, the best performing GAM variant included river as the only class variable and splines for month, dissolved oxygen saturation, and salinity (Table 9). For salinity, significant predictor variables included river, month, and the river\*month interaction as class variables in addition to splines of dissolved oxygen saturation and temperature (Table 10). Significant predictor variables for dissolved oxygen saturation were the class variables of river and month, and splines of temperature and sampling depth (Table 11).

**Table 8.** Environmental model fitting results for water temperature, salinity and % dissolved oxygen saturation showing initial linear model (LM) and generalized additive model (GAM) results (Dev Ex – Deviance explained).

Type	Parameter	Equation	df	Adj. R <sup>2</sup>	
LM	Temperature	G	104	0.98	
LM	Salinity	H	104	0.62	
LM	Dissolved Oxygen	I	105	0.52	
Type	Parameter	Equation	df	Adj. R <sup>2</sup>	Dev Ex
GAM	Temperature	J	11.64	0.98	98.2%
GAM	Salinity	K	14.9	0.65	69.0%
GAM	Dissolved Oxygen	L	14.6	0.73	61.4%

**Table 9.** Environmental GAM fitting results for water temperature (Equation J, Table 8). Spline abbreviations: s(sat)= %dissolved oxygen spline, s(sal)= salinity spline, and s(month)= month spline.

Splines	edf	Ref.df	F	p
s(sat)	2.13	2.62	14.21	<0.0001
s(sal)	3.54	4.45	17.11	<0.0001
s(month)	3.97	4.00	1079.32	<0.0001
Parametric Terms	df		F	p
River	1.00		2.86	0.09

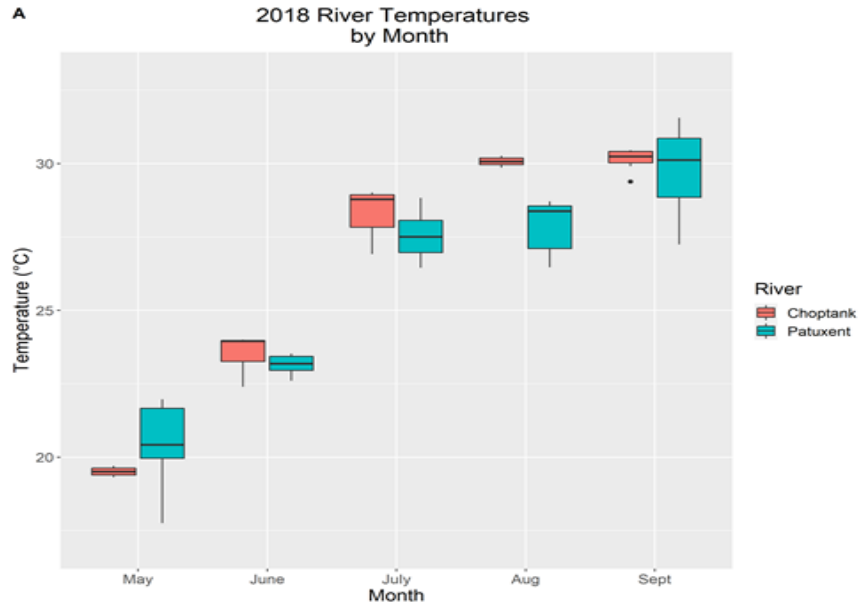
**Table 10.** Environmental GAM fitting results for salinity (Equation K, Table 8). Spline abbreviations: s(sat)= %dissolved oxygen spline, s(temp)= temperature spline.

Splines	edf	Ref.df	F	p
s(sat)	1.72	2.12	3.49	0.09
s(temp)	4.19	5.22	19.28	<0.0001
Parametric Terms	df		F	p
Month	3.00		23.55	<0.0001
River	1.00		49.59	<0.0001
Month:River	4.00		12.88	<0.0001

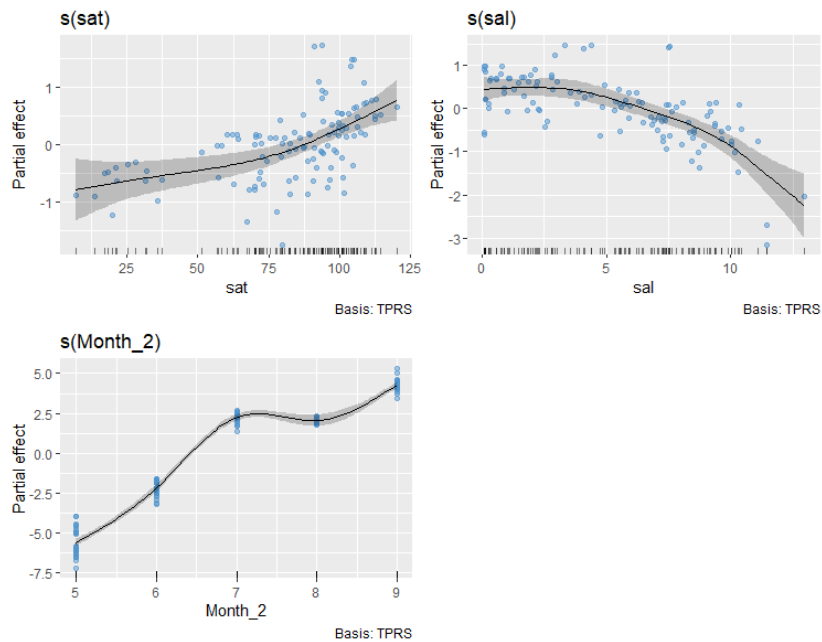
**Table 11.** Environmental GAM fitting results for dissolved oxygen saturation (Equation L, Table 8). Spline abbreviations: s(temp)= temperature spline, s(depth)= water depth spline.

<b>Splines</b>	<b>edf</b>	<b>Ref.df</b>	<b>F</b>	<b>p</b>
s(temp)	5.26	6.35	15.62	<0.0001
s(depth)	3.34	4.09	13.82	<0.0001
<b>Parametric Terms</b>	<b>df</b>		<b>F</b>	<b>p</b>
Month	4.00		13.36	<0.0001
River	1.00		0.07	0.79

Average water column temperatures increased somewhat linearly from May to July during the first half of the sampling 2018 sampling season (Fig. 3, 4). This pattern occurred in both Choptank and Patuxent rivers. From July to August, temperatures remained steady before increasing again in September. The late summer increase in water temperature was more apparent in the Patuxent River than in the Choptank River (Fig. 3), otherwise water temperature was comparable between rivers during corresponding months. Throughout the study period, water temperature was positively associated with dissolved oxygen saturation and negatively associated with salinity (Fig. 4).

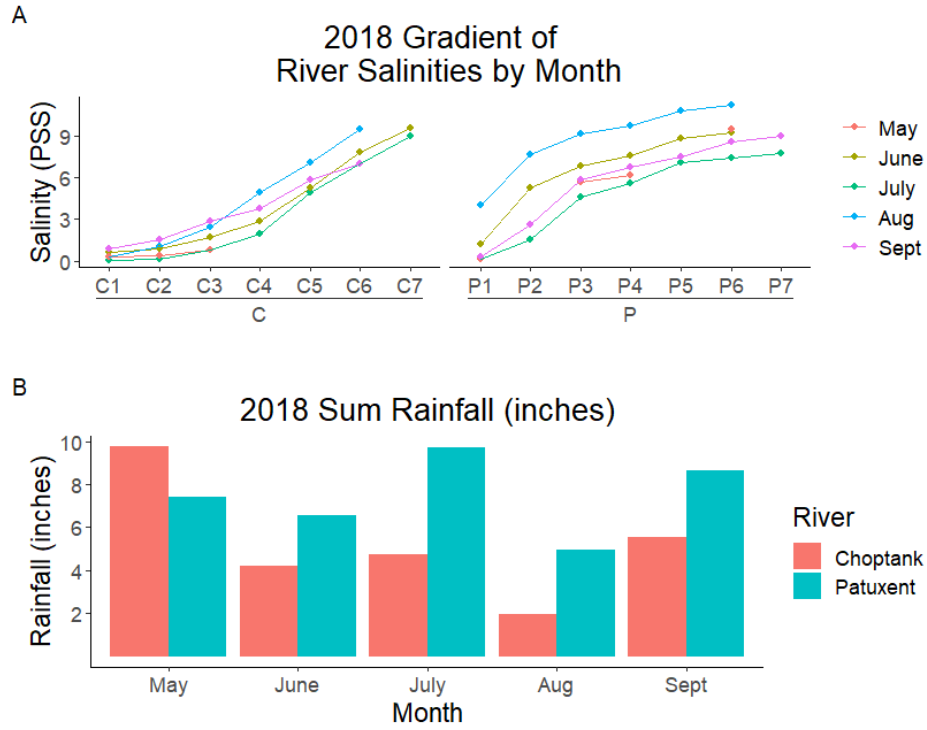


**Figure 3.** Boxplots of water column temperature distributions with interquartile range whiskers of Choptank and Patuxent at stations 1-7 during the 2018 sampling season. \*Station 7 was not consistently sampled (Table 2).



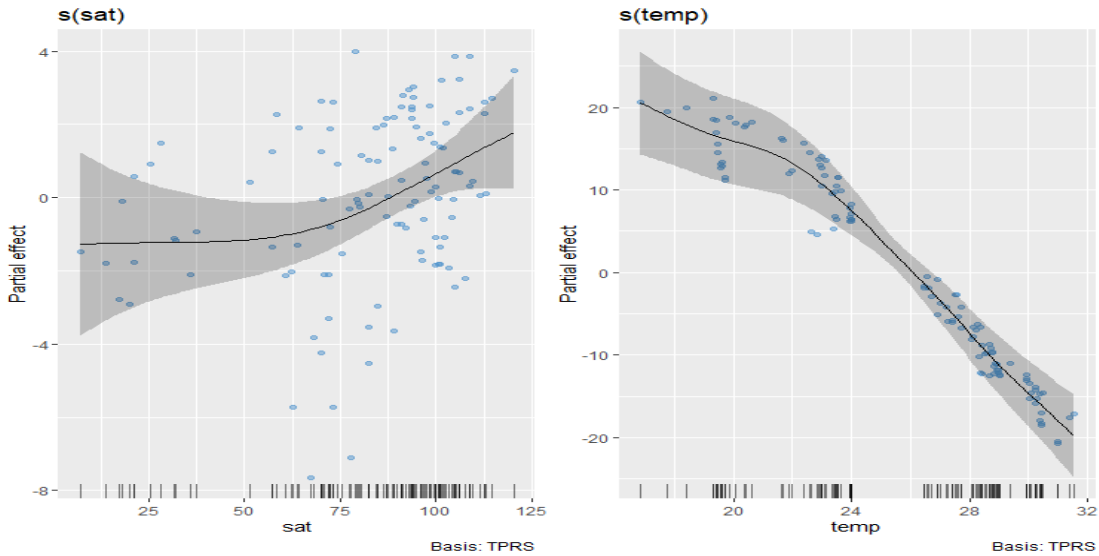
**Figure 4.** Partial effect plots for Equation J (see Table 8), the generalized additive model of water temperature. Black line represents modeled partial effect on temperature for each predictor (%DO saturation – s(sat); salinity – s(sal), Month – s(Month\_2)), shaded bands represent 95% confidence intervals.

Average water column salinity generally increased with proximity to the river mouths in both Choptank and Patuxent rivers, regardless of sampling month (Fig. 5A). Mean Choptank salinity ranged from 3.4 in August to 4.6 in May and Patuxent salinity ranged from 4.5 in August to 8.8 in May. Although the study was designed to target the same salinity regime between rivers, mean monthly salinities were significantly higher in Patuxent River compared to Choptank River (paired *t*-test,  $t=6.45$ ,  $df=4$ ,  $p<0.003$ ). In most instances, the highest monthly salinities were observed at a given station in August with the exception being salinities at Choptank stations C1-C3 in September (Fig. 5A). These monthly patterns aligned with monthly precipitation records from both river basins, with the month of highest salinity (August) experiencing the lowest recorded total rainfall in each basin (Fig. 5B). Salinity was qualitatively higher at greater depth each month in each river when comparing mean salinity at the surface to midwater depth. Throughout the study period, salinity was positively (albeit weakly) associated with dissolved oxygen saturation and negatively associated with water temperature (Fig. 6).



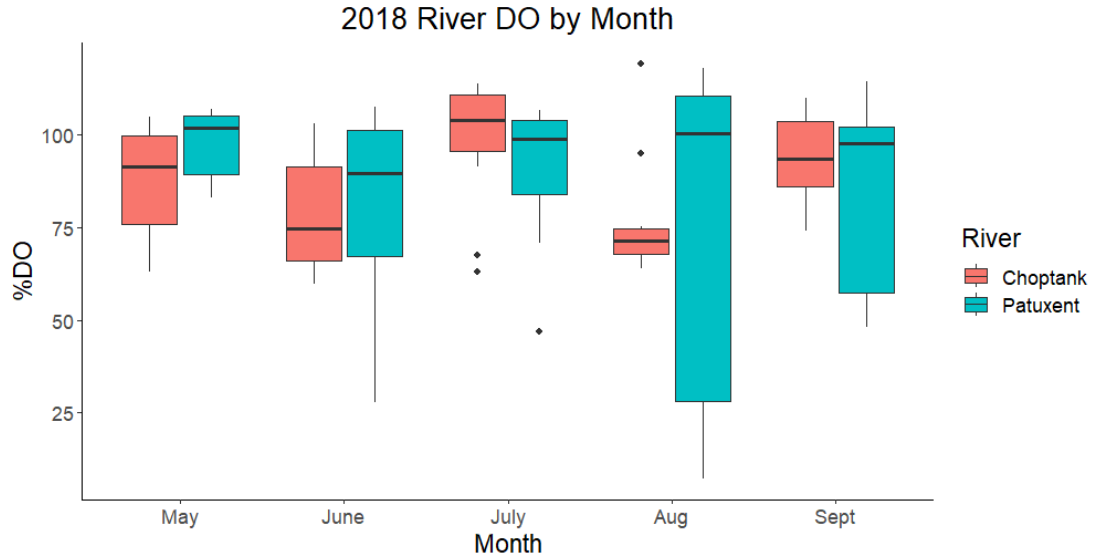
**Figure 5.** Average water column salinity (A) of Choptank and Patuxent stations 1-7 during the 2018 sampling season and monthly sum rainfall (B; based on Salisbury Ocean City Wicomico Regional Airport Station and St. Leonard Station Weather Underground data).



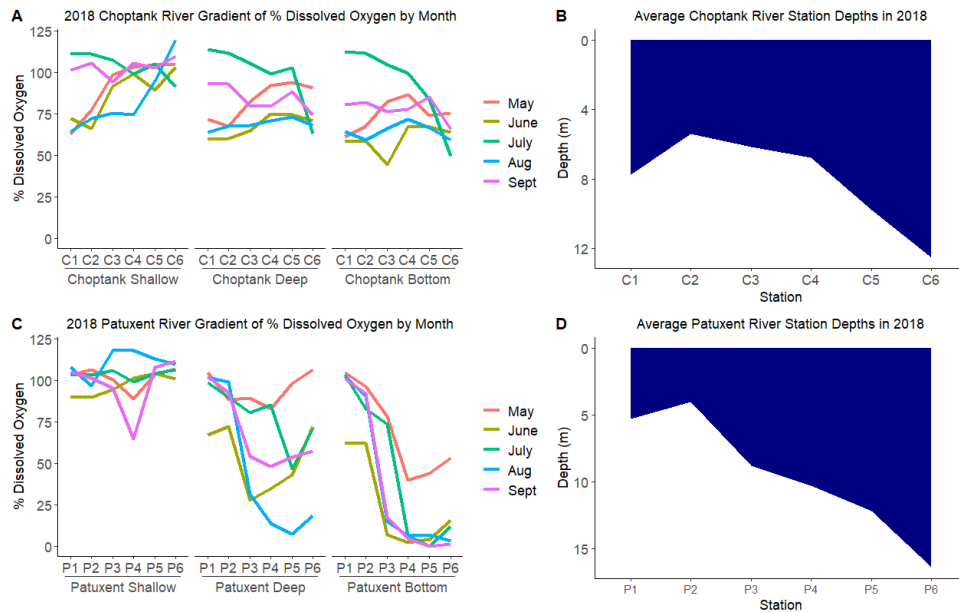


**Figure 6.** Partial effect plots for Equation K (see Table 8) generalized additive model (salinity). Black line represents modeled partial effect on temperature for each predictor (%DO saturation –  $s(\text{sat})$ ; temperature –  $s(\text{temp})$ ), shaded bands represent 95% confidence intervals.

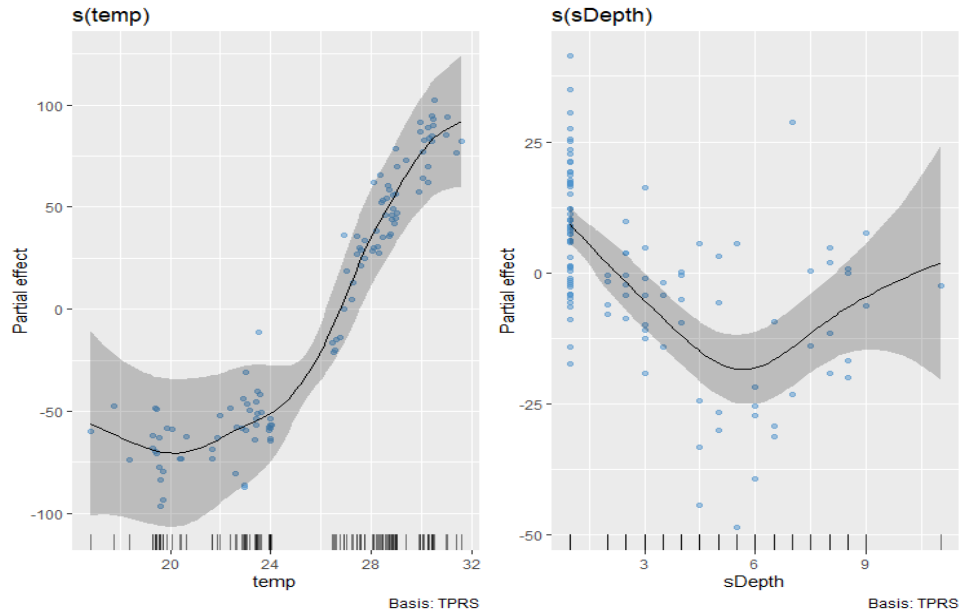
Variability of average water column dissolved oxygen generally increased by month in the Patuxent River (Fig. 7). Conversely, monthly measures of dissolved oxygen saturation in the Choptank River were less variable over time and less variable overall than those measurements made in the Patuxent River (Fig. 7). Low observed monthly mean dissolved oxygen occurred in the late summer in both rivers. The lowest mean values occurred for both Choptank and Patuxent rivers during August (76.0% and 77.9% respectively). Spatially, dissolved oxygen saturations were lowest at the deepest stations in both rivers, a pattern particularly apparent for the lower Patuxent stations P3-P6 (Fig. 8). Within the water column, dissolved oxygen saturation was typically higher at the surface and lower at mid-depth at a given station (Fig. 8). During the study, dissolved oxygen saturation was positively associated with water temperature and negatively associated with station depth (Fig. 9).



**Figure 7.** Boxplots of dissolved oxygen saturation (%DO) sample distributions with interquartile range whiskers by month in Choptank and Patuxent rivers in 2018.



**Figure 8.** Average dissolved oxygen saturation (%) by depth category of plankton tow (shallow: just below the surface, deep: midpoint between surface and bottom at each station, bottom: readings within 0.5m of bottom) of (A) Choptank River, (C) Patuxent River during the sampling season of 2018 \* and average (B) Choptank and (D) Patuxent station depths recorded in 2018.  
\*day cruise temps used for patching Aug values in this dataset



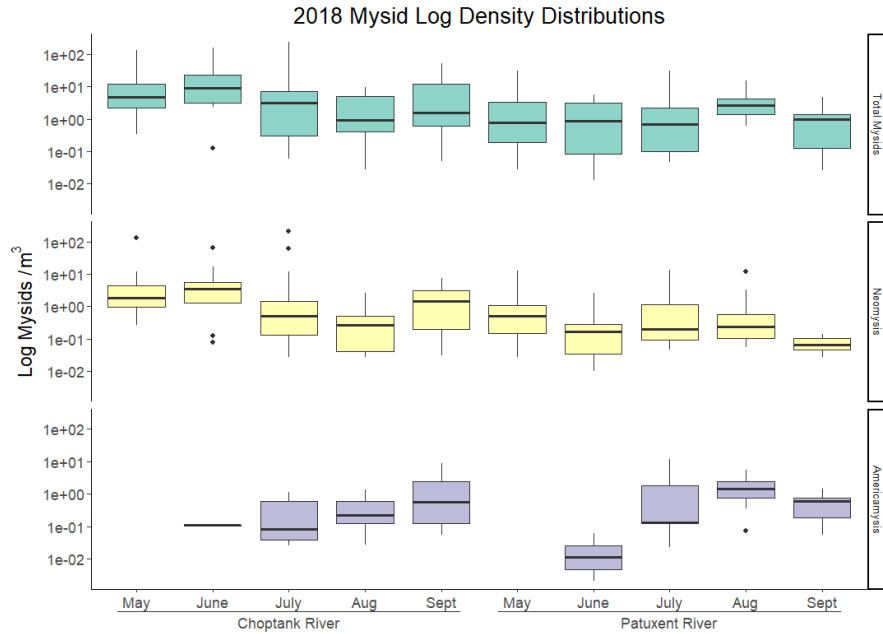
**Figure 9.** Partial effect plots for Equation K (see Table 8) generalized additive model of dissolved oxygen saturation. Black line represents modeled partial effect on temperature for each predictor (temperature –  $s(\text{temp})$ ; depth –  $s(\text{sDepth})$ ), shaded bands represent 95% confidence intervals.

#### Spatial and Temporal Patterns in Mysid Abundance

Using the 2018 samples, over 13,800 mysids were isolated and sorted into taxonomic and demographic categories. Results of a Kruskal-Wallis rank sum test revealed a significant difference between the total mysid group ( $H=12.02$ ,  $p=0.0005$ ) and *Neomysis* ( $H=7.51$ ,  $p=0.006$ ) between rivers. *Americamysis* spp. abundances did not differ between rivers ( $H=0.84$ ,  $p=0.4$ ) (Table 12). For the Total mysids and *Neomysis* groups, abundances were greater in the Choptank River than the Patuxent River (Fig. 10). This was reversed for *Americamysis* spp., where the test indicated greater abundances in the Patuxent River.

**Table 12.** Results from signed Kruskal-Wallis rank sum test for comparisons of differences of total mysid, *Neomysis americana*, and *Americamysis* spp. abundance between the Choptank and Patuxent rivers.

Taxon	df	H	p
Total mysids	1.00	12.02	0.0005
<i>Neomysis americana</i>	1.00	7.51	0.0006
<i>Americamysis</i> spp.	1.00	0.84	0.36



**Figure 10.** Monthly abundance distributions with interquartile range whiskers of all (total) mysids, and *Neomysis americana* and *Americamysis* spp. caught during sampling in the Choptank and Patuxent rivers during 2018.

Total mysid abundances were typically higher in Choptank River than the Patuxent River throughout the sampling season (Fig. 11). The exception to the pattern occurred in August, when Choptank total mysid abundance reached its lowest value of 30.3 mysids/m<sup>3</sup> and Patuxent total total mysid abundance peaked at 49.3 mysids/m<sup>3</sup> (Fig. 11). During the study period, Choptank total mysid abundance

peaked in June and July, while Patuxent mysid abundance peaks occurred in May and August.

Monthly abundances within rivers of Choptank and Patuxent river total mysids, *Neomysis*, and *Americamysis* spp. were compared using non-parametric two-tailed Wilcoxon signed-rank tests with continuity correction after residuals from paired *t*-tests failed to satisfy the assumption of normality. *Neomysis* occurred in greater numbers than *Americamysis* spp. from May to July of 2018 in Choptank River (Fig. 11, Table 13). There were no statistically significant differences between *Neomysis* and *Americamysis* spp. abundances in the Choptank River during August and September (Table 13). In the Patuxent River, *Neomysis* occurred in greater abundance than *Americamysis* spp. during May and June, there were no statistical differences between the abundances in July, and during August and September, *Americamysis* spp. occurred in greater abundance than *Neomysis* (Table 14).

In both rivers, mean abundances of *Neomysis* showed a similar, undulating pattern over time (Fig. 10). Abundances were high at the start of the survey before declining by 40% or more in June. Abundances then increased again to local maxima in each river in July. In August, *Neomysis* abundances declined abruptly and remained very low in the Patuxent River. In the Choptank River, abundances of *Neomysis* declined slightly but remained relatively high in August before declining rapidly in September.

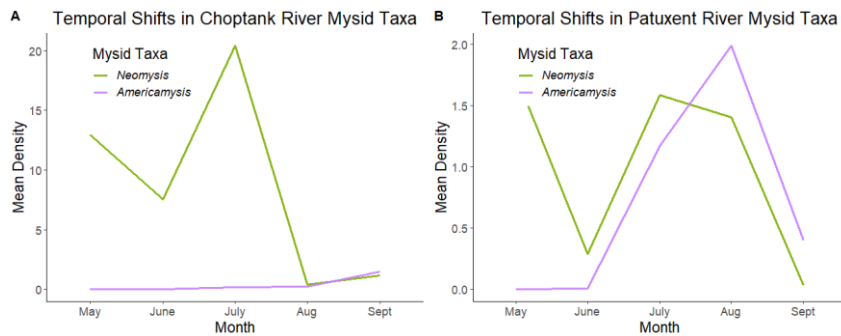
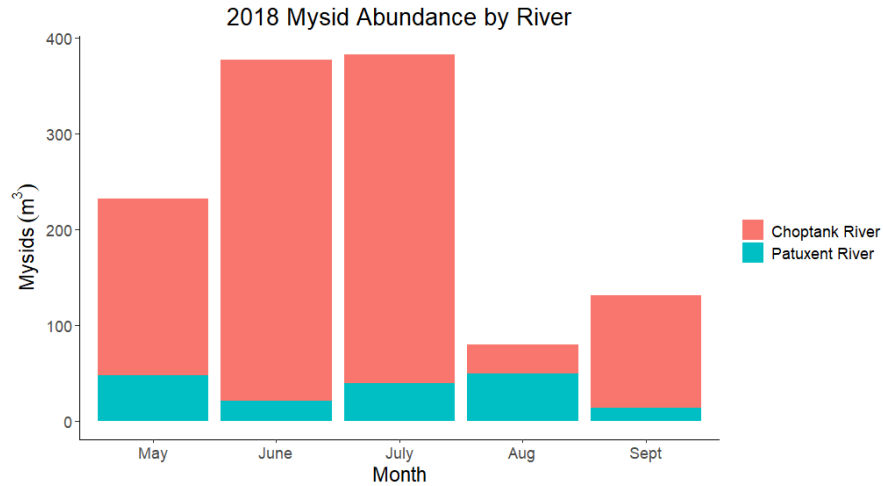
**Table 13.** Differences between *Neomysis americana* (neo) and *Americamysis* spp. (amer) monthly mean abundances in the Choptank River using the Wilcoxon rank sum test with continuity correction.

<b>Month</b>	<b>W</b>	<b>p</b>	<b>Relationship</b>
May	12	0.0001	neo > amer
June	26	0.0004	neo > amer
July	30.5	0.002	neo > amer
Aug	85.5	0.57	neo = amer
Sept	123.5	0.24	neo = amer

**Table 14.** Differences between *Neomysis americana* (neo) and *Americamysis* spp. (amer) monthly mean abundances in the Patuxent River using the Wilcoxon rank sum test with continuity correction.

<b>Month</b>	<b>W</b>	<b>p</b>	<b>Relationship</b>
May	0	<0.0001	neo > amer
June	28	0.0005	neo > amer
July	53	0.26	neo = amer
Aug	112	0.02	neo < amer
Sept	143	0.03	neo < amer

Unlike *Neomysis*, *Americamysis* spp. abundances generally increased over the study period (Fig. 11A, B). In both rivers, no *Americamysis* spp. were observed in May. By June, small numbers of the genera were present in both rivers, followed by relatively rapid increases during the mid-late summer months of July and August. Abundances of *Americamysis* spp. continued to increase in September in the Choptank but declined in the Patuxent.

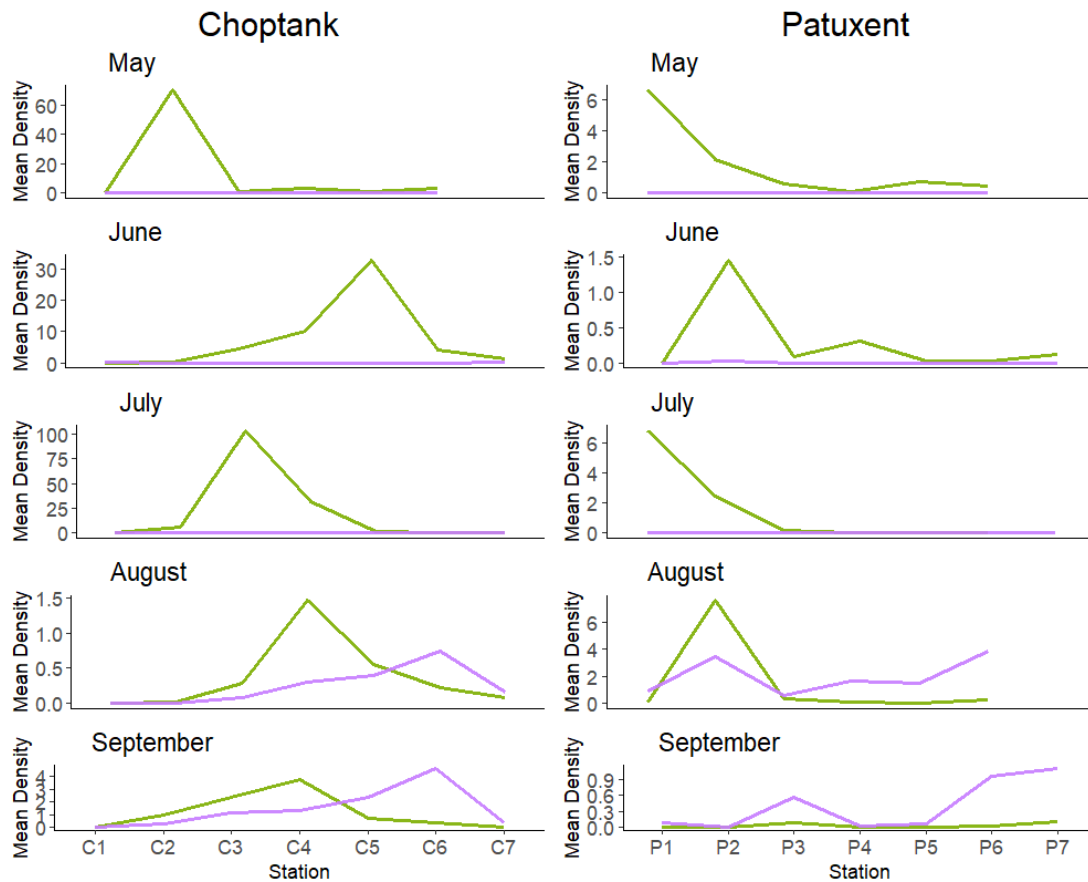


**Figure 11.** Mean monthly abundances (shallow and deep tow samples averaged across all sites for each month) of all (total) mysids (Top panel), and *Neomysis americana* and *Americamysis* spp. (Bottom panels, A & B) caught during sampling in the Choptank and Patuxent rivers during 2018. \* Differences in mysids (m<sup>3</sup>) due to inclusion of juvenile counts in top panel (total mysid sample population); juveniles were excluded from *Neomysis* and *Americamysis* abundances in bottom panels (also see Table 5).

Within rivers, abundances of each mysid taxon differed monthly among stations (Figure 12). In the Choptank, *Neomysis* abundance peaks appeared from station C2 (upstream) to C5 (downstream) over the sampling season while *Neomysis* abundance peaks in the Patuxent occurred predominantly at the more upstream sites (stations P1, P2). With the exception of May, peak *Neomysis* abundances occurred at mid-to-downstream stations (C3 to C5). *Neomysis* abundance did not differ

significantly between months in the Choptank River according to results of a Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment (Table A2), but did differ in abundance between June–July and July–August (Table A4). *Americamysis* spp. abundance peaks were typically observed at more downstream stations in both rivers (Fig. 12). This pattern was more apparent in the Choptank River, where there was a clear peak in *Americamysis* spp. abundances at station C6 in August and September. Despite this peak, *Americamysis* spp. were present in declining abundances at upstream stations C2–C5. According to results of a Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment, Choptank *Americamysis* spp. abundance did not differ between consecutive months, but did differ between June–Sept and May–Sept (Table A3). In both cases, the abundance was greater in September. In the Patuxent, *Americamysis* spp. were more widely distributed when present with peaks occurring from stations P2 to P7. There was some evidence of multiple modes of *Americamysis* spp. in the Patuxent, with localized peaks at upstream and downstream stations in the same month. A statistically significant increase in *Americamysis* spp. abundance occurred between July and August in the Patuxent River. Non-consecutive month differences were detected between June–August, May–August, and May–Sept for Patuxent River *Americamysis* spp. abundances. Significances of these differences were determined using a Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment (Table A5).



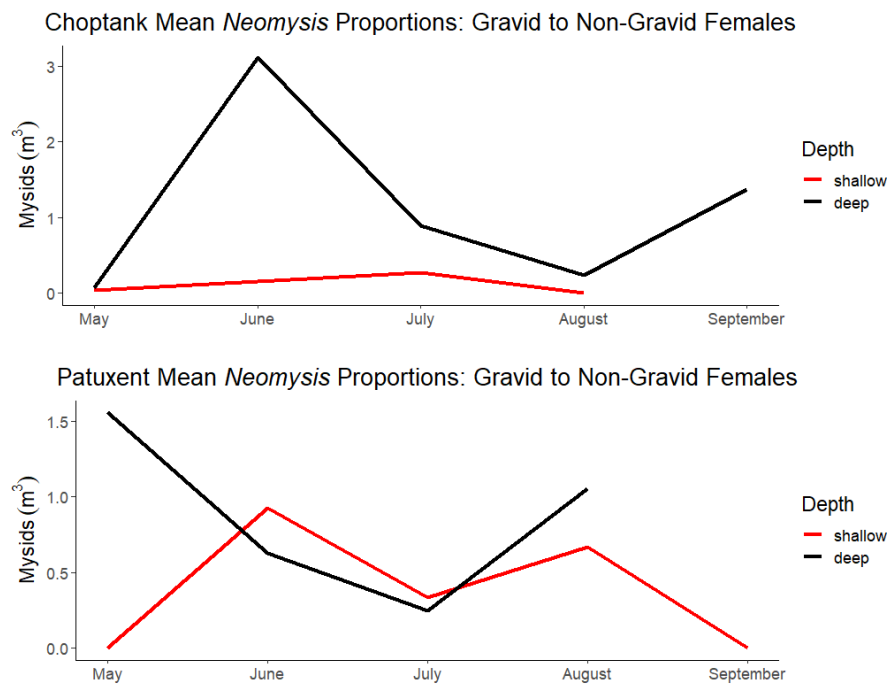


**Figure 12.** Mean monthly *Neomysis americana* (green line) and *Americamysis* spp. (purple line) abundances observed at each sampling station in each river (note differences in y-axes by river and month).

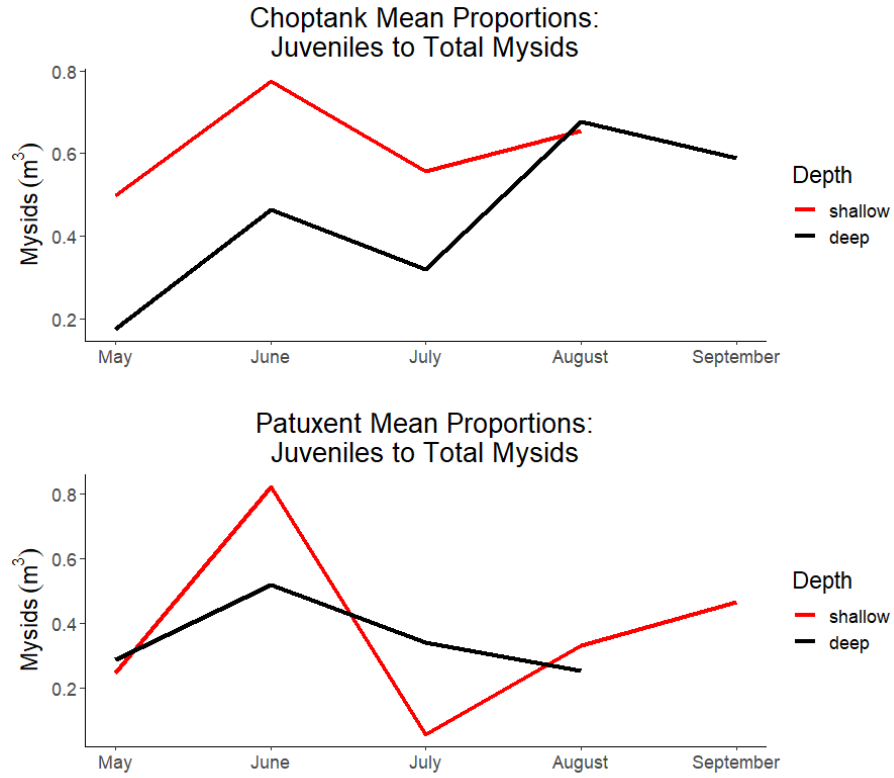
#### Mysid Demographic Patterns

The greatest monthly mean ratio of gravid to non-gravid *Neomysis* females peaked in catches from the deep net collections (mid-water column) in both rivers, but it occurred during May in the Patuxent ( $1.55 \pm 0.66$  [SE]) and during June in the Choptank ( $3.11 \pm 2.25$ ) (Fig. 13). The monthly mean proportion of total mysids contributed by juveniles was greatest ( $0.78 \pm 0.12$ ) in June's shallow tow of Patuxent River and in September's shallow tow ( $0.82 \pm 0.06$ ) of the Choptank (Fig. 14). The monthly proportion of total *Neomysis* contributed by females *Neomysis* in the

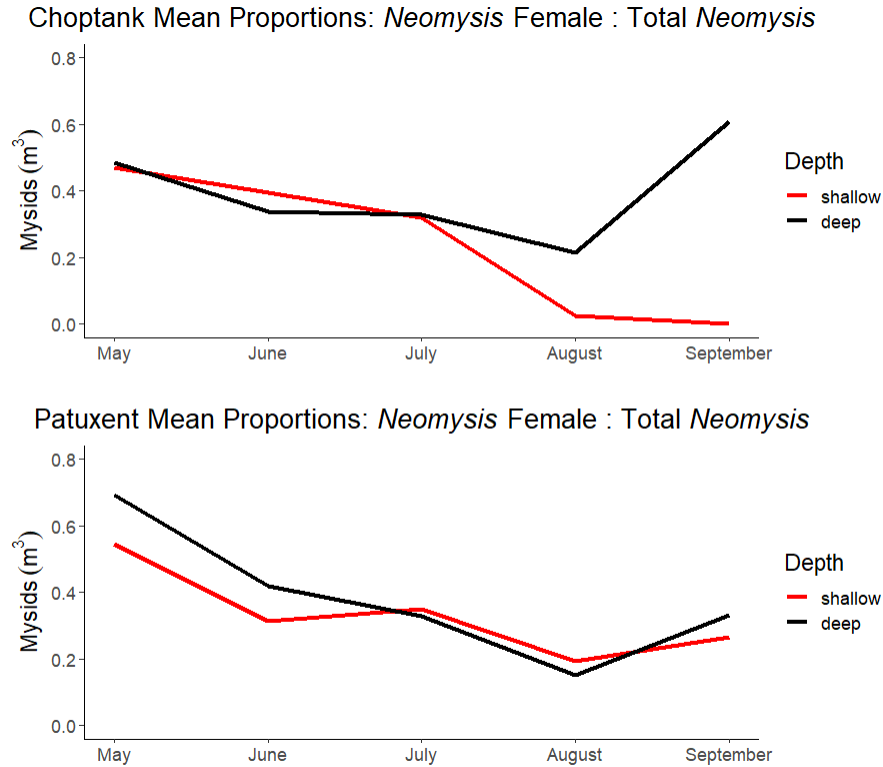
Choptank River were greatest in September's deep tow ( $0.61 \pm 0.03$ ) and Patuxent proportions were greatest in May's's deep tow ( $0.69 \pm 0.61$ ) (Fig. 15). The greatest proportion of juveniles contributing to total mysids occurred in September's shallow tow of the Choptank River (1.00) and in June's shallow tow (1.00) of the Patuxent. The greatest proportion of *Neomysis* female contributing to total *Neomysis* in the Choptank occurred in July's shallow tow (0.69) and the greatest Patuxent proportion occurred in May's shallow tow (1.00). Kruskal-Wallis rank sum tests revealed no differences in ratios between rivers (Table 15,  $p \geq 0.11$ ).



**Figure 13.** Ratio of gravid to non-gravid female *N.americana* by depth category (shallow: surface sample, deep: mid-water sample) and month.



**Figure 14.** Proportion of total mysids composed of juveniles by depth category (shallow: surface sample, deep: mid-water sample) and month.



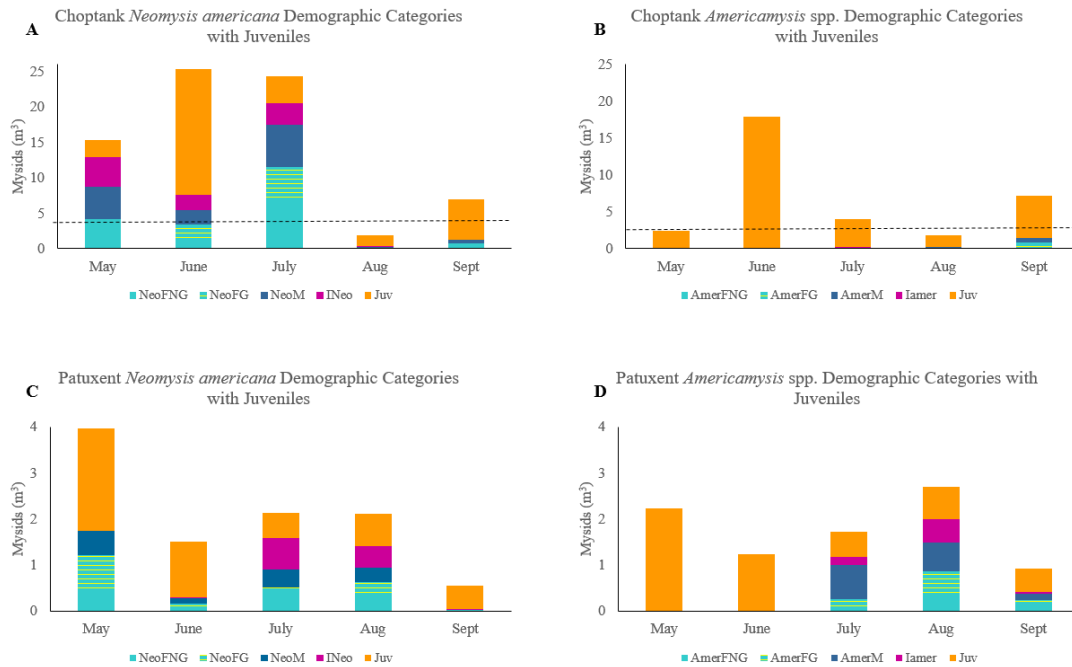
**Figure 15.** Proportion of total mysids composed of juveniles by depth category (shallow: surface sample, deep: mid-water sample) and month.

Comparison of the same 3 proportions across months revealed significant differences. The system-wide juvenile proportion differed significantly between July and June ( $Z=-3.34$ ,  $p=0.0085$ ) and June and May ( $Z=2.91$ ,  $p=0.033$ ) according to Dunn (1964) Kruskal-Wallis multiple comparison with Holm's adjustment. The Choptank juvenile proportion did not differ between months, but the Patuxent juvenile proportion differed between July and June ( $Z=-3.18$ ,  $p=0.015$ ). Ratios of gravid to non-gravid *Neomysis* females did not differ significantly between months according to Kruskal-Wallis rank sum tests, but differed between May and September in the Choptank ( $Z=-2.97$ ,  $p=0.03$ ). Monthly ratios of gravid *Neomysis* females to non-gravid *Neomysis* females did not differ in distribution medians (Kruskal-Wallis

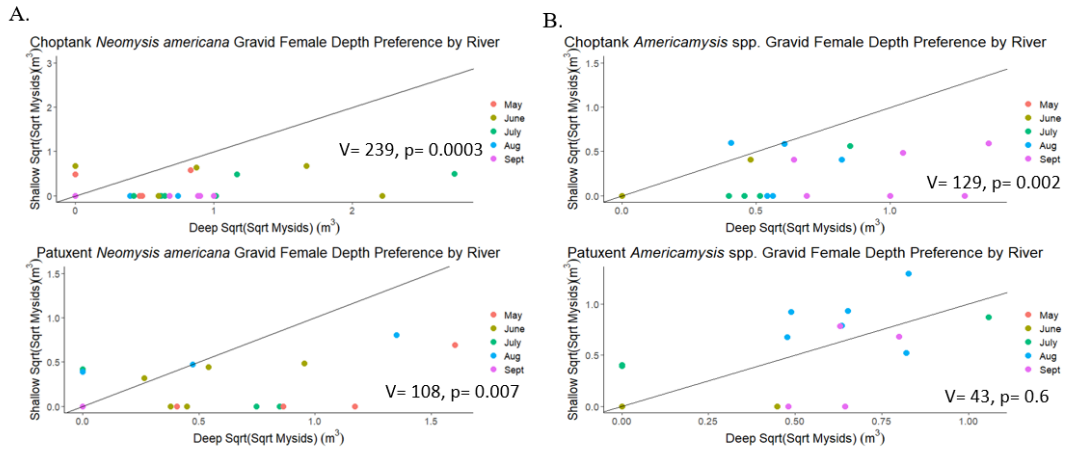
H=5.5.19, df=4, p=0.27) between months system-wide. Significant differences among months in ratios of female *Neomysis* to total *Neomysis* were observed between May and September (Z=-2.97, p=0.03)

**Table 15.** Kruskal-Wallis rank sum tests statistics from comparisons of distribution median differences between Choptank and Patuxent river ratios for juveniles (unspciated), total mysids, and *Neomysis americana* (*Neomysis*) total, females, gravid females, and non-gravid females.

Demographic Ratio	Kruskal-Wallis $\chi^2$	df	p
juvenile : Total mysids	2.50	1	0.11
<i>Neomysis</i> female : <i>Neomysis</i> total	0.25	1	0.62
<i>Neomysis</i> non-gravid : <i>Neomysis</i> gravid	1.9	1	0.17



**Figure 16.** Mysid abundances by demographic group (see Table 4) observed in the Choptank (A, B) and Patuxent (C, D) rivers from May to September 2018. Dashed line in the Choptank/top panels designates the maximum observed mysid abundance in the Patuxent River as a reference.



**Figure 17.** Abundance of *Neomysis americana* (A) and *Americamysis* spp. (B) gravid female abundance in deep vs shallow tows with 1:1 reference line and Wilcoxon signed rank test with continuity correction test statistics and significance values.

#### Environmental Correlations with Mysid Abundances

Significant correlations between water temperature and station depth, and the abundances of several mysid demographic groups were observed (Table 16). For *Neomysis* total and non-gravid females, abundances were negatively correlated with water temperature. Total and gravid *Neomysis* showed a positive correlation with depth. All *Americamysis* spp. groups were positively correlated with water temperature, and *Americamysis* spp. total and gravid females were also positively correlated (prior to Bonferroni correction) with station depth (Table 16). Aggregated groups of all mysids and all juveniles (across genera) did not show any significant correlations with water temperatures, salinity, dissolved oxygen, or depth. Gravid females of both *Neomysis* and *Americamysis* spp. showed preferences for the mid-water (“deep”) sampling depth compared to the surface (“shallow”) sampling depth except for *Americamysis* spp. in the Patuxent, which displayed no statistically significant preference (Fig. 17).

**Table 16.** Kendall’s rank correlation analysis results using a subset of mysid demographic groups (Total: Mysids, *Neomysis americana*, *Americamysis* spp.; non-gravid females: *Neomysis*, *Americamysis* spp.; gravid females: *Neomysis*, *Americamysis* spp., sexually immature juveniles [both genera]), and the environmental variables: temperature, dissolved oxygen saturation, salinity, and sample collection depth. Bolded text denotes significant correlations at  $\alpha = 0.05$ , Italic text denotes Bonferroni-corrected  $\alpha = 0.0016$ .

<b>Demographic</b>	<b>Variable</b>	<b>p</b>	<b>z</b>	<b>tau</b>
All	Temperature (°C)	<b>0.02</b>	-2.27	-0.16
<i>Neomysis</i>	Oxygen Saturation (%)	0.81	-0.24	-0.02
	Salinity	0.74	0.34	0.02
	Depth (m)	<b>0.02</b>	2.32	0.17
<i>Neomysis</i>	Temperature (°C)	<b>0.046</b>	-1.99	-0.14
Non-gravid	Oxygen Saturation (%)	0.74	0.33	0.02
	Salinity	0.43	-0.79	-0.05
	Depth (m)	0.25	1.15	0.09
<i>Neomysis</i>	Temperature (°C)	0.12	-1.57	-0.12
gravid	Oxygen Saturation (%)	0.22	-1.24	-0.09
	Salinity	0.82	-0.22	-0.02
	Depth (m)	<b>0.004</b>	2.88	0.22
All	Temperature (°C)	<b>&lt;0.0001</b>	4.54	0.34
<i>Americamysis</i>	Oxygen Saturation (%)	1	0	0
	Salinity	0.34	0.95	0.07
	Depth (m)	<b>0.05</b>	1.96	0.15
<i>Americamysis</i>	Temperature (°C)	<b>&lt;0.0001</b>	4.59	0.35
non-gravid	Oxygen Saturation (%)	0.68	-0.41	-0.03
	Salinity	0.41	0.82	0.06
	Depth (m)	0.13	1.52	0.12
<i>Americamysis</i>	Temperature (°C)	<b>0.0004</b>	3.57	0.27
gravid	Oxygen Saturation (%)	0.36	-0.91	-0.07
	Salinity	0.41	0.82	0.06
	Depth (m)	<b>0.002726</b>	3.00	0.24
All Juveniles	Temperature (°C)	0.53	-0.63	-0.04
	Oxygen Saturation (%)	0.81	-0.24	-0.02
	Salinity	0.87	0.16	0.01
	Depth (m)	0.45	0.75	0.05
All Mysids	Temperature (°C)	0.62	-0.50	-0.03
	Oxygen Saturation (%)	0.94	0.08	0.01
	Salinity	0.75	0.32	0.02
	depth (m)	0.10	1.66	0.12

## Discussion

The goal of my study was to describe spatiotemporal patterns of mysids, a key prey group for ecologically, economically, and culturally important fish species, (Binion-Rock et al., 2019; Buchheister & Latour, 2015; Pagenkopp Lohan et al., 2023) within two Chesapeake Bay tributaries. I hypothesized that mysid abundances would be higher in the Choptank River because previous research has shown the Patuxent River experiences relatively worse water quality in deep channel waters during the summer, a key putative habitat for the diel vertically migrating mysids in these rivers. Further, I hypothesized that mysid assemblages would be dominated by *Neomysis* based on historical reporting (Cowles 1930). I collected plankton and water quality samples from 6–7 stations in each tributary once a month for five months (May–September, 2018). Samples were also collected during the same months of 2019, but sample preservation failed in some instances, leading to an incomplete dataset. Therefore, the 2019 data were not used as part of my thesis.

Analyses of the over 13,800 mysids examined revealed previously unreported details regarding the spatial and temporal patterns of mysid abundance in Chesapeake Bay. Overall, I found significant differences in the abundance of mysids between the Choptank and Patuxent rivers with total mysid and *Neomysis* abundances being greater in the Choptank River and *Americamysis* spp. not differing between rivers, partially supporting the initial hypothesis. Reproduction appears to be temporally offset between the two genera, with *Neomysis* reproducing earlier in the spring and *Americamysis* spp. reproducing later in the summer. Further, I documented significant correlations between station temperature and the abundances of *Americamysis* spp.



females (Kendall's tau; gravid:  $\tau=0.27$ ,  $p<0.0001$ ; non-gravid:  $\tau=0.35$ ,  $p<0.0001$ ) (Table 16).

#### Spatiotemporal Shifts

The dominant mysid species in both rivers for the majority of the sampling season was *Neomysis*. While the scale at which these abundances occurred differed between the rivers (abundances were greater in the Choptank than in the Patuxent), this pattern of taxonomic dominance was similar. *Neomysis* dominated both rivers in May and June, then dropped to near or below *Americamysis* spp. abundances from July to September. A shifting seasonal dominance pattern of *Neomysis* and *Americamysis* spp. observed in this study was also documented in a previous study of mysid dynamics within the geographically proximal (but non-contiguous) Maryland coastal lagoons (Mayor et al., 2017). This temporal shift in dominance suggests each taxon undergoes temporally-offset population events (i.e. breeding, migration) or experiences dissimilar population constraints (e.g., environmental controls). For example, *Neomysis* and *Americamysis* spp. were observed to display asynchronous breeding periods in the MD coastal lagoons, which resulted in offset abundance peaks (Mayor et al., 2017). In addition to differences in breeding intervals, relatively rapid movements into and out of the tributaries could contribute to the apparent quick turnover in species dominance in the assemblage. For example, *Neomysis*, when compared to that of other predominant mysid species of Georges Bank, showed a strong association with tidal fronts (Lough & Aretxabaleta, 2014). This association with tidal movement was also observed in the Delaware River Estuary, where study

findings suggested mysid movement into the basin originated from an off-shore population (Hulburt, 1957). In the case of *Neomysis*, onshore migration has been hypothesized to be facilitated by mysids' preference for more benthic habitats and layered estuarine circulation wherein mysids are carried into the basin with the net up-estuary movement of deeper water and subsequent avoidance of outflowing surface waters (Hulburt, 1957).

Given the similarity in body size and overlap in habitat for *Neomysis* and *Americamysis*, it is unlikely that taxon-specific predation pressure was responsible for this shift in dominance of one mysid taxon over the other within rivers. A large number of studies have demonstrated the importance of mysids as prey but few, if any, have specifically looked for evidence of diet selectivity of one species of mysid over another by fish predators. Likely this is due to the highly digested nature of mysids in the dissected stomachs of fish, making positive identification at the species level difficult. Fine-scale vertical or horizontal separation of mysids may have been present in the field but at scales too fine for my sampling to detect. Therefore, it is possible that seasonal changes in predation pressure could have contributed to differences in seasonal patterns between rivers.

The broad distribution of Choptank *Neomysis* abundance peaks and the greater mean abundance ranges (~32–104 mysids/m<sup>3</sup>) from May-July suggests that this population is less restricted by environmental factors within the study area than its Patuxent counterpart, which exhibited abundance peaks limited to the Patuxent's more upstream stations (P1 and P2). In addition to the more limited range of peak abundance locations, the magnitudes of abundance peaks were much smaller in the

Patuxent. Choptank *Neomysis* abundance peaks occur above 30 mysids/m<sup>3</sup> until July, after which point their mean abundance peaks drop below 4 mysids/m<sup>3</sup>. This is also the point at which Choptank *Americamysis* spp. abundances begin to increase relative to *Neomysis* abundances. Like the Choptank *Americamysis* spp., the Patuxent *Americamysis* spp. abundances began to increase relative to *Neomysis* abundances during August, and they remained the dominant taxa through September (Fig. 16).

In both rivers, *Neomysis* and *Americamysis* spp. abundances (particularly gravid females) tended to associate positively with sampling depth. The positive correlation of gravid female abundance of both taxa with depth is interesting and appears to reflect a shared life history strategy. It appears that gravid females remain deeper in the water column when releasing larvae however future work is required to explore this question. The co-occurrence of these two taxa at similar depths may result in either competition or niche partitioning during the period of transition from *Neomysis* dominance to *Americamysis* spp. dominance. Niche partitioning occurs when competition leads to dissimilar patterns of resource use by competitors (Vacher et al., 2016). The opportunistic and highly adaptable feeding behaviors of mysids may allow multiple species to coexist and mitigate the potential effects of competition (Calliari et al., 2007). For example, mysids can shift from raptorial depredation of copepods to filter feeding on phytoplankton (or vice versa) depending on resource availability (Viherluoto et al., 2000; Winkler et al., 2007). Further, Winkler et al. (2007) demonstrated field and experimental evidence of prey partitioning between *Neomysis* and a sympatric estuarine mysid species in the St. Lawrence River.

## Mysid responses to environmental conditions

The positive association of *Neomysis* and *Americamysis* spp. abundances (particularly gravid females) with sampling depth, and the mature gravid and non-gravid female demographic groups associating positively with temperature, possibly influenced the observed seasonal dominance shift. The developmental phases within the marsupium of the predominant *Americamysis* spp. found in the study area (*A. bahia*) are generally described in 3 phases: embryonic, nauplius, and post-nauplius (Mauchline, 1980). Wortham-Neal and Price (2002) found that the embryonic phase became longer with increasing temperatures, and higher (compared to another experimental temperature of 20°C) temperature (29°C) lengthened the post-nauplius phase but shortened overall incubation periods. Mean temperatures in August and September (Choptank: 30±0.03°C, 30±0.19°C and Patuxent: 27±0.09°C, 30±0.26°C, respectively) may explain the *Americamysis* spp. dominance during these months as their populations may be responding to a favorable temperature range that reduces brooding times.

Lower mysid abundances in Patuxent River may be explained by bathymetric differences between it and Choptank River. The Patuxent River has a wider and more consistently deep channel and despite both rivers receiving substantial anthropogenic nutrient inputs, the deeper bathymetry of the Patuxent River leads to the recurring seasonal formation of hypoxia in the Patuxent River (Breitburg et al., 2003; Keister et al., 2000; Testa et al., 2008). While hypoxia does occur in the Choptank River, the Choptank does not experience the same consistent, spatially extensive annual hypoxia that is observed in the Patuxent River (Fisher et al. 2006).

The presence of hypoxia in the Patuxent River was one of the primary factors underlying my initial hypothesis that mysid abundances would be higher in the Choptank, however hypoxia can also lead to more pervasive ecological problems such as benthic-pelagic decoupling (the loss of connectivity between benthic and pelagic ecosystems or food webs). Benthic macrofauna tend to migrate upward in the benthic sediment porewater or even into the water column to escape prolonged exposure to hypoxia in their preferred, deeper habitats, movements that can result in increased predatory encounter rate and a reduction of benthic community biomass and richness (Diaz et al., 1992; Karna, 2003; Riedel et al., 2014). An increase in predation upon displaced benthic or demersal organisms due to hypoxia has been documented in multiple studies (Pierson et al., 2022). Support for these observations comes, in part, from comparing predator diets during non-hypoxic and hypoxic time periods (Pierson et al., 2022). Changes in diet associated with hypoxia can alter the nutritional quality of prey or restrict access to high quality prey, leading to physiological consequences for predators (Pierson et al., 2022; Quillen et al., 2022). This may explain the higher tissue C:N composition observed in mysids from the Choptank River as compared to the Patuxent River (Quillen et al., 2022). Given that mysids in the Choptank River are less likely to experience habitat and resource restrictions than those of the Patuxent, where hypoxia could be directly limiting access to preferred benthic habitat or indirectly limiting food resources, these individuals may be better able to store excess energy gained through feeding as lipids to be used for other functions such as reproduction (Quillen et al., 2022).

Salinity generally increased along a sampling station gradient from “C1” and “P1” (most upstream locations) to “C7” and “P7” (most downstream locations). The more downstream the station, the closer in proximity the station is to the river mouth, and thus, confluence with the much saltier Chesapeake Bay. Tidal salt intrusion into the rivers was expected to diminish with distance from the intrusion source, and that pattern was observed. Monthly variation in salinity tended to correlate with differences in monthly rainfall (Fig 4). As rain dilutes salinity, monthly rainfall correlated inversely with salinity. It should be noted that 2018 was the wettest year on record for the Chesapeake basin, which almost certainly affected salinities therein. According to non-parametric rank correlations, mysid abundances were neither correlated with oxygen saturation nor salinity. This suggests that the parameter thresholds for these taxa were not present during sampling and thus, both taxa exhibited a wide tolerance of both oxygen saturation and salinity ranges. The wide salinity tolerance range for *Neomysis* has been observed in other systems and support these findings (Schiariti et al., 2006). However, salinity tolerance may be location-dependent as high availability of food in areas characterized by sharp, significant changes in salinity may be offsetting the increased energetic costs of regulating osmotic pressure in such environments (Schiariti et al., 2006), and temperature-dependent with respect to ontogenetic stages as these variables were found to correlate for *Neomysis* in the Laguna de Rocha estuary, Uruguay (Paul & Calliari, 2017) and hatchery-supplied *Americamysis* spp. (Modlin & Froelich, 1997). The magnitude of the dissolved oxygen influence on Chesapeake Bay mysid presence, abundance, and demographic dynamics may have been missed due to the project’s

sampling scheme. While water quality was measured from surface to bottom, mysids were only collected from surface and mid-water depths. Without a bottom mysid sample to pair with the depths that are most likely experiencing hypoxia, the effect of hypoxia's presence may have been missed.

#### Mysid Demographics

The proportion of *Neomysis* female to total *Neomysis*, ratio of *Neomysis* non-gravid female: *Neomysis* gravid female, and the proportion of juvenile to total mysids (hereafter referred to as female proportions, gravid ratios, and juvenile proportions, respectively) were not found to differ between rivers. The *Neomysis* demographic structure (with respect to the demographic proportion and ratio categories tested) appeared to be similar between the Choptank and Patuxent rivers. Mayor et al., (2017) found a similar pattern in mysid demographic ratios within Maryland's coastal lagoons. The largest ratio of gravid females occurring in deeper water, in May in the Patuxent River and in June in the Choptank River follows patterns observed in other studies and systems (Espinosa et al., 2019; Herman, 1963). The maximum juvenile ratio in the Choptank River was observed in September and in the Patuxent was observed in June, both in shallow water.

Differences of mysid demographics by depth have been attributed to developmental phase, body size, and event cues such as increased vertical migration of females during breeding events and less migration during the rest of the year (Herman, 1963; Lough & Aretxabaleta, 2014; Mauchline, 1980). The total female ratio maxima occurred in the shallow, July tow in the Choptank River and in the May,

shallow tow of the Patuxent River. While larger, mature mysids show an affinity for more benthic habitats, even during the night (Herman, 1963), Patuxent mysids were more likely to experience seasonal hypoxia in their preferred habitat (Fig. 7; Breitburg et al., 2003; Keister et al., 2000; Quillen et al., 2022; Testa et al., 2008). The presence of hypoxia could force the mature, more benthic individuals closer to the surface as an avoidance strategy to mitigate potential effects of low oxygen exposure (Diaz et al., 1992; LaRow, 1970; Taylor et al., 2003).

The system-wide ratio of juveniles significantly increased between June and July as well as between May and June, however, mean juvenile densities do not differ significantly between months system-wide or in either river. The variability in proportion between months is likely due to changes in other demographic groups. The system-wide ratio of gravid females to non-gravid females was consistent throughout the sampling season, suggesting that fecund *Neomysis* are present throughout the summer and likely engaged in continuous reproduction in this environment. Significant differences were detected in the system-wide ratio of total females between May and August, August and September, and July and September. The female ratio increased from May to August, and decreased between July and September, and August and September. This pattern, when considered with the juvenile monthly ratios, suggest the possibility that either, a) a single spring cohort of females may mature, then reproduce multiple times before dying, or b) that continuous reproduction coupled with rapid, temperature-dependent maturation of females leads to the relatively stable ratio of gravid females in the population during



the summer. Similar patterns of increasing and decreasing female ratios over time were observed in Canada and Argentina, where *Neomysis* are invasive (Bouchard & Winkler, 2018; Viñas et al., 2005; Wittmann, 1984). As stated earlier, future efforts should evaluate whether the later summer cohort are the result of multiple broods being produced by the same female cohort or if generations are overlapping during the summer period.

Once it is determined which species are present in target areas throughout the year, more studies can be done on species and organismal levels. For example, of the two known life history strategies of *Neomysis* females, more investigation is required to determine which they exhibit in the Chesapeake Bay system. The two strategies affect the growth rate, size at maturation, and clutch size of females (Bouchard & Winkler, 2018). The size of females and the presence of newly-released juvenile shrimp throughout a project's sampling seasons may lend insight into which life history strategies are being employed and their respective drivers.

### Conclusions

Mysids are a critical forage species for important Chesapeake Bay fisheries species (Buchheister & Latour, 2015; Friedland et al., 1988; Torre & Targett, 2017; Walter et al., 2003; Woodland & Secor, 2013). Despite their importance, mysid species are under-sampled and thus, their population dynamics are less understood than more easily sampled taxa. The difficulty in accurately estimating mysid populations lies in their horizontal and vertical diel migrations, as well as their seasonal migrations and complex life histories (Jumars, 2007; Sato & Jumars, 2008). This study aimed to examine not only abundances of mysids present, but the

population structures of the mysid taxa observed. Studies such as this, that build understanding of which mysids are present, when they are present, in what abundances they might be present, their correlations with biotic and abiotic environmental variables, and their limiting factors within the Chesapeake Bay tributaries provides the information necessary to meaningfully incorporate these forage taxa into ecosystem-based models.

Expanding current monitoring activities is required to extend our understanding of mysid distributions and abundance beyond the Patuxent and Choptank rivers. Year-round sampling, increasing sampling frequency, and increasing the number of stations in each river would provide a more complete dataset from which to draw conclusions. In addition to net sampling, using more sophisticated techniques would provide a more complete picture of spatiotemporal shifts in mysid assemblage. Multi-frequency acoustics and acoustic imaging have been utilized to identify mysid swarms (Kaltenberg & Benoit-Bird, 2013; Rogissart et al., 2023; Sato & Jumars, 2008). A preliminary collection of adaptive resolution sonar imaging data was collected during this study and could provide valuable additional insights. These data were collected during daylight hours when mysids often exhibit aggregating and vertical migration behaviors.

Stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analysis is one tool that could further be used to study habitat suitability for mysids within Chesapeake Bay. Using  $\delta^{13}\text{C}$  to identify food sources (or regions where food sources originated) and  $\delta^{15}\text{N}$  to estimate relative trophic position, could reveal additional insight into mysid foraging strategies. Using traditional stomach contents analysis, Fulton (1982) found that while other mysid

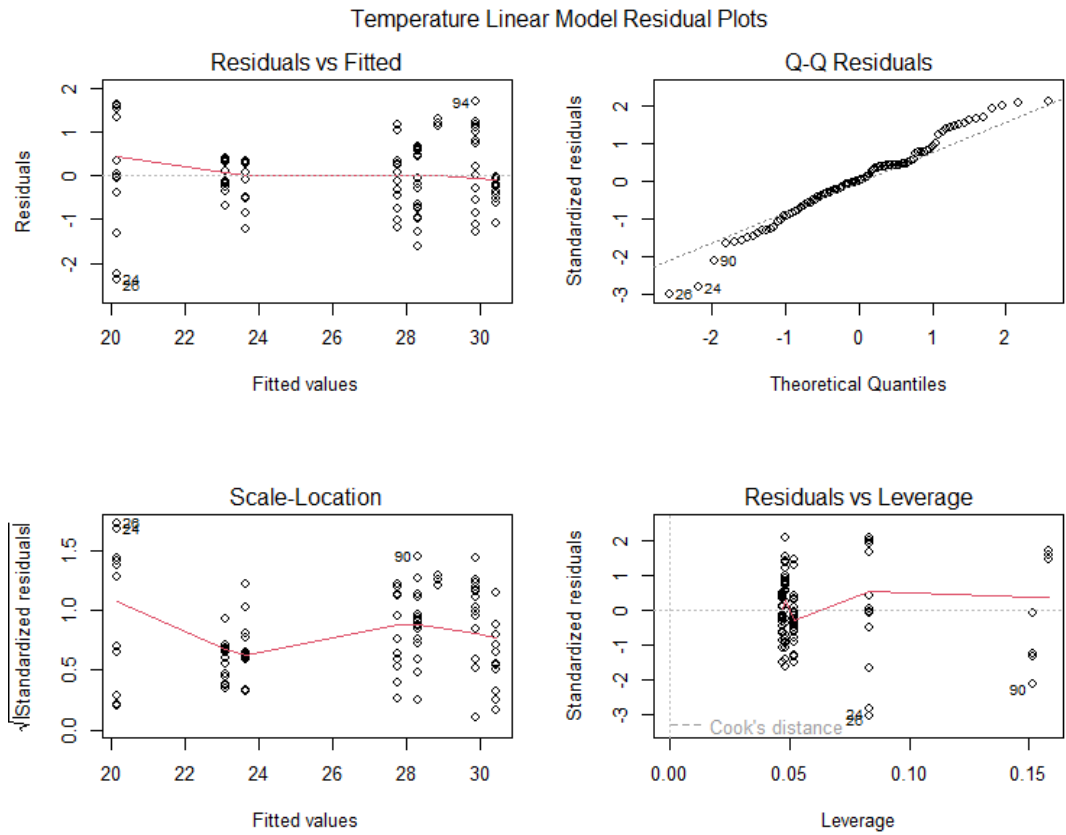
species tend to be carnivorous, *Neomysis* tends toward omnivory. Stomach contents analysis of mysids is difficult due to the grinding of prey within the gastric mill following ingestion, a process that can hinder visual identification of prey. Stable isotope analysis and similar biomarker approaches such as fatty acid profiles would avoid some of these issues and provide time-integrated data on assimilate diet. Quillen et al. (2022) used this approach to evaluate benthic-pelagic coupling of Patuxent and Choptank *Neomysis*, showing decoupling of mysids from benthic food webs in the presence of hypoxia. Studies such as that of Quillen et al. (2022) and Woodland and Secor (2013) that documented coupling of benthic and pelagic food webs by mysids demonstrates their flexibility in both nutrient acquisition and habitat utilization (Jumars, 2007). Uncovering the details of this flexibility specific to Chesapeake Bay's seasonal mysid migrants would allow for more targeted and comprehensive ecosystem-based fishery management models for Chesapeake Bay.

Establishing a comprehensive understanding of Chesapeake Bay mysid population dynamics and species contributions would allow for more effective conservation strategies of ecologically and economically important Bay species. As sampling techniques evolve and ecosystem-based management becomes more widely implemented in coastal ecosystems, there will be an increasing need for more complete studies of previously understudied, lower trophic level creatures such as mysids.

## Appendices

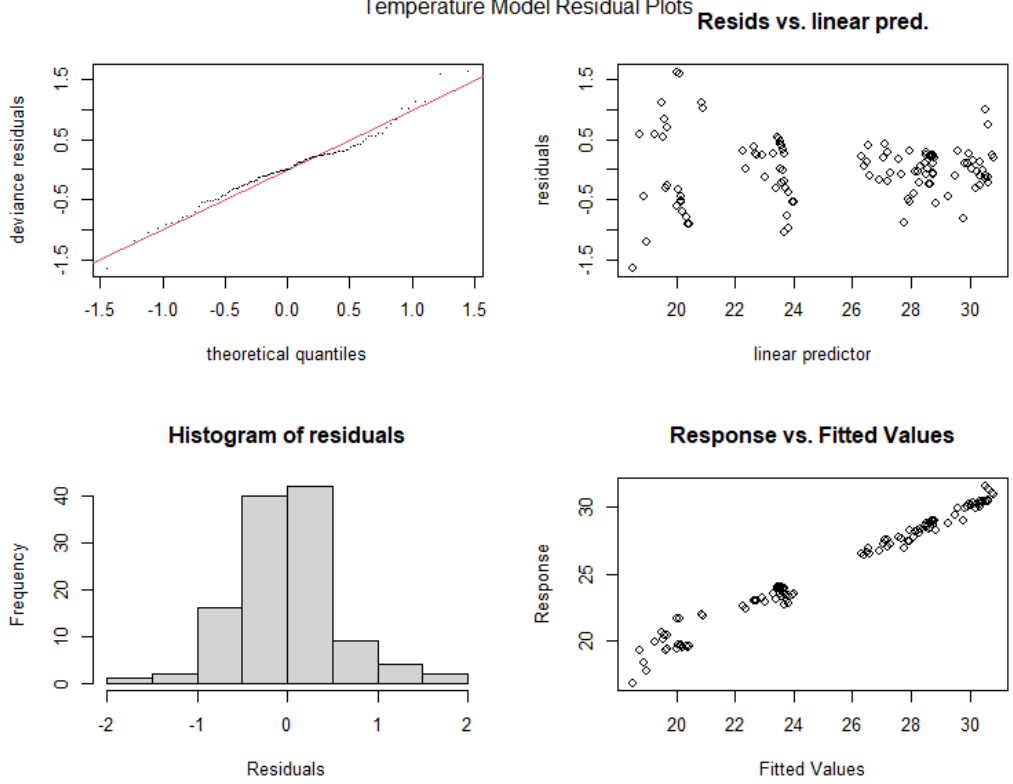
**Table A1.** Environmental patching data sources by variable(s) patched.

<b>Data Source</b>	<b>Station Name</b>	<b>Station ID</b>	<b>Table 6. Predictor Variable (s)</b>
MD DNR Eyes on the Bay NOAA Tides & Currents UMCES	Patuxent River - Jug Bay	PXT0455	EOTB temp, EOTB sal
Horn Point Laboratory UMCES	Solomons Island, MD	8577330	NOAA temp
Chesapeake Biological Laboratory	Oyster Hatchery	N/A	HPL temp, HPL sal
USGS Water Data for the Nation	CBL Pier	N/A	CBL sal
USGS Water Data for the Nation	Patuxent River Near Bowie, MD	1594440	Pax river flow
USGS Water Data for the Nation	Choptank River Near Greensboro, MD	1491000	Chop river flow

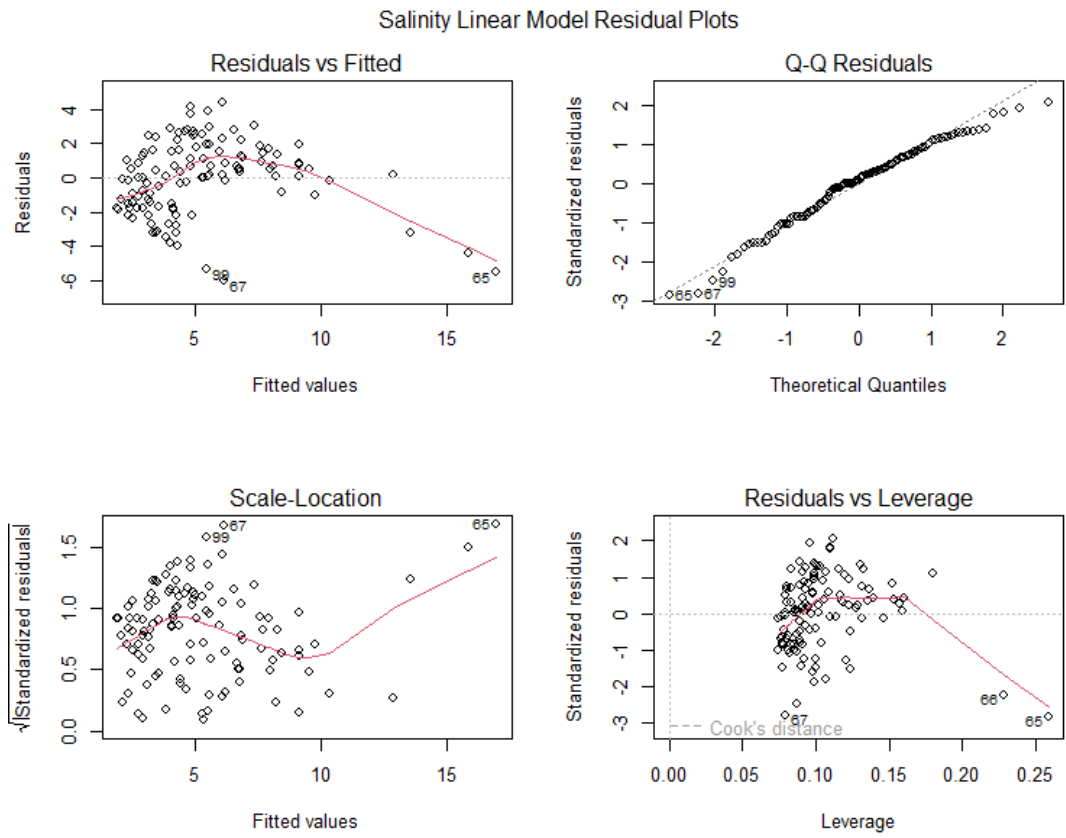


**Figure A1.** Residual plots for Equation G (Table 5) linear temperature model, (Shapiro-Wilk normality test,  $W = 0.9163$ ,  $p\text{-value} = 9.892e-06$ ).

Temperature Model Residual Plots

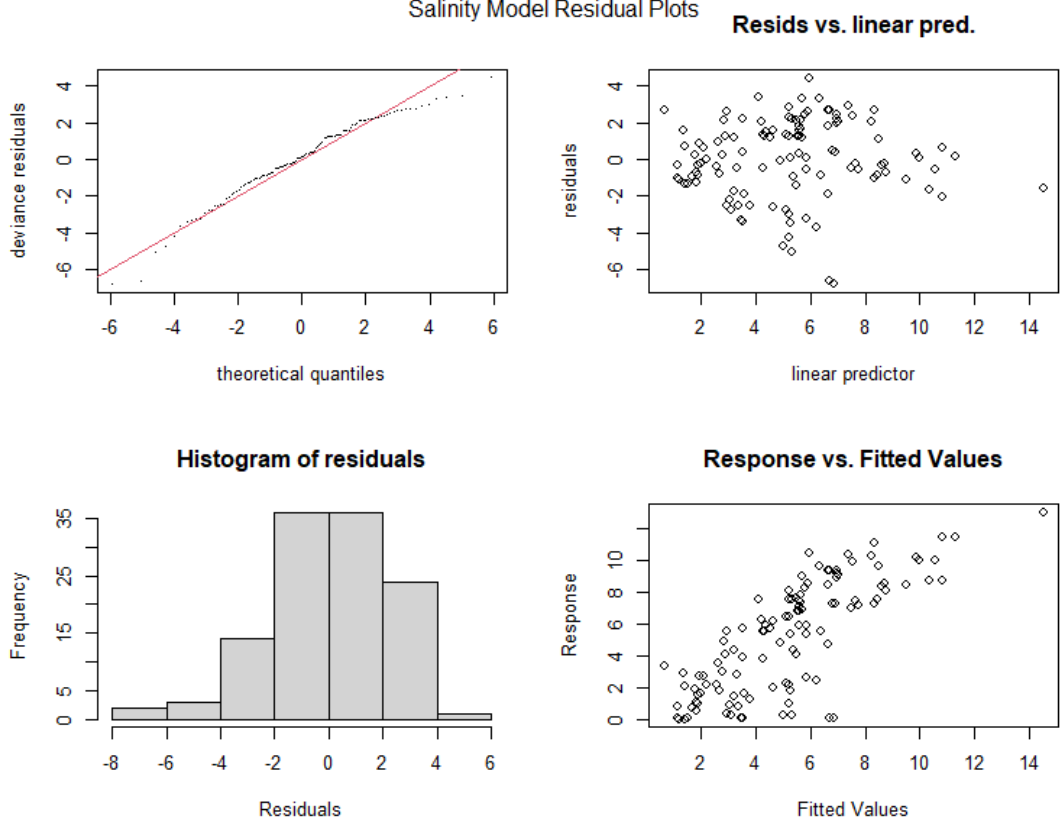


**Figure A2.** Residual plots for Equation J (Table 6) generalized additive model for water temperature.



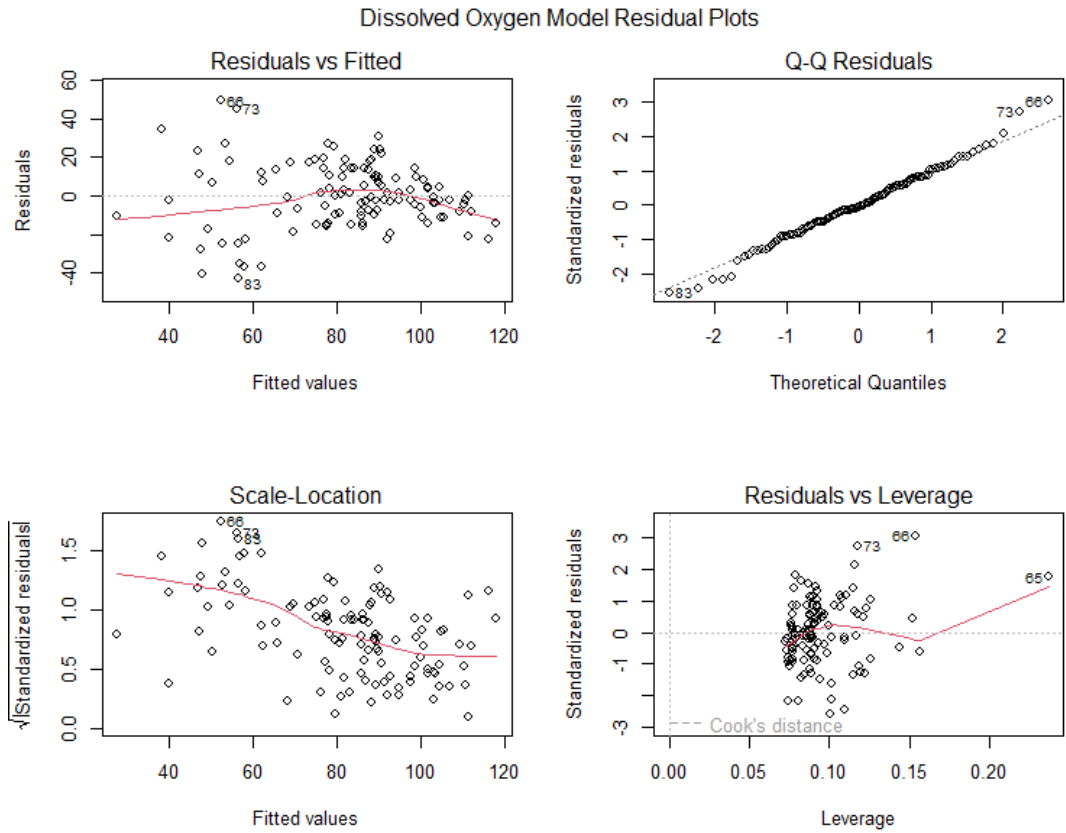
**Figure A3.** Residual plots for Equation H (Table 5 linear salinity model, (Shapiro-Wilk normality test,  $W = 0.93285$ ,  $p\text{-value} = 1.068e-05$ ).

Salinity Model Residual Plots



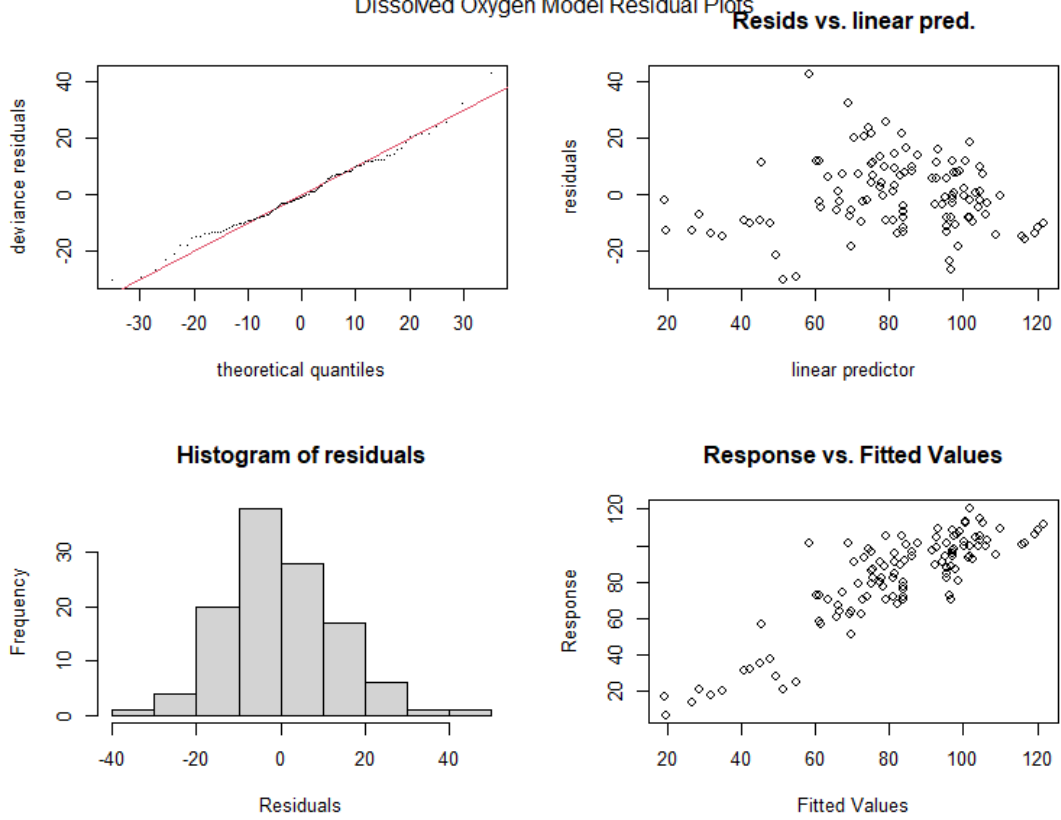
**Figure A4.** Residual plots for Equation K (Table 7) generalized additive model for salinity.





**Figure A5.** Residual plots for Equation I (Table 5) linear % dissolved oxygen model, (Shapiro-Wilk normality test,  $W = 0.93285$ ,  $p\text{-value} = 1.068e-05$ ).

Dissolved Oxygen Model Residual Plots



**Figure A6.** Residual plots for Equation L (Table 8) generalized additive model for % dissolved oxygen.

**Table A2.** *Neomysis americana* mean abundance differences by month in the Choptank River using the Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment.

<b>Months</b>	<b>Z</b>	<b>p</b>	<b>p adjusted</b>
Aug - July	-2.08	0.04	0.38
Aug - June	-2.24	0.03	0.25
July - June	-0.16	0.87	1.00
Aug - May	-2.40	0.02	0.16
July- May	-0.41	0.69	1.00
June - May	-0.25	0.80	1.00
Aug - Sept	-0.18	0.86	1.00
July - Sept	1.90	0.06	0.57
June - Sept	2.06	0.04	0.40
May - Sept	2.23	0.03	0.26

**Table A3.** *Americamysis* spp. mean abundance differences by month in the Choptank River using the Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment.

<b>Months</b>	<b>Z</b>	<b>p</b>	<b>p adjusted</b>
Aug - July	0.33	0.74	1.00
Aug - June	2.26	0.02	0.24
July - June	1.93	0.05	0.53
Aug - May	2.79	0.005	0.05
July- May	2.50	0.01	0.13
June - May	0.62	0.53	1.00
Aug - Sept	-1.42	0.16	1.00
July - Sept	-1.75	0.08	0.80
June - Sept	-3.68	0.0002	0.002
May - Sept	-4.16	<0.0001	0.0003

**Table A4.** *Neomysis americana* mean abundance differences by month in the Patuxent River using the Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment.

<b>Months</b>	<b>Z</b>	<b>p</b>	<b>p adjusted</b>
Aug - July	0.38	0.70	1
Aug - June	0.79	0.43	1
July - June	0.40	0.69	1
Aug - May	-1.36	0.17	1
July- May	-1.74	0.08	1
June - May	-2.20	0.03	0.28
Aug - Sept	2.47	0.01	0.14
July - Sept	2.07	0.04	0.39
June - Sept	1.74	0.08	0.82
May - Sept	3.88	<0.0001	0.00106

**Table A5.** *Americamysis* spp. mean abundance differences by month in the Patuxent River using the Dunn (1964) Kruskal-Wallis multiple comparison test with Bonferroni adjustment.

<b>Months</b>	<b>Z</b>	<b>p</b>	<b>p adjusted</b>
Aug - July	3.39	0.0007	0.007
Aug - June	5.00	<0.0001	<0.0001
July - June	1.48	0.14	1.00
Aug - May	5.24	<0.0001	<0.0001
July- May	1.84	0.07	0.65
June - May	0.43	0.67	1.00
Aug - Sept	2.52	0.01	0.12
July - Sept	-1.00	0.32	1.00
June - Sept	-2.58	0.01	0.10
May - Sept	-2.91	0.004	0.034

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