

ABSTRACT

Title of Dissertation:

SURVIVING THE DEAD ZONE:
INTERACTIONS AMONG JELLYFISH,
COPEPODS, AND FISH IN THE
CHESAPEAKE BAY

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The oxygen-deficient areas (dissolved oxygen $< 2 \text{ mg L}^{-1}$) in oceans and estuaries have been increasing worldwide in recent decades and are especially common in populated and developed areas due to eutrophication and warming. The objectives of this dissertation were to understand the effects of hypoxia on zooplankton and the plankton foodweb in the Chesapeake Bay. The study focused on copepod (*Acartia tonsa*) and its major predators bay anchovy (*Anchoa mitchilli*), comb jellyfish (*Mnemiopsis leidyi*), and bay nettle (*Chrysaora chesapeakii*) with data collected during six cruises in 2010 and 2011 and an individual-based model. Oxygen deficiency was evaluated with both dissolved oxygen concentration ($\text{DO} < 2 \text{ mg L}^{-1}$) and the oxygen supply and demand of the copepod ($p\text{O}_2 < P_{\text{crit}}$). The effects of hypoxia on zooplankton concentrations were estimated with net tows, and the impact

of hypoxia on the plankton foodweb were quantified by comparing copepods' nonpredatory mortality (estimated with neutral red experiments) and predatory mortality (estimated with gut contents of comb jellyfish and bay anchovy). A copepod behavior model was also built to examine how stress-induced behavior affected copepod vertical distributions and the tradeoffs between avoiding both hypoxia and predation. The results indicated the impact of oxygen deficiency could be underestimated using solely the metric of dissolved oxygen, especially under warm and saline conditions. Both copepod and planktivorous fish concentrations were lower under hypoxic conditions, but gelatinous zooplankton concentrations were higher. Both nonpredatory and predatory mortality of copepods were higher under hypoxic conditions, suggesting a direct linkage between hypoxia and decreasing copepod abundance. Most importantly, the source of copepod mortality changed with both hypoxic severity and season: the relative importance shifted from nonpredatory in spring to a combination of predatory and nonpredatory in summer and autumn, and the dominant predators shifted from juvenile bay anchovies under moderate hypoxia to comb jellyfish under warm and severely hypoxic conditions. The model demonstrated how enhancing stress avoidance would result in aggregating at a shallower depth and thus increasing predation risk, supporting the hypothesis that behavior change under hypoxia may increase predatory mortality. Overall my research has shown that hypoxia directly decreases zooplankton abundance and increases predation impact, and avoiding hypoxia could contribute to higher predation impact.

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by

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Dedication

Dedicate to James Liou and Lydia Chiu, my loving and selfless parents.

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Most importantly, I would like to thank my parents, James Liou and Lydia Chiu, for their selfless support and unconditional love throughout my whole life. I also want to thank my husband, Nick Slater, for his love, encouragement, and understanding during my time in graduate school. Because my family believes in me, I could overcome difficulties, bounce back after setbacks, and finally reach the goal. Nobody has been more supportive than my family, and I dedicate this dissertation to them.

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Chapter One. Introduction and Overview

The oxygen-deficient area in the ocean known as the “dead zone” (dissolved oxygen $< 2 \text{ mg L}^{-1}$) has been increasing worldwide in recent decades; so far, more than 400 systems and 245,000 km² of aquatic ecosystems are affected by oxygen deficiency (Diaz & Rosenberg 2008, Breitburg et al. 2018). In coastal areas, including the Chesapeake Bay, oxygen deficiency is especially common in populated and developed areas due to eutrophication and warming (Rabalais et al. 2010, Rhein et al. 2013). Expansion of hypoxic water causes habitat degradation and sometimes leads to mass mortality of benthos and fish (reviewed in (Breitburg et al. 2018), the consequences of which could be expensive. For example, Lipton & Hicks (2003) estimated US\$200,000 net losses of value to the recreational striped bass (*Morone saxatilis*) fishery in the Patuxent River due to hypoxia; these losses would be >US\$145 million if projected to the whole Chesapeake Bay.

The environmental changes under eutrophication and oxygen deficiency may be systematic. With excessive anthropogenic nutrient, the primary producer community shifts from perennial macroalgae and seagrasses to fast-growing phytoplankton (Borum 1996), and mixotrophic phytoflagellates and dinoflagellates are often favored in the plankton community (Baird et al., 2004; Capriulo et al., 2002; Stoecker et al., 2017). This fuels future summer hypoxia and put oxygen-demanding species such as fast-swimming fish in a disadvantage compared with hypoxia-tolerant species like slow-drifting jellyfish (Breitburg et al. 1994). Such a shift alters the

foodweb structure towards a zooplankton-dominated system that favors planktivorous and filter feeders, with more production directed toward microbial loops and gelatinous zooplankton than finfish (Justić et al. 1995, Glibert & Burkholder 2006, Glibert 2010, Roman et al. 2019).

Copepod plays an important role in the foodweb by transferring primary production to higher trophic levels, and thus the abundance of copepods and the directions of copepod's energy flow influence the resilience of ecosystem. However among many eutrophic coastal ecosystems, a decrease in the copepod population is often concurrent with peak hypoxia and jellyfish blooms (Shoji et al. 2010, Dong et al. 2010, Purcell 2012, Pierson 2017), but the proposed explanations vary. Many studies have suggested hypoxia directly increases copepod mortality and results in a smaller population (Roman et al. 1993, 2005a 200, Elliott et al. 2013a), while some have indicated hypoxia favors jellyfish, and thus their predation upon copepods increases under hypoxic conditions (Decker et al. 2004, Kolesar et al. 2010). Some studies also have proposed behavior changes under hypoxic conditions, like decreasing diel vertical migration or avoidance of the hypoxic bottom, which may increase the spatial overlap between organisms and result in increased predator-prey encounter rates, and consequently, increased mortality (Keister et al. 2000, Breitburg et al. 2003). Further research is still needed to determine how hypoxia affects the interactions of the zooplankton community and to elucidate the related mechanisms. Does hypoxia cause a decrease in copepod populations? If so, of what magnitude, and through what mechanisms (direct mortality, predation)? Does behavior change play a role, and if so, how?

The overarching goal of this dissertation is to understand how hypoxia affects zooplankton communities and their interactions by quantifying the impact of hypoxia on zooplankton community and elucidating the mechanisms with field observations, onboard experiments, gut content analyses, and individual-based simulations. Six week-long research cruises were conducted in the main stem of the Chesapeake Bay in May, August/July, and September of 2010 and 2011. Hourly CTD casts and Scanfish surveys were conducted to collect data on water temperature, salinity, dissolved oxygen, and chlorophyll-a content to evaluate the onset, development, and dissipation of hypoxia. Cruise details, net deployments, and hydrological measurements were uploaded to the Biological and Chemical Oceanography Data Management Office (DOI: 10.1575/1912/bco-dmo.687991, Pierson et al. 2017). Oxygen deficiency was evaluated by both dissolved oxygen and the supply and demand of copepod *Acartia tonsa*. Neutral red treatment was applied to copepods collected with Niskin bottles to estimate copepods' nonpredatory mortality. The research vessel anchored at two stations, termed North (38° 31.32' N, 076° 24.48' W) and South (37° 43.68' N, 076° 12.0' W).

To estimate the effects of hypoxia on concentrations of copepod *Acartia tonsa*, larval and juvenile bay anchovy *Anchoa mitchilli*, bay nettle *Chrysaora chesapeakei* (formerly known as *C. quinquecirrha*), and comb jelly *Mnemiopsis leidyi* (as discussed in Chapter Two), at least five series of trawling operations were conducted at each station, including hauls with a MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System), a Tucker Trawl, and a Mid-Water Trawl. Gut samples were also collected with Reeve nets (for *M. leidyi*),

MOCNESS (for larval *A. mitchilli*), and mid-water trawl (for juvenile *A. mitchilli*) to understand predation's impact upon copepods under hypoxic conditions (as discussed in Chapter Three). An individual-based model was built to understand how different stress avoidance behavior may future affect copepod's vertical distribution and their encounter with predators (as discussed in Chapter Four). The conclusions and synthesis of these studies are presented in Chapter Five.

The null hypotheses that I tested were 1) there is no difference in zooplankton concentrations under different levels of oxygen deficiency; 2) there is no difference in copepods' nonpredatory mortality under different conditions of oxygen deficiency; 3) there is no difference in ctenophore predation or anchovy predation on copepods under different levels of oxygen deficiency; 4) there is no difference in copepods' vertical distribution and mortality risk (estimated with time spending in stress patches) under different stress avoidance behaviors. The main chapters of the dissertation are organized as follows:

- II. Fewer copepods, fewer anchovies, and more jellyfish: how does hypoxia impact the Chesapeake Bay zooplankton community?
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- III. Hypoxia increases ctenophore and fish predation on copepods: a case study in the Chesapeake Bay
- IV. Avoiding hypoxia and escaping predators: Examining behavior trade-offs with an individual-based model

References

- Baird D, Christian RR, Peterson CH, Johnson GA (2004) Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecol Appl* 14:805–822.
- Borum J (1996) Shallow waters and land/sea boundaries. *Eutrophication Coast Mar Ecosyst* 52:179–203.
- Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240.
- Breitburg DL, Adamack A, Rose KA, Kolesar SE, Decker B, Purcell JE, Keister JE, Cowan JH (2003) The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. *Estuaries* 26:280–297.
- Breitburg DL, Steinberg N, DuBean S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar Ecol Prog Ser* 104:235–246.
- Capriulo GM, Smith G, Troy R, Wikfors GH, Pellet J, Yarish C (2002) The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. In: *Nutrients and Eutrophication in Estuaries and Coastal Waters*. Orive E, Elliott M, de Jonge VN (eds) Springer Netherlands, Dordrecht, p 263–333
- Decker MB, Breitburg D, Purcell JE (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 280:163–72.
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *science* 321:926–929.
- Dong Z, Liu D, Keesing JK (2010) Jellyfish blooms in China: Dominant species, causes and consequences. *Mar Pollut Bull* 60:954–963.
- Elliott DT, Pierson JJ, Roman MR (2013) Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. *J Plankton Res* 35:1027–1034.
- Glibert PM (2010) Long-term changes in nutrient loading and stoichiometry and their relationships with changes in the food web and dominant pelagic fish species in the San Francisco estuary, California. *Rev Fish Sci* 18:211–232.
- Glibert PM, Burkholder JM (2006) The complex relationships between increases in fertilization of the earth, coastal eutrophication and proliferation of harmful algal blooms. *Ecol Harmful Algae*:341–354.

- Justić D, Rabalais NN, Turner RE, Dortch Q (1995) Changes in nutrient structure of river-dominated coastal waters: stoichiometric nutrient balance and its consequences. *Estuar Coast Shelf Sci* 40:339–356.
- Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. *Mar Ecol Prog Ser* 205:43–59.
- Kolesar S, Breitburg D, Purcell J, Decker M (2010) Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: clearance rates and vertical habitat overlap. *Mar Ecol Prog Ser* 411:173–188.
- Lipton D, Hicks R (2003) The cost of stress: Low dissolved oxygen and economic benefits of recreational striped bass (*Morone saxatilis*) fishing in the Patuxent River. *Estuaries* 26:310–315.
- Pierson J (2017) Zooplankton from hypoxic waters of Chesapeake Bay. 10.1575/1912/bco-dmo.687996
- Pierson J, Slater W, Elliott D, Roman M (2017) Synergistic effects of seasonal deoxygenation and temperature truncate copepod vertical migration and distribution. *Mar Ecol Prog Ser* 575:57–68.
- Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu Rev Mar Sci* 4:209–235.
- Rabalais NN, Diaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J (2010) Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7:585–619.
- Rhein M al, Rintoul SR, Aoki S, Campos E, Chambers D, Feely RA, Gulev S, Johnson GC, Josey SA, Kostianoy A, others (2013) Observations: ocean. *Clim Change*:255–315.
- Roman M, Zhang X, McGilliard C, Boicourt W (2005) Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. *Limnol Oceanogr*:480–492.
- Roman MR, Brandt SB, Houde ED, Pierson JJ (2019) Interactive Effects of Hypoxia and Temperature on Coastal Pelagic Zooplankton and Fish. *Front Mar Sci* 6.
- Roman MR, Gauzens AL, Rhinehart WK, White JR (1993) Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnol Oceanogr* 38:1603–1614.
- Shoji J, Kudoh T, Takatsuji H, Kawaguchi O, Kasai A (2010) Distribution of moon jellyfish *Aurelia aurita* in relation to summer hypoxia in Hiroshima Bay, Seto Inland Sea. *Estuar Coast Shelf Sci* 86:485–490.
- Stoecker DK, Hansen PJ, Caron DA, Mitra A (2017) Mixotrophy in the Marine Plankton. *Annu Rev Mar Sci* 9:311–335.

Chapter Two. Fewer copepods, fewer anchovies, and more jellyfish: how does hypoxia impact the Chesapeake Bay zooplankton community?

Abstract

To understand dissolved oxygen deficiency in Chesapeake Bay and its direct impact on zooplankton and planktivorous fish communities, six research cruises were conducted at two sites in the Chesapeake Bay from spring to autumn in 2010 and 2011. Temperature, salinity, and dissolved oxygen were measured from hourly CTD casts, and crustacean zooplankton, planktivorous fish and gelatinous zooplankton were collected with nets and trawls. CTD data were grouped into three temperature groups and two dissolved oxygen-level subgroups using principal component analysis (PCA). Species concentrations and copepod nonpredatory mortalities were compared between oxygenated conditions within each temperature group. Under hypoxic conditions there usually were significantly fewer copepods *Acartia tonsa* and bay anchovies *Anchoa mitchilli*, but more bay nettles *Chyrsaora chesapeakei* and lobate ctenophores *Mnemiopsis leidyi*. Neutral red staining of copepod samples confirmed that copepod nonpredatory mortalities were higher under hypoxic conditions than under normoxia, indicating that the sudden decline in copepod concentration in summer was directly associated with hypoxia. Because comparisons were made within each temperature group, the effects of temperature were isolated, and hypoxia

was clearly shown to have contributed to copepod decreases, planktivorous fish decreases, and gelatinous zooplankton increases. This research quantified the direct effects of hypoxia and explained the interactions between seasonality and hypoxia on the zooplankton population.

Introduction

Hypoxia in the Chesapeake Bay

The amount of oxygen-deficient water (i.e., dissolved oxygen $< 2 \text{ mg L}^{-1}$) in coastal areas has been increasing worldwide in recent decades largely due to eutrophication and warming (Rabalais et al. 2010, Rhein et al. 2013). In more than 400 coastal systems covering a 245,000 km² area, hypoxia has been recognized as a key stressor in many aquatic ecosystems, especially along populated and developed coasts (Diaz & Rosenberg 2008). Chesapeake Bay, the largest estuary in the United States, is prone to hypoxia due to its linear shape and its low rates of seasonal flushing, which strengthens stratification and impedes full circulation (Libes 2011). In addition to these natural causes of hypoxia, anthropogenic drivers, such as eutrophication and warming, have also contributed to hypoxia in the Bay (Cowan & Boynton 1996). Chesapeake Bay has a surface area of 3500 km² and a three-month duration of deoxygenated bottom water annually (Diaz & Rosenberg 2008). The volume of hypoxic water has been increasing, and the seasonal onset has been earlier since the 1950s (Hagy et al. 2004, Kemp et al. 2005, Murphy et al. 2011). With both temperature and human population (the major source of eutrophication) projected to

increase, the hypoxic volume of the Bay could increase in the future (Rabalais et al. 2010, Najjar et al. 2010, Deutsch et al. 2011, Breitburg et al. 2018).

The consequences of hypoxia are both environmental and economic, and the environmental changes under hypoxic conditions may be systematic (Roman et al. 2019). For example, eutrophic-induced hypoxia could alter ecosystem structure by decreasing suitable habitats for hypoxia-sensitive species such as striped bass (*Morone saxatilis*) and favoring hypoxia-tolerant and filter-feeding species like jellyfish (Breitburg et al. 1997, Kimmel et al. 2012). It was proposed that under hypoxic conditions, K-selected species could be replaced by r-selected species and a complex foodweb replaced by a simpler foodweb (Wu 2002). Hypoxia can negatively impact fisheries in some ecosystems, for example Alabama's oyster (*Crassostrea virginica*), North Carolina's brown shrimp (*Farfantepenaeus aztecus*), and the Black Sea's Norway lobster (*Nephrops norvegicus*) fisheries (Noone et al. 2013). A 10-year study also indicated that chronic hypoxia in the Chesapeake Bay was concurrent with substantial reductions in landings and catch rates of demersal fish species (Buchheister et al. 2013). Lipton and Hicks projected a net present value loss of US\$145 million from the recreational striped bass (*M. saxatilis*) fishery in the Chesapeake Bay if DO were consistently lower than 3 mg L⁻¹ (Lipton & Hicks 2003). Although it is difficult to quantify all economic losses due to hypoxia and the diverse reasons for these losses, most studies agree that expansion of hypoxic water causes habitat degradation and therefore compresses the distributions of fisheries species and their prey, and sometimes leads to mass mortality of benthos and pelagic fish (Diaz & Rosenberg 1995, Breitburg et al. 2018).

Zooplankton and planktivores diversity in the Bay

Chesapeake Bay is very productive and diverse in crustacean zooplankton (> 50 species), fish (> 350 species), and gelatinous zooplankton (> 30 species). Crustacean zooplankton are the most abundant mesozooplankton in the Chesapeake Bay, and copepods are the dominant taxa. There have been more than 50 copepod species identified in Chesapeake Bay, and the most commonly found genera are *Acartia* and *Eurytemora*, while other dominant taxa include *Centropages* spp., *Oithona* spp., and *Paracalanus* spp. (Wilson & Museum 1932, Heinle 1966, Olson 1987, Lippson & Lippson 2006, Steinberg & Condon 2009). While the calanoid copepod *E. carolleae* (previously *E. affinis*, (Alekseev & Souissi 2011) is dominant in winter and spring, the calanoid copepod *A. tonsa* is the most abundant copepod in summer and autumn, reaching peak densities of approximately 100,000 ind. m⁻³ (Heinle 1966, Olson 1987, Kimmel & Roman 2004). The life cycle of *A. tonsa* is short in warm summers, taking approximately 7 days for an egg to develop into an adult when the water temperature is above 25°C. The estimated *A. tonsa* production in summer is 180.7 – 199.4 mg m⁻² day⁻¹, assuming an average depth of 3m (Heinle 1966). In summer, copepod nauplii and *A. tonsa* adults together could graze approximately half (205.6 mg C m⁻² d⁻¹) of the *in situ* primary production (White & Roman 1992).

Chesapeake Bay gelatinous zooplankton are in the phyla Cnidaria (hydromedusae and scyphomedusae) and Ctenophora. The most commonly surveyed gelatinous species in the Bay include the large medusoid species, such as bay nettle (*Chrysaora chesapeakei*, formerly sea nettle *C. quinquecirrha* (Bayha et al. 2017),

lion's mane jelly (*Cyanea capillata*), and moon jelly (*Aurelia aurita*), and the ctenophores *Mnemiopsis leidyi* and *Beroe ovate*. In addition, 27 hydromedusa species have been identified in the Chesapeake Bay (Mayer 1910, Mayor 1912, Calder 1971, Morales-Alamo & Haven 1974, Burrell & Van Engel 1976, Purcell & Nemazie 1992, Purcell et al. 2001b).

Among approximately 350 fish species living in the Chesapeake Bay, bay anchovy (*Anchoa mitchilli*) is the most abundant pelagic fish (Stone 1994, Wang & Houde 1994, Newberger & Houde 1995, Murdy et al. 1997, Jung & Houde 2003). During *A. mitchilli*'s spawning season (May to September), *A. mitchilli* eggs and larvae can make up to 80% and 75%, respectively, of the fish eggs and larvae collected in ichthyoplankton surveys (Olney 1983). In addition to *A. mitchilli*, Atlantic croaker (*Micropogonias undulatus*), white perch (*Morone americana*), spot (*Leiostomus xanthurus*), weakfish (*Cynoscion regalis*), and Atlantic menhaden (*Brevoortia tyrannus*) are also commonly found pelagic fish in the Chesapeake Bay (Jung & Houde 2003).

Direct effects of seasonal hypoxia

Seasonal hypoxia in the Chesapeake Bay usually establishes in spring, peaks in summer, and dissipates in autumn (Kemp et al. 2005). Dissolved oxygen concentrations vary spatially, with the upper Bay containing a higher percentage volume of hypoxic water than the lower Bay (Kemp et al. 2005). Seasonal low dissolved oxygen negatively affects many organisms in the Bay. For example, *A. tonsa* produced fewer eggs and the egg hatching is delayed when DO is ≤ 2 mg L⁻¹ in

Chesapeake Bay, and egg hatching ceased when DO is $< 0.1 \text{ mg L}^{-1}$ (Roman et al. 1993). Additionally, copepod ingestion rates were lower under hypoxic conditions, which led to smaller adult sizes (Elliott et al. 2013a). As a result, copepod populations decline under hypoxic conditions due to lower egg production, reduced hatching success, slower growth and development, and increased mortality (Vargo & Sastry 1977, Lutz et al. 1992, Roman et al. 1993, Marcus et al. 2004, Richmond et al. 2006, Ekau et al. 2010).

Similarly, hypoxia also negatively affects *A. mitchilli* growth, survival, behavior, population distributions, and recruitment (Chesney & Houde 1989, Houde & Zastrow 1991, MacGregor & Houde 1996, Jung & Houde 2004, Taylor et al. 2007, Ludsin et al. 2009, Adamack et al. 2012). Trawl surveys indicate that *A. mitchilli* occurs most abundantly at $\text{DO} > 3 \text{ mg L}^{-1}$, and *A. mitchilli* densities decrease along with decreasing DO concentrations (Jung & Houde 2004). In addition, *A. mitchilli* larvae avoided $\text{DO} < 1 \text{ mg L}^{-1}$ under laboratory and field conditions (Breitburg 1994, North & Houde 2004). Lab results also indicate that DO concentrations less than 2.4 and 1.6 mg L^{-1} , respectively, were lethal to *A. mitchilli* eggs and larvae, respectively (Chesney & Houde 1989).

By contrast, laboratory experiments and field surveys indicate that gelatinous zooplankton are more tolerant of hypoxic conditions than their copepod prey and fish competitors (Purcell et al. 2001a). For example, *M. leidyi* occurs in hypoxic bottom water as low as $\text{DO} 1 \text{ mg L}^{-1}$ while copepods and both larval *A. mitchilli* and larval *Gobiosoma bosc* avoid DO concentrations $< 2 \text{ mg L}^{-1}$ (Breitburg 1994, Keister et al. 2000, Breitburg et al. 2003). Experimental studies also found that moderate hypoxia

did not affect predation ability of gelatinous zooplankton (Breitburg et al. 1994, Decker et al. 2004, Purcell et al. 2001a, Shoji et al. 2005b a).

In this paper, we evaluate the effects of bottom hypoxia on Chesapeake Bay zooplankton and planktivorous fish. Our objectives were to determine if the concentrations and distributions of *A. tonsa* and its predators *A. mitchilli*, *M. leidyi*, and *C. chesapeakei* vary with respect to levels of dissolved oxygen, and to estimate the direct impact of hypoxia on *A. tonsa* populations by quantifying the non-predation mortality rates of *A. tonsa* under different DO conditions.

Methods

Cruises and environmental data

Six week-long cruises were conducted on the R/V Hugh R. Sharp in the mainstem of the Chesapeake Bay from late spring to autumn (May, July/August, and September) in 2010 and 2011. The vessel anchored at two stations which are approximately 90 km apart, designated North (38° 31.32' N, 076° 24.48' W, depth 28m) and South (37° 43.68' N, 076° 12.0' W, depth 35m) (Figure 2.1). These two stations were selected because both stations were at the mainstem of Chesapeake Bay with comparatively deeper water columns that allow persistent stratification to form, and the North was expected to experience more severe oxygen deficiency over a longer duration compared with the South.

Both biological and hydrographic data were collected. Approximately 2.5 days were spent at each station, with ~27 hours at anchor and ~33 hours underway near the station conducting net collections for zooplankton and fish. While at anchor,

a total of 229 and 223 hourly CTD casts were conducted during the six cruises (Appendix 2.1) to obtain temperature, salinity, and dissolved oxygen at 0.5-m depth intervals. Cruise details, gear and instrument deployments, and measurements were submitted to the Biological and Chemical Oceanography Data Management Office (BCO-DMO) (Pierson et al. 2017).

Evaluation of environmental oxygen supplies and copepod's physiological oxygen needs

The temperature-specific oxygen demands for the *A. tonsa* copepod were estimated at each half-meter CTD measurement. First, Q_{10} of *A. tonsa* was calculated with respect to salinity (Equation 2.1, Elliott et al. 2013c), and oxygen solubility (O2Sat, Weiss 1970) was calculated using the “sw_satO2.m” in the SeaWater MATLAB toolbox (McDougall & Barker 2011). From oxygen solubility, the percentage of oxygen saturation (O_2P_{ct} , Equation 2.2) and saturation partial pressure of environmental oxygen (pO_2 , Equation 2.3) were calculated. From Q_{10} and temperature, the temperature-specific critical oxygen partial pressure (P_{crit} , Equation 2.4) and the lethal oxygen partial pressure (P_{leth} , Equation 2.5) could be estimated (Elliott et al. 2013b, Pierson et al. 2017, Roman et al. 2019). By comparing pO_2 with P_{crit} and P_{leth} , the differences between *A. tonsa* oxygen supply and oxygen demand based on ambient temperature and salinity could be estimated. If $pO_2 > P_{crit}$, the metabolism of the copepod *A. tonsa* is independent of the surrounding pO_2 . If $pO_2 < P_{crit}$ (biological hypoxia), *A. tonsa*'s metabolism decreases, which may cause copepods to suffer from sublethal effects. If $pO_2 < P_{leth}$, the concentration of dissolved

oxygen is insufficient to support copepod respiration, causing hypoxia-induced mortality to increase.

$$Q_{10} = 0.053 \times \text{Salinity} + 0.705 \quad (\text{Equation 2.1})$$

$$O_2\text{Pct (\%)} = \frac{\text{DO}}{O_2\text{Sat}} \quad (\text{Equation 2.2})$$

$$pO_2 = (159.27 \times O_2\text{Pct} - 0.0141) \times 133.322 / 1000 \quad (\text{Equation 2.3})$$

$$P_{crit} = 7.49Q_{10}^{0.1(T-18)} + 0.59 \quad (\text{Equation 2.4})$$

$$P_{leth} = 2.61Q_{10}^{0.1(T-18)} + 0.59 \quad (\text{Equation 2.5})$$

Estimation of zooplankton and planktivorous fish concentrations

To document seasonal changes in populations of crustacean zooplankton, gelatinous zooplankton and ichthyoplankton in the mainstem Chesapeake Bay, net collections were conducted at the two stations (North and South) during each cruise; the resulting copepod, gelatinous zooplankton and anchovy datasets were uploaded to the Biological and Chemical Oceanography Data Management Office (BCO-DMO) (Pierson & Houde 2015, Pierson 2017, Pierson & Decker 2017). CTD casts were conducted before each series of net tows to determine pycnocline depth and DO levels that guided the selection of net-sampling depths (described in Pierson et al. 2017)). Each net-collection series included tows with a MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System), a Tucker Trawl, and a mid-water trawl (Appendix 2.2). Copepod concentration data were obtained primarily from the MOCNESS tows. However, copepod concentrations in May-2010 (South) were estimated from the Tucker Trawl tows and Sep-2010 (North) from Z-trap

deployments (described in Barba 2015) because of MOCNESS mechanical problems. Larval bay anchovies were collected by both the MOCNESS and Tucker Trawl, whereas juvenile and adult bay anchovies were sampled by the mid-water Trawl. Gelatinous zooplankton, primarily bay nettles and ctenophores, were collected by Tucker Trawl. Our study focused on the whole water column; thus, abundances of copepods, jellyfish, ctenophores, and fish were expressed in concentrations (ind. m⁻³) estimated for the entire water depth sampled by each tow.

The MOCNESS (Wiebe 1976) had a 0.25 m²-mouth and was fitted with six 150- μ m mesh nets, and with sensors to measure pressure, temperature, salinity, dissolved oxygen, chlorophyll *a* fluorescence, flow, turbidity, and photosynthetically active radiation (PAR) in real-time. The MOCNESS was deployed to collect copepods from three layers (above, within, and below pycnocline) and to collect larval bay anchovy from two layers (above and below pycnocline). After each tow, the nets were rinsed, and most adult gelatinous zooplankton were removed by pouring the sample through a 5-mm mesh sieve. The remainder of each sample was concentrated with a 200- μ m mesh sieve, preserved in a 4% formaldehyde and seawater solution, and later enumerated in the laboratory. The MOCNESS was inoperative at the South Station during the 2010-May cruise and the 2011-May cruise, and the Tucker Trawl was deployed instead.

The 1-m² Tucker Trawl was fitted with two opening and closing 280 μ m-mesh nets and a flowmeter for each net to collect gelatinous zooplankton. During each deployment, each net was opened for two minutes to determine gelatinous zooplankton concentrations from three to four water depth intervals, depending on

hydrographic conditions. The nets were rinsed after each trawl and gelatinous zooplankton were separated. If there were more than 30 gelatinous zooplankton of each species, the total numbers of each species were estimated by measuring the wet biovolume of the first 30 randomly selected gelatinous zooplankton and then the total biovolume of all gelatinous zooplankton.

The mid-water trawl, with 18-m² mouth opening and 4-mm cod-end mesh, was deployed twice during each sampling-station occupation. An above- and below-pycnocline trawl deployments collected juvenile and adult bay anchovy at each of the sampling stations during summer and fall cruises. Each deployment was of 20-min duration; the trawl was fished obliquely in two-minute steps within each sampling depth. The effective volume sampled in a 20-min tow was 989 m³ (Jung & Houde 2004). The number of fish in each trawl sample and relative concentrations (individuals per 20 min) were recorded. Total lengths were measured from a sample of 30 bay anchovies, or all individuals were measured if fewer than 30 were collected from each trawl tow. A representative sample of juvenile and adult bay anchovy was preserved in ethanol for subsequent stomach analysis in the laboratory.

Nonpredatory mortality rates

Neutral red uptake experiments were conducted to estimate the proportion of living and dead copepods in each layer and to calculate the non-predatory mortality rates of copepods (Elliott & Tang 2009, Elliott et al. 2013a). Copepods were collected with a CTD rosette by combining water from three 10-L Niskin bottles in each of three discrete layers: surface layer, base of the oxycline, and near the bottom. 90-L

were collected in total, 30 L from each layer. Sampling was repeated three times at each station during all cruises except the spring cruise in 2010. Copepod non-predatory mortality rates (M_{np} , Equation 2.6) were estimated from the percentage of copepod carcasses present in the sample divided by the estimated *in situ* carcass decomposition time (τ), a function of copepod dry weight and water temperature (Equation 2.7, Elliott & Tang 2009, Elliott 2010)

$$M_{np} (\% d^{-1}) = \frac{\% \text{ dead from neutral red dye}}{\text{carcass turn over time } (\tau)} \quad (\text{Equation 2.6})$$

$$\tau = \frac{\text{Dry Weight}_t - \text{Dry Weight}_i}{-4.116 \times (1 - e^{-0.008 \text{ Temp}})} - 1.39 \quad (\text{Equation 2.7})$$

Statistical analysis

Principal Component Analysis (PCA) was applied to assign data from cruises and stations into groups representing comparatively similar environmental conditions. Temperature, salinity, and dissolved oxygen from above, at, and below the pycnocline, selected as the depth of the maximum density gradient for each hourly CTD cast were analyzed in R (Team 2013). Based on the PCA results, cruises and stations were first grouped into three temperature groups, designed Cool (C), Temperate (T), and Warm (W), according to their PC1 scores for which the major loading was temperature. Then, each temperature group was divided into two subgroups, termed less-oxygenated (LO) and more-oxygenated (MO), according to their PC2 scores for which the biggest loading was bottom dissolved oxygen. These

groups were then used to compare the zooplankton, fish, and gelatinous zooplankton concentrations, as well as the nonpredatory mortality rates.

Differences in the concentrations of copepods, larval and juvenile anchovies, ctenophores, and bay nettles were compared between the LO and MO subgroups within each temperature group (C, T, W) with Kruskal-Wallis test (Kruskal & Wallis 1952) performed in R to test the null hypothesis of no differences among zooplankton concentrations in different oxygenated conditions. Likewise, copepod nonpredatory mortality rates were also compared between hypoxia subgroups within each temperature group to test the null hypothesis of no differences in copepod nonpredatory mortalities under different hypoxic conditions. Note that within the biological hypoxia matrix ($pO_2 < P_{crit}$, Elliott et al. 2013c), the comparisons between the hypoxia subgroups in the C and T groups were made between normoxic ($pO_2 > P_{crit}$) and hypoxic conditions ($pO_2 < P_{crit}$), but the comparisons in the W group were made between moderately ($pO_2 < P_{crit}$) and severely hypoxic ($pO_2 < P_{crit}$) conditions.

To assess the effect of different nets on capture of larval anchovies, we conducted a permutation t-test, using a 10,000-time rearrangement simulation, using larval anchovy length data from 10 MOCNESS samples and 20 Tucker trawl samples collected at the North station in May 2010.

Results

General environmental conditions

Water temperature varied with seasons and years: summer was warmer than spring and fall, and 2011 was warmer than 2010 (Figure 2.2). The recorded water temperature ranged from 15.5°C to 34.5°C, with the highest water temperature observed at the surface of North Station during the 2011-Summer cruise, and the lowest was observed near the bottom of North Station during the 2011-Spring cruise. Salinity primarily varied by depth, station and year: the North Station was less saline than the South Station, especially at the surface, and 2011 was less saline than 2010 (Figure 2.2). Salinity ranged from 4 to 25, with the highest salinity found near the bottom of the South Station during the 2010-Autumn cruise, and the lowest salinity found at the surface of the North Station during the 2011-Spring cruise.

Dissolved oxygen also varied with depths, stations, seasons, and years. In general, dissolved oxygen was 1) lower at the North Station than at the South Station, 2) was lower during summer than the other seasons, and 3) was lower in 2011 than in 2010 (Figure 2.3). Dissolved oxygen ranged from below detectable limits to 15.5 mg L⁻¹; the highest dissolved oxygen was recorded at the surface of the North Station during the 2011-Autumn cruise and the lowest during the 2010-Summer and 2011-Spring and 2011-Summer cruises (Figure 2.3).

Our two hypoxia indicators (DO and pO_2) mapped different “dead zones” in the Bay, and the volume and duration of the dead zone were more extensive with the biological (pO_2) standard. If only DO concentration was considered as an indicator, oxygen-deficient water in the Chesapeake Bay was mostly confined to the bottom water (Figure 2.3). However, if the temperature-dependent oxygen demands of the copepod *A. tonsa* are considered, oxygen-deficient water in the Chesapeake Bay

occurred above the pycnocline, and sometimes even near the surface (Figure 2.3). For example, during the 2011 summer cruise at the South Station, two-thirds of the water column was categorized as biologically hypoxic, and thus, *A. tonsa* that occurred below 5-m would be stressed by oxygen deficiency. Using the DO indicator, hypoxia was only prevalent in summer; however, if oxygen demand and supply are considered (i.e., pO_2), hypoxic conditions extended into autumn in both years (Figure 2.3).

Zooplankton and fish concentrations

In general, there were more copepods and larval bay anchovies observed in spring, more gelatinous zooplankton in summer, and more juvenile bay anchovy in autumn. Overall, there were more crustacean zooplankton and fish in 2010 and more gelatinous zooplankton in 2011 (Figure 2.4 - 2.6; Appendix 2.3).

The MOCNESS survey documented the temporal succession of adult *A. tonsa*, which varied with the development of hypoxia (Figure 2.4a). In 2010, when hypoxia was more pronounced in summer, the concentrations of adult copepods declined by more than 75% at the North Station and by 20% at the South Station and then began to recover in autumn at both stations (Figure 2.4a). The oxygen deficiency was worse in 2011 when hypoxic water was observed at the North Station beginning in spring. In addition, Hurricane Irene and Tropical Storm Lee passed Chesapeake Bay approximately one month and two weeks, respectively, before the 2011 autumn cruise. As a result, *A. tonsa*'s concentrations were low in spring, slightly increased in summer, and declined again in autumn (Figure 2.4a). The temporal changes of *A. tonsa* copepodites resembled the pattern of adults (Figure 2.4b). In 2010, the

concentrations of copepodites were high at the North Station in spring, lower in summer, and increased in September, while in 2011 the copepodite concentrations remained low in spring and summer and then increased at the South Station in autumn (Figure 2.4b).

A. mitchilli larvae were most abundant in spring 2010. Juveniles were most abundant in summer 2010 and autumn 2011 (Figure 2.5). In 2010, the highest concentrations of larval *A. mitchilli* were observed in May, and abundance declined in summer and remained low in autumn. A similar seasonal pattern was observed in 2011, but concentrations were much lower (Figure 2.5). In 2010, the highest concentrations of juvenile *A. mitchilli* occurred in summer; in 2011, the highest concentrations occurred in autumn (Figure 2.5). The permutation t-test to determine whether the Tucker Trawl or MOCNESS net caught larval anchovies of different sizes resulted in a p-value of 0.676, indicating that the larval anchovy's length distribution (as collected by these two nets) are not significantly different.

Unlike the temporal changes of crustacean zooplankton and planktivorous fish, gelatinous zooplankton peaked during summer, and they were more abundant at the South Station than at the North Station in both years (Figure 2.6). The highest concentrations of both *M. leidy* and *C. chesapeakei* were observed at the South Station in the summer of 2011. No gelatinous zooplankton were collected in spring, and only a few were found in autumn. In any single Tucker-trawl tow during the six cruises, *M. leidy* was at least 50 times more abundant than *C. chesapeakei* (Appendix 2.3).

Grouping with PCA results

Among the nine principal components in our analysis, PC1 explained 56% of the variance, and PC2 explained 26% of the variance; together, these two principal components explained 82% of the variability in environmental conditions. Because only PC1 and PC2 had eigenvalues larger than 1, and the cumulative sum increased slowly after PC2, only PC1 and PC2 were retained for further analysis. The top three loadings of PC1 were water temperatures in the bottom layer, pycnocline, surface layer, indicating water temperature was the major driving factor of PC1 (Table 2.1). The top three loadings of PC2 included dissolved oxygen of the bottom layer as well as the salinity of the bottom and surface layers (Table 2.1), indicating that bottom dissolved oxygen and salinity in both the bottom and surface layers were the major drivers of PC2.

The scatter plot of PC1 and PC2 scores for 335 CTD casts is provided (Figure 2.7). Because the major loading in PC1 was water temperature, which was negatively related to PC1 (Table 2.1b), all data were grouped into three temperature categories approximately corresponding to PC1 scores -4 to -2 , -2 to 0 , and 0 to 2 , named “Warm (W)”, “Temperate (T)”, and “Cool (C)”, respectively. Because bottom dissolved oxygen was the highest loading on PC2 and dissolved oxygen was positively related to PC2 (Table 2.1b), each temperature group was further divided into two oxygen subgroups approximately at $PC2 = 0$, labeled “Less-Oxygenated (LO,)” and “More-Oxygenated (MO)”, respectively, from bottom to top on PC2. The cruises and stations and their corresponding groups are listed in Table 2.2

Re-examining the environmental conditions with PCA grouping, the temperature variations among C, T, W group were bigger than the changes among vertical water layers and between LO and MO (Figure 2.8a). The mean water temperatures were approximately 20°C, 23°C, and 26°C in the C, T, and W groups, respectively. In general, the W group also had higher salinity than the other groups, and the MO subgroups also had higher salinity than the LO subgroup especially in the surface layer (Figure 2.8b). In each temperature group, the mean dissolved oxygen concentration was higher in the MO subgroup than in the LO subgroup (approximately 7 mg L⁻¹ vs 5 mg L⁻¹, respectively, Figure 2.8c). Mean dissolved oxygen concentrations were lower in the W group than in the C group, approximately 4.6 mg L⁻¹ in W vs 7.0 mg L⁻¹ in C (Appendix 2.4). By calculating the gap between oxygen demand at the given temperature and salinity (P_{crit}) and oxygen supply (pO_2) in the bottom of the water column, the largest oxygen deficiency was observed in C – LO, W – LO, T – LO, in order of severity (Appendix 2.4).

All spring cruises were characterized as cool (“C”), and most of the data from spring cruises belong to C-MO except 2011-Spring-North, where the bottom of the water column was severely hypoxic (DO close to 0 mg L⁻¹ and $pO_2 < P_{leth}$, Table 2.2 & Figure 2.3). All summer cruises and the 2010-Autumn cruise fell in the W group. All data from 2010-Autumn and 2010-Summer-South were grouped into W-MO, while data from 2011-Summer and 2010-Summer-North were grouped into W-LO. Only the data from the 2011-Autumn cruise belonged to the T group, and the North Station was characterized as “T-LO,” whereas data collected at the South Station fell into the T-MO group (Table 2.2). According to the biological hypoxia matrix ($pO_2 <$

P_{crit} , Elliott et al. 2013c) and the PCA results, the comparisons between the oxygen deficiency subgroups in the C and T groups were made between normoxic ($pO_2 > P_{crit}$) and moderate hypoxic ($pO_2 < P_{crit}$), while the comparisons between the oxygen subgroups in the W group were made between moderate and severe hypoxia ($pO_2 < P_{leth}$) conditions (Appendix 2.4).

Effects of hypoxia

Overall, the less-oxygenated subgroups (LO) had fewer crustacean zooplankton, fewer planktivorous fish, but more gelatinous zooplankton than the more-oxygenated (MO) subgroups (Figure 2.9 - 2.11). In all temperature groups, *A. tonsa* concentrations were lower in the LO than in the MO subgroups; the lowest concentration was found in the T - LO group and highest occurred in the C - MO group (Figure 2.9a). In both the C and the T groups, adult *A. tonsa* concentrations in the LO groups were only one-third of the copepod concentrations of the MO groups (both $p < 0.05$, Table 2.3). In the warm group, the bottom water column was hypoxic in both oxygen subgroups but differed in severity ($pO_2 < P_{crit}$ in W - MO and $pO_2 < P_{leth}$ in W - LO, Appendix 2.4), and mean *A. tonsa* concentrations did not differ significantly in the W-LO and W- MO subgroups (Table 2.3). Similarly, *A. tonsa* copepodite concentrations were always at least 50% lower in the LO subgroups than in the MO subgroups in all temperature groups (Figure 2.3b), and the differences between the two oxygenated subgroups were significant in all temperature groups (Table 2.3).

The concentrations of larval *A. mitchilli* were also lower in LO subgroups in each temperature group (Figure 2.10a). Mean larval *A. mitchilli* concentrations were highest in the C - MO group and lowest in the C - LO and T - LO group. The differences in larval concentrations among the oxygenated subgroups were significant in the C and T groups ($p = 0.0102$ and $p = 0.0034$), but not in the W group ($p = 0.4522$) (Table 2.3). The mean densities of juvenile *A. mitchilli* were highest in the T - MO group and lowest in the W - LO group (Figure 2.10b). Although there were more juvenile *A. mitchilli* in the MO subgroup, only the concentrations in the warm group showed a significant difference ($p=0.0376$, Table 2.3).

Unlike the concentrations of copepods and anchovies, there were more gelatinous zooplankton in the LO subgroups (Figure 2.11). The highest *M. leidyi* and *C. chesapeakei* concentrations were found in the W - LO group, while the lowest concentrations were observed in the C - LO group (only *M. leidyi* and no *C. chesapeakei*). The LO groups had significantly more *M. leidyi* associated with the W and T groups (both $p < 0.0001$, Table 2.3). The patterns were similar for *C. chesapeakei*, although the differences between oxygenated subgroups were not significant (Figure 2.11b & Table 2.3). The difference in concentration between *M. leidyi* and *C. chesapeakei* for the oxygenated subgroups increased with temperature, with the biggest difference found in the W - MO group, in which the concentration of *M. leidyi* was 968 times that of *C. chesapeakei* (Figure 2.11).

Copepod non-predatory mortalities were higher under less-oxygenated conditions than under more-oxygenated conditions (Figure 2.12). The highest daily

non-predatory mortality was found in T - LO and lowest in W - MO (50 % and 2 %, respectively). When compared within the same temperature group, nonpredatory mortality in each LO group was at least twice that of the nonpredatory mortality in the MO group, but only the difference in the warm group was significantly different ($p=0.008$, Table 2.4).

Discussion

Hydrographical and biological hypoxia

In our analysis, the low-dissolved oxygen “dead zone” in the mid-Chesapeake Bay was considerably larger, and the hypoxia event duration lasted longer, if a biological standard ($pO_2 < P_{crit}$) was used instead of the commonly adopted hydrographical hypoxia standard ($DO < 2 \text{ mg L}^{-1}$). If we solely applied the hydrographical threshold in our study, the low oxygen regions would be primarily be confined to summertime conditions below the pycnocline. By contrast, using the biological hypoxia threshold, the zone of low oxygen that we surveyed was larger, especially in summer and, at times was also expressed above the pycnocline (Figure 2.3). For example, during the 2011 summer cruise at the South Station, two-thirds of the water column was categorized as biologically hypoxic, and more than half of the vertical water column had DO below lethal levels for *A. tonsa* ($pO_2 < P_{leth}$), indicating a highly stressful and even harmful environment to copepods throughout most the water column (Figure 2.3). Therefore, in 2011 summer at the South Station, *A. tonsa* lived below 5m would be affected by oxygen deficiency even when the DO was above 2 mg L^{-1} . In 2011, the hypoxia threshold (P_{crit}) at the South Station was

approximately 4 mg L⁻¹ and not 2 mg L⁻¹ if considering *A. tonsa*'s metabolic needs and the ambient temperature and salinity.

Although DO < 2 mg L⁻¹ is a commonly-adopted standard for studies of hypoxia effects in estuaries (Gray et al. 2002), this hydrographical standard does not consider that oxygen solubility varies with temperature and salinity (Lange et al. 1972) and that diverse species have different oxygen deficiency tolerances (Diaz 2001). Since oxygen solubility decreases as temperature and salinity increase, using DO < 2 mg L⁻¹ as a definition of hypoxia likely underestimates the severity of oxygen deficiency in warm and saline ecosystems (Roman et al. 2019). Compared with other seasonally hypoxic ecosystems, such as the Gulf of Mexico, temperature and salinity in the Chesapeake Bay are moderate. However, Chesapeake Bay can be warm and saline during summer in its down-estuary region, where hypoxia is often considered less severe compared to more the up-estuary portions of the Bay. For example, during the 2011 summer cruise, DO concentrations at the South station were similar to those measured at the same depth at the North station. But by contrast, a much higher percentage of the water column was biologically hypoxic at the South station due to high salinity in the deeper water column of the South station (Pierson et al. 2017). Under these conditions, the water column of the South station provided a less suitable habitat for *A. tonsa* than that of the North station, even though the DO concentration at the North station was similar or higher. Consequently, habitat degradation due to hypoxia in the lower Chesapeake Bay may be underestimated if the fixed hydrographical standard (i.e., 2 mg L⁻¹) for defining hypoxia is used.

In addition to oxygen supply varying with temperature and salinity, oxygen demands also vary among species and life stages. Typically, fast-swimming species and younger individuals require more oxygen at the same temperature and salinity than do drifting species and older individuals (Ekau et al. 2010). In this study, we compared the oxygen supply and demand of adult *A. tonsa* and concluded that the area and duration of biological hypoxia ($pO_2 < P_{crit}$) was larger and longer than hydrographical hypoxia ($DO < 2 \text{ mg L}^{-1}$). In contrast, gelatinous zooplankton are known to be more tolerant of hypoxia (Purcell et al. 2001a) than copepods. For example Decker et al. (2004) observed *A. tonsa*'s jumping frequency decreased with decreasing dissolved oxygen, while the clearance rate of the gelatinous planktivore *M. leidy* was little affected by low dissolved oxygen concentrations. The P_{crit} of *M. leidy*, an important gelatinous predator in the mainstem Chesapeake Bay during summer, is 7 kPa At 25°C (Purcell et al. 2001a, Thuesen et al. 2005), which is about half the P_{crit} of *A. tonsa* at the same temperature (13 kPa, Elliott et al. 2013c). Accordingly, the biologically-defined hypoxic regions for *M. leidy* would be smaller than the hydrographically-defined zone of hypoxia in the Bay. Applying this same reasoning, areas where biologically hypoxic conditions occur for large and fast swimming species, like striped bass, would be larger than the hydrographically-determined zone of hypoxia in the Bay. Considering that responses of organisms to low-dissolved oxygen are not universal, we recommend that future studies of hypoxia impacts on ecosystems should not only focus on dissolved oxygen concentrations but should also consider the species-specific effects of temperature and salinity and biologically-relevant hypoxic conditions.

Seasonal and episodic hypoxia

Species respond differently to hypoxia at various temporal scales. In a permanently hypoxic ecosystem, e.g., in the ocean's oxygen minimum zone, many organisms evolve physiological adaptations and genetic modifications to cope with a low-dissolved oxygen environment through enhancing oxygen absorption (i.e., increasing hemoglobin O₂ affinity and gill surface area) and decreasing oxygen demands (i.e., reducing red blood cell ATP concentration) (Wood & Johansen 1972, Powers 1980, Gracey et al. 2001, Mandic et al. 2009). Many species in the oxygen minimum zone, particularly krill and myctophid fishes, use hypoxic conditions to their advantage and take refuge from visually predators during daytime (Gilly et al. 2013). On the other hand, organisms living in non-permanent hypoxic conditions tend to rely on behavioral adaptations or metabolic suppression to cope with temporary adverse conditions (Childress & Seibel 1998). Thus, oxygen deficiency acts as a stressor rather than a refuge for organisms living in episodic or seasonally hypoxic ecosystems, often characterized as coastal dead zones.

Hypoxia in the Chesapeake Bay is seasonal and especially pronounced in summer. The PCA analysis indicated that in 2010 and 2011, water during summer was distinguished from water in spring as being warmer, more saline, and having less dissolved oxygen in the bottom layers. Although the oxygen deficiency is temporary and localized, many studies have found adverse effects of summer bottom hypoxia on vertical distributions of organisms (Breitburg 1992, Keister et al. 2000, Purcell et al. 2014), abundance (Roman et al. 1993), and diversity (Cooper & Brush 1993). Previous studies found that copepods show different diel migration patterns under

seasonal hypoxia (Pierson et al. 2017) and increased non-predatory mortality in summer (Elliott et al. 2013a).

The PCA results also indicated that water during the 2011 autumn cruise, which occurred after Hurricane Irene (August 27, 2011) and Tropical Storm Lee (September 7–10, 2011) affected the region, could be distinguished from water conditions during our other cruises (Figure 2.7). The water column was cooler, less saline, and less oxygenated in September 2011 relative to water samples collected in 2010 at the same location and season. Significant weather events like hurricanes and tropical storms could cause a hypoxia event by introducing large amounts of freshwater runoff and organic matter. Palinkas et al. described Hurricane Irene as a wind and sediment-resuspension event, while Tropical Storm Lee was a hydrographical and sediment-deposition event (Palinkas et al. 2014). Tropical Storm Lee brought high streamflow ($22,002 \text{ m}^3 \text{ s}^{-1}$) to the Susquehanna River and resulted in the second-highest recorded discharge behind Tropical Storm Agnes in 1972 (Hirsch 2012). As a result, salinities measured during the 2011 autumn cruise were much lower than those measured in the previous year. Other studies in estuaries also have observed short-term hypoxia after hurricanes (Peierls et al. 2003, Stevens et al. 2006), and sometimes the recovery to baseline conditions took months (Mallin et al. 1999). Similarly, early-fall hypoxia was soon reestablished after Hurricane Isabel impacted the Chesapeake Bay, and the resuspension of nutrients into the upper water column led to a large diatom bloom, followed by a dinoflagellate bloom (Roman et al. 2005b). The effects of episodic hypoxia resulting from storms are less studied. While unplanned, we may have observed the effects of Hurricane Irene and Tropical Storm

Lee on the Chesapeake Bay ecosystem during the 2011 autumn cruise. In this study both seasonal and episodic hypoxia were observed, but differences found were dictated by snapshots of the two stations during the 3 seasons in 2 years. More research, such as higher frequency sampling before and after weather events and long-term observation at more stations across different geographic conditions, are needed to assess the variability and to understand the differences and similarities of seasonal hypoxia and episodic hypoxia on zooplankton composition and foodweb interactions.

Strengths and limitations of the PCA grouping method and our sampling regime

Because temperature, salinity, and dissolved oxygen varied differently with depths, stations, season, and years, a PCA method was adopted to help group data, enabling comparison of different hypoxic conditions while temperature and salinity were comparatively similar. By only comparing the oxygenated subgroups within the same temperature group, we could understand the effects of hypoxia on organisms, while isolating effects of temperature. Although we were not able to isolate the effects of salinity, all species examined in this study were euryhaline species and are native to this partially mixed estuary. For example, Chesapeake Bay organisms occur at a wide range of salinities: *A. tonsa* < 5 – 38, *M. leidy* 3.4 – 33, *C. chesapeakei* 10 – 26, and *A. mitchilli* 0 – 45, in the Chesapeake Bay (Bishop 1972, Miller 1974, Robinette 1983, Houde & Zastrow 1991, Purcell et al. 1999, Cervetto et al. 1999). The salinity of the sampling region ranged from 8 to 25 (Figure 2.2), which is within the range of salinity habitat of the species studied. Although *A. tonsa*'s oxygen demands increase when salinity diverges from its natural habitat and their mortality

increases when exposed to salinity changes >10 - 15 (Lance 1965, Farmer & Reeve 1978, Cervetto et al. 1999), the salinity differences between LOs and MOs in our study were small (i.e., 3-5, Figure 2.8). By comparison, the differences in bottom dissolved oxygen between LOs and MOs in this study provided either insufficient or sufficient oxygen concentrations to support the basic metabolism of *A. tonsa* (Appendix 2.4). The loading of salinity in the PCA analysis was smaller than the temperature in PC1 and less than bottom dissolved oxygen in PC2, and thus, differences in bottom dissolved oxygen were larger than the differences in salinities between the LO and the MO subgroups. Therefore, we reasoned that the moderate salinity fluctuations observed in the six cruises would have a smaller influence than temperature and bottom dissolved oxygen on zooplankton and planktivorous fish concentrations and copepod non-predatory mortality. More research is needed to clarify the effects of interactions of salinity and dissolved oxygen on organism occurrence and concentration.

The time sensitive nature of research cruise sampling meant that if we missed a sampling opportunity, we may not have been able to do it again. So, when presented with mechanical failures we decided to collect the samples in the best possible way, even if it was not optimal. Thus, different nets were used at certain times in order to not miss a sampling opportunity. Skjodal et al. (2013) suggest that net mesh should effectively retain organisms whose smallest dimension is approximately 2/3 of the mesh size. In the case of the Tucker Trawl used here, with 280 μm mesh, we expect it to retain organisms > 187 μm in size. The MOCNESS mesh size was 200 μm . Estimated widths for adult *A. tonsa* from Chesapeake Bay during May 2010, when

the Tucker Trawl was used a substitute for the MOCNESS, was 297 and 279 μm for female and male *A. tonsa*, respectively (Pierson, unpubl.), and Elliott et al. (2013) estimated a width of 262 μm for adult *A. tonsa* from the same region (Elliott et al. 2013a). These widths are well above the minimum size for capturing *A. tonsa* adults and thus suggest no difference in catchability between the MOCNESS and Tucker Trawl, which were both towed in an oblique manner. The Z-trip was used to collect zooplankton samples in a vertical manner, and sampled a lower volume of water, but as it had the same mesh size as the MOCNESS, and we anticipate similar catchability between these nets. Our test of the catchability of larval between the Tucker Trawl and the MOCNESS indicated no differences in the sizes of individuals caught, based on a permutation t-test of 10,000 simulations of the data, which further gives us confidence in our sampling despite the fact that we were compelled to use different nets at certain times.

Copepod's predators in hypoxia

A. tonsa's predators responded differently toward hypoxia in our study: more *M. leidy* and *C. chesapeakei* but fewer *A. mitchilli* under hypoxic conditions. The reasons of fewer larval and juvenile *A. mitchilli* were observed under hypoxic conditions could be decreasing habitat, reducing growth rates, and increasing mortality at young stages, which could also result in declining species diversity (Breitburg et al. 2001, Eby et al. 2005, Pollock et al. 2007). An individual-based model developed for Chesapeake Bay indicated that the mortality rate of *A. mitchilli* larvae would increase, as would spatial overlaps among *A. mitchilli* and its predators when bottom waters were hypoxic (Breitburg et al. 2001, Adamack et al. 2012). On

the contrary, more gelatinous zooplankton were found under hypoxic conditions, and overall larger ctenophore populations than those of *C. chesapeakei*. Long-term decreases in *C. chesapeakei* have been observed in the Chesapeake Bay mainstem region, leading to reduced predation impact upon *M. leidyi* and a corresponding increase in the *M. leidyi* population in the mainstem region (Purcell & Decker 2005, Kimmel et al. 2012). Hypoxia could contribute to the population decline in *C. chesapeakei* observed in the Chesapeake Bay, because ctenophores are known to be better oxyregulators than medusae (Thuesen et al. 2005), and *M. leidyi*'s life cycle does not have a benthic stage like *C. chesapeakei*, whose polyp stage has been shown to be vulnerable to hypoxia when held at 0.5 mg L⁻¹ for more than 5 days (Condon et al. 2001). Other potential contributing factors to the population shift include decreased availability of benthic habitat (i.e., oyster shell) for *C. chesapeakei*'s polyps due to declining oyster populations (Grove & Breitburg 2005, Breitburg & Fulford 2006). Additionally, the declining oyster population is hypothesized to exacerbate the effects of anthropogenic nutrient enrichment on phytoplankton production (Newell 1988). Resulting eutrophication, in addition to favoring increased hypoxia, may favor microzooplankton and filter feeders like *M. leidyi* (McNamara et al. 2014). Furthermore, warmer and shorter winters, in the long-term, could strengthen stratification and increase the severity and duration of summer hypoxia, while also increasing *M. leidyi*'s over-winter survival rate and contributing to its reproductive capacity in earlier and warmer springs (Sullivan et al. 2001, Oviatt 2004). Although *M. leidyi* has received less attention from the general public relative to the more noticeable, stinging *C. chesapeakei*, the shift in population sizes of these two

gelatinous species is important because *M. leidy* is able to prey more heavily on copepods than is *C. chesapeakei* of the same size. Thus, *M. leidy*'s impact on the plankton foodweb is expected to increase with its growing population (Purcell et al. 2001b, Purcell & Decker 2005). The impact of eutrophication-induced hypoxia on an ecosystem can be systemic, ranging from species to habitat to food web structure. Such an ecosystem is less resilient and is usually dominated by pelagic algae, microbial loops, smaller zooplankton, filter feeders, and smaller fish (McClelland & Valiela 1998, Wu 2002, Breitburg 2002, Kemp et al. 2005, Uye 2011, Kimmel et al. 2012). More research is still needed to understand the interaction of hypoxia and predator-prey interaction in the field.

Conclusion

Crustacean zooplankton (*A.tonsa*) and planktivorous fish (larval and juvenile *A. mitchilli*) concentrations tended to be lower under hypoxia, while gelatinous zooplankton populations (both *M. leidy* and *C. chesapeakei*) increased under the same conditions. These population trends relative to hypoxia were consistent among different temperature conditions and were pronounced relative to the influence of seasonality. Neutral red staining indicated high non-predatory copepod mortality under hypoxic conditions and implied a direct linkage between low dissolved oxygen and reduced copepod abundances. These findings confirm the role of hypoxia as a source of direct mortality for copepods in the Chesapeake Bay, and hypoxia directly associates with more gelatinous zooplankton population and less planktivorous fish in

addition to seasonality, implying potential predator-prey dynamic changes in this system.

References

- Adamack A, Rose K, Breitburg D, Nice A, Lung W (2012) Simulating the effect of hypoxia on bay anchovy egg and larval mortality using coupled watershed, water quality, and individual-based predation models. *Mar Ecol Prog Ser* 445:141–160.
- Alekseev VR, Souissi A (2011) A new species within the *Eurytemora affinis* complex (Copepoda: Calanoida) from the Atlantic Coast of USA, with observations on eight morphologically different European populations. *Zootaxa* 2767:41–56.
- Barba AP (2015) Responses of the copepod *Acartia tonsa* to hypoxia in Chesapeake Bay. University of Maryland, College Park
- Bayha KM, Collins AG, Gaffney PM (2017) Multigene phylogeny of the scyphozoan jellyfish family Pelagiidae reveals that the common U.S. Atlantic sea nettle comprises two distinct species (*Chrysaora quinquecirrha* and *C. chesapeakei*). *PeerJ* 5:e3863.
- Bishop JW (1972) Ctenophores of the Chesapeake Bay. *Chesap Sci* 13:S98–S100.
- Breitburg D (2002) Effects of Hypoxia, and the Balance between Hypoxia and Enrichment, on Coastal Fishes and Fisheries. *Estuaries* 25:767–781.
- Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240.
- Breitburg DL (1994) Behavioral response of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Mar Biol* 120:615–625.
- Breitburg DL (1992) Episodic Hypoxia in Chesapeake Bay: Interacting Effects of Recruitment, Behavior, and Physical Disturbance. *Ecol Monogr* 62:525–546.
- Breitburg DL, Adamack A, Rose KA, Kolesar SE, Decker B, Purcell JE, Keister JE, Cowan JH (2003) The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. *Estuaries* 26:280–297.
- Breitburg DL, Fulford RS (2006) Oyster-Sea Nettle Interdependence and Altered Control within the Chesapeake Bay Ecosystem. *Estuaries Coasts* 29:776–784.
- Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying Effects of Low Dissolved Oxygen on Trophic Interactions in an Estuarine Food Web. *Ecol Monogr* 67:489–507.
- Breitburg DL, Pihl L, Kolesar SE (2001) Effects of Low Dissolved Oxygen on the Behavior, Ecology and Harvest of Fishes: A Comparison of the Chesapeake Bay and Baltic-Kattegat Systems. *Coast Hypoxia Consequences Living Resour Ecosyst*:241–267.

- Breitburg DL, Steinberg N, DuBean S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar Ecol Prog Ser* 104:235–246.
- Buchheister A, Bonzek CF, Gartland J, Latour RJ (2013) Patterns and drivers of the demersal fish community of Chesapeake Bay. *Mar Ecol Prog Ser* 481:161–180.
- Burrell VG, Van Engel WA (1976) Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River estuary. *Estuar Coast Mar Sci* 4:235–242.
- Calder DR (1971) Hydroids and hydromedusae of southern Chesapeake Bay.
- Cervetto G, Gaudy R, Pagano M (1999) Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). *J Exp Mar Biol Ecol* 239:33–45.
- Chesney EJ, Houde ED (1989) Laboratory studies on the effects of hypoxic waters on the survival of eggs and yolk-sac larvae of the bay anchovy, *Anchoa mitchilli*. Center for Environmental Science, Chesapeake Biological Laboratory.
- Childress JJ, Seibel BA (1998) Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *J Exp Biol* 201:1223–1232.
- Condon RH, Decker MB, Purcell JE (2001) Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (*Chrysaora quinquecirrha*). *Jellyfish Blooms Ecol Soc Importance*:89–95.
- Cooper SR, Brush GS (1993) A 2,500-year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries Coasts* 16:617–626.
- Cowan JL, Boynton WR (1996) Sediment-water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: seasonal patterns, controlling factors and ecological significance. *Estuaries Coasts* 19:562–580.
- Decker MB, Breitburg D, Purcell JE (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 280:163–72.
- Deutsch C, Brix H, Ito T, Frenzel H, Thompson L (2011) Climate-Forced Variability of Ocean Hypoxia. *Science* 333:336–339.
- Diaz RJ (2001) Overview of hypoxia around the world. *J Environ Qual* 30:275–281.
- Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr Mar Biol Annu Rev* 33:245–03.
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *science* 321:926–929.
- Eby LA, Crowder LB, McClellan CM, Peterson CH, Powers MJ (2005) Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Mar Ecol Prog Ser* 291:249–262.

- Ekau W, Auel H, Poertner H, Gilbert D (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7:1669–1699.
- Elliott DT (2010) Copepod carcasses, mortality and population dynamics in the tributaries of the Lower Chesapeake Bay. The College of William and Mary
- Elliott DT, Pierson JJ, Roman MR (2013a) Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. *J Plankton Res* 35:1027–1034.
- Elliott DT, Pierson JJ, Roman MR (2013b) Predicting the Effects of Coastal Hypoxia on Vital Rates of the Planktonic Copepod *Acartia tonsa* Dana. *PLoS ONE* 8:e63987.
- Elliott DT, Tang KW (2009) Simple staining method for differentiating live and dead marine zooplankton in field samples. *Limnol Oceanogr Methods* 7:585–594.
- Farmer L, Reeve MR (1978) Role of the free amino acid pool of the copepod *Acartia tonsa* in adjustment to salinity change. *Mar Biol* 48:311–316.
- Gilly WF, Beman JM, Litvin SY, Robison BH (2013) Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone. *Annu Rev Mar Sci* 5:393–420.
- Gracey AY, Troll JV, Somero GN (2001) Hypoxia-induced gene expression profiling in the euryoxic fish *Gillichthys mirabilis*. *Proc Natl Acad Sci* 98:1993–1998.
- Gray JS, Wu RS, Or YY (2002) Effects of hypoxia and organic enrichment on the coastal marine environment. *Mar Ecol Prog Ser* 238:249–279.
- Grove M, Breitburg DL (2005) Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. *Mar Ecol Prog Ser* 301:185–198.
- Hagy JD, Boynton WR, Keefe CW, Wood KV (2004) Hypoxia in Chesapeake Bay, 1950–2001: Long-term change in relation to nutrient loading and river flow. *Estuaries* 27:634–658.
- Heinle DR (1966) Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River estuary. *Chesap Sci* 7:59–74.
- Hirsch RM (2012) Flux of nitrogen, phosphorus, and suspended sediment from the Susquehanna River Basin to the Chesapeake Bay during Tropical Storm Lee, September 2011, as an indicator of the effects of reservoir sedimentation on water quality. US Geological Survey.
- Houde ED, Zastrow CE (1991) Bay anchovy, *Anchoa mitchilli*. In: *Habitat Requirements for Chesapeake Bay Living Resources. Chesapeake Bay Program, Annapolis, MD.*, 2nd ed. p 8.1-8.14
- Jung S, Houde ED (2004) Recruitment and spawning-stock biomass distribution of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay. *Fish Bull* 102:63–77.

- Jung S, Houde ED (2003) Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. *Estuar Coast Shelf Sci* 58:335–351.
- Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. *Mar Ecol Prog Ser* 205:43–59.
- Kemp WM, Boynton WR, Adolf JE, Boesch DF, Boicourt WC, Brush G, Cornwell JC, Fisher TR, Glibert PM, Hagy JD, others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Mar Ecol Prog Ser* 303:1–29.
- Kimmel DG, Boynton WR, Roman MR (2012) Long-term decline in the calanoid copepod *Acartia tonsa* in central Chesapeake Bay, USA: An indirect effect of eutrophication? *Estuar Coast Shelf Sci* 101:76–85.
- Kimmel DG, Roman MR (2004) Long-term trends in mesozooplankton abundance in Chesapeake Bay, USA: influence of freshwater input. *Mar Ecol Prog Ser* 267:71–83.
- Kruskal WH, Wallis WA (1952) Use of Ranks in One-Criterion Variance Analysis. *J Am Stat Assoc* 47:583–621.
- Lance J (1965) Respiration and osmotic behaviour of the copepod *Acartia tonsa* in diluted sea water. *Comp Biochem Physiol* 14:155–165.
- Lange R, Staaland H, Mostad A (1972) The effect of salinity and temperature on solubility of oxygen and respiratory rate in oxygen-dependent marine invertebrates. *J Exp Mar Biol Ecol* 9:217–229.
- Libes S (2011) Introduction to marine biogeochemistry. Academic Press.
- Lippson AJ, Lippson RL (2006) Life in the Chesapeake Bay. JHU Press.
- Lipton D, Hicks R (2003) The cost of stress: Low dissolved oxygen and economic benefits of recreational striped bass (*Morone saxatilis*) fishing in the Patuxent River. *Estuaries* 26:310–315.
- Ludsin SA, Zhang X, Brandt SB, Roman MR, Boicourt WC, Mason DM, Costantini M (2009) Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implications for food web interactions and fish recruitment. *J Exp Mar Biol Ecol* 381:S121–S131.
- Lutz RV, Marcus NH, Chanton JP (1992) Effects of low oxygen concentrations on the hatching and viability of eggs of marine calanoid copepods. *Mar Biol* 114:241–247.
- MacGregor JM, Houde ED (1996) Onshore-offshore pattern and variability in distribution and abundance of bay anchovy *Anchoa mitchilli* eggs and larvae in Chesapeake Bay. *Mar Ecol Prog Ser* Oldendorf 138:15–25.

- Mallin MA, Posey MH, Shank GC, McIver MR, Ensign SH, Alphin TD (1999) Hurricane effects on water quality and benthos in the Cape Fear watershed: natural and anthropogenic impacts. *Ecol Appl* 9:350–362.
- Mandic M, Todgham AE, Richards JG (2009) Mechanisms and evolution of hypoxia tolerance in fish. *Proc R Soc B Biol Sci* 276:735–744.
- Marcus NH, Richmond C, Sedlacek C, Miller GA, Oppert C (2004) Impact of hypoxia on the survival, egg production and population dynamics of *Acartia tonsa* Dana. *J Exp Mar Biol Ecol* 301:111–128.
- Mayer AG (1910) *Medusae of the World: The Scyphomedusae*. Carnegie Institution of Washington.
- Mayor AG (1912) *Ctenophores of the Atlantic coast of North America*. Carnegie Institution of Washington.
- McClelland JW, Valiela I (1998) Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. *Mar Ecol Prog Ser*:259–271.
- McDougall TJ, Barker PM (2011) Getting started with TEOS-10 and the Gibbs Seawater (GSW) oceanographic toolbox. *SCORIAPSO WG* 127:1–28.
- McNamara M, Lonsdale D, Cerrato R (2014) Role of eutrophication in structuring planktonic communities in the presence of the ctenophore *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 510:151–165.
- Miller RJ (1974) Distribution and Biomass of an Estuarine Ctenophore Population, *Mnemiopsis leidyi* (A. Agassiz). *Chesap Sci* 15:1–8.
- Morales-Alamo R, Haven DS (1974) Atypical mouth shape of polyps of the jellyfish, *Aurelia aurita*, from Chesapeake Bay, Delaware Bay, and Gulf of Mexico. *Chesap Sci* 15:22–29.
- Murdy EO, Birdsong RS, Musick JA (1997) *Fishes of Chesapeake Bay*. Smithsonian Institution Press.
- Murphy RR, Kemp WM, Ball WP (2011) Long-term trends in Chesapeake Bay seasonal hypoxia, stratification, and nutrient loading. *Estuaries Coasts* 34:1293–1309.
- Najjar RG, Pyke CR, Adams MB, Breitburg D, Hershner C, Kemp M, Howarth R, Mulholland MR, Paolisso M, Secor D, Sellner K, Wardrop D, Wood R (2010) Potential climate-change impacts on the Chesapeake Bay. *Estuar Coast Shelf Sci* 86:1–20.
- Newberger TA, Houde ED (1995) Population biology of bay anchovy *Anchoa mitchilli* in the mid Chesapeake Bay. *Mar Ecol Prog Ser* 116:25–37.
- Newell RI (1988) Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*. *Underst Estuary Adv Chesap Bay Res* 129:536–546.

- Noone KJ, Diaz RJ, Sumaila UR (2013) Managing ocean environments in a changing climate: sustainability and economic perspectives, First edition. Elsevier, Burlington, MA.
- North EW, Houde ED (2004) Distribution and transport of bay anchovy (*Anchoa mitchilli*) eggs and larvae in Chesapeake Bay. *Estuar Coast Shelf Sci* 60:409–429.
- Olney JE (1983) Eggs and early larvae of the bay anchovy, *Anchoa mitchilli*, and the weakfish, *Cynoscion regalis*, in lower Chesapeake Bay with notes on associated ichthyoplankton. *Estuaries Coasts* 6:20–35.
- Olson MM (1987) Ecological studies in the middle reach of Chesapeake Bay. pringer-Verlag.
- Oviatt CA (2004) The changing ecology of temperate coastal waters during a warming trend. *Estuaries* 27:895–904.
- Palinkas CM, Halka JP, Li M, Sanford LP, Cheng P (2014) Sediment deposition from tropical storms in the upper Chesapeake Bay: Field observations and model simulations. *Cont Shelf Res* 86:6–16.
- Peierls BL, Christian RR, Paerl HW (2003) Water quality and phytoplankton as indicators of hurricane impacts on a large estuarine ecosystem. *Estuaries* 26:1329–1343.
- Pierson J (2017) Zooplankton from hypoxic waters of Chesapeake Bay. 10.1575/1912/bco-dmo.687996
- Pierson J, Decker MB (2017) DeZoZoo Cruise Data. 10.1575/1912/bco-dmo.687984
- Pierson J, Houde ED (2015) Anchovy data of Chesapeake Bay. 10.1575/1912/bco-dmo.687979
- Pierson J, Slater W, Elliott D, Roman M (2017) Synergistic effects of seasonal deoxygenation and temperature truncate copepod vertical migration and distribution. *Mar Ecol Prog Ser* 575:57–68.
- Pollock MS, Clarke LMJ, Dubé MG (2007) The effects of hypoxia on fishes: from ecological relevance to physiological effects. *Environ Rev* 15:1–14.
- Powers DA (1980) Molecular ecology of teleost fish hemoglobins: strategies for adapting to changing environments. *Am Zool*:139–162.
- Purcell J, Decker M, Breitburg D, Broughton K (2014) Fine-scale vertical distributions of *Mnemiopsis leidyi* ctenophores: predation on copepods relative to stratification and hypoxia. *Mar Ecol Prog Ser* 500:103–120.
- Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ, Raskoff KA (2001a) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: *Coastal and Estuarine Studies*. p 77–100

- Purcell JE, Decker MB (2005) Effects of Climate on Relative Predation by Scyphomedusae and Ctenophores on Copepods in Chesapeake Bay during 1987-2000. *Limnol Oceanogr* 50:376–387.
- Purcell JE, Nemazie DA (1992) Quantitative feeding ecology of the hydromedusan *Nemopsis bachei* in Chesapeake Bay. *Mar Biol* 113:305–311.
- Purcell JE, Shiganova TA, Decker MB, Houde ED (2001b) The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. In: *Jellyfish Blooms: Ecological and Societal Importance*. Springer, p 145–176
- Purcell JE, Shiganova TA, Decker MB, Houde ED (2001c) The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. *Hydrobiologia* 451:145–176.
- Purcell JE, White JR, Nemazie DA, Wright DA (1999) Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Mar Ecol Prog Ser* 180:187–196.
- Rabalais NN, Diaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J (2010) Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7:585–619.
- Rhein M al, Rintoul SR, Aoki S, Campos E, Chambers D, Feely RA, Gulev S, Johnson GC, Josey SA, Kostianoy A, others (2013) Observations: ocean. *Clim Change*:255–315.
- Richmond C, Marcus NH, Sedlacek C, Miller GA, Oppert C (2006) Hypoxia and seasonal temperature: Short-term effects and long-term implications for *Acartia tonsa* dana. *J Exp Mar Biol Ecol* 328:177–196.
- Robinette HR (1983) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico): Bay anchovy and Striped anchovy.
- Roman MR, Boicourt WC, Kimmel DG, Miller WD, Adolf JE, Bichy J, Harding LW, Houde ED, Jung S, Zhang X (2005) Chesapeake Bay plankton and fish abundance enhanced by Hurricane Isabel. *Eos Trans Am Geophys Union* 86:261.
- Roman MR, Brandt SB, Houde ED, Pierson JJ (2019) Interactive Effects of Hypoxia and Temperature on Coastal Pelagic Zooplankton and Fish. *Front Mar Sci* 6.
- Roman MR, Gauzens AL, Rhinehart WK, White JR (1993) Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnol Oceanogr* 38:1603–1614.
- Shoji J, Masuda R, Yamashita Y, Tanaka M (2005a) Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*. *Mar Biol* 147:863–868.

- Shoji J, Masuda R, Yamashita Y, Tanaka M (2005b) Predation on fish larvae by moon jellyfish *Aurelia aurita* under low dissolved oxygen concentrations. *Fish Sci* 71:748–753.
- Steinberg DK, Condon RH (2009) Zooplankton of the York River. *J Coast Res*:66–79.
- Stevens PW, Blewett DA, Casey JP (2006) Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of hurricane Charley. *Estuaries Coasts* 29:997–1003.
- Stone SL (1994) Distribution and abundance of fishes and invertebrates in Mid-Atlantic estuaries. US Department of Commerce, National Oceanic and Atmospheric Administration.
- Sullivan BK, Keuren DV, Clancy M (2001) Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. *Hydrobiologia* 451:113–120.
- Taylor JC, Rand PS, Jenkins J (2007) Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. *Mar Biol* 152:939–957.
- Team RC (2013) R: A language and environment for statistical computing.
- Thuesen EV, Rutherford LD, Brommer PL (2005) The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. *J Mar Biol Assoc U K* 85:627–633.
- Uye S (2011) Human forcing of the copepod–fish–jellyfish triangular trophic relationship. *Hydrobiologia* 666:71–83.
- Vargo SL, Sastry AN (1977) Acute temperature and low dissolved oxygen tolerances of brachyuran crab (*Cancer irroratus*) larvae. *Mar Biol* 40:165–171.
- Wang SB, Houde ED (1994) Energy storage and dynamics in bay anchovy *Anchoa mitchilli*. *Mar Biol* 121:219–227.
- Weiss RF (1970) The solubility of nitrogen, oxygen and argon in water and seawater. In: *Deep Sea Research and Oceanographic Abstracts*. Elsevier, p 721–735
- White JR, Roman MR (1992) Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. *Mar Ecol-Prog Ser* 86:251–251.
- Wiebe PH (1976) A multiple opening/closing net and environment sensing system for sampling zooplankton. *J Mar Res* 34:313–326.
- Wilson CB, Museum USN (1932) The copepod crustaceans of Chesapeake Bay. Smithsonian Institution Press.
- Wood SC, Johansen K (1972) Adaptation to hypoxia by increased HbO₂ affinity and decreased red cell ATP concentration. *Nature* 237:278–279.

Wu RS (2002) Hypoxia: from molecular responses to ecosystem responses. Mar Pollut Bull 45:35–45.

Tables and figures

Table 2.1. Eigenvalue (a) and eigenvectors (b) of the principal component analysis of temperature, salinity, and dissolved oxygen (DO) of water sampled by CTD from above, at, and below pycnocline at both the North and South Stations.

(a)

	Eigenvalue	Difference	Proportion	Cumulative
1	5.01	2.68	0.56	0.56
2	2.33	1.68	0.26	0.82
3	0.66	0.16	0.07	0.89
4	0.50	0.21	0.06	0.95
5	0.30	0.21	0.03	0.98
6	0.08	0.04	0.01	0.99
7	0.05	0.01	0.01	0.99
8	0.04	0.02	0.00	1.00
9	-	0.02	0.00	1.00

(b)

	Principal Component 1	Principal Component 2
DO above pycnocline	0.35	0.20
DO at pycnocline	0.27	0.33
DO below pycnocline	0.14	0.51
Temp. above pycnocline	- 0.38	- 0.26
Temp. at pycnocline	- 0.39	- 0.12
Temp. below pycnocline	- 0.42	- 0.06
Salinity above pycnocline	- 0.33	0.41
Salinity at pycnocline	- 0.33	0.39
Salinity below pycnocline	- 0.30	0.45

Table 2.2. Grouping cruises, Year-Season (Station), according to the PCA grouping results. All cruises were designated for three temperature groups according to their PC1 scores (C = Cool, T = Temperate, W = Warm), and each group was divided into two subgroups according to their PC2 scores (LO = Less-oxygenated, MO = More-oxygenated). Underlined text indicates the averaged bottom DO < 2 mg L⁻¹, bold text indicates bottom $pO_2 < P_{crit}$, and italic text indicates $pO_2 < P_{leth}$.

	LO	MO
C	<u>2011-Spring (N)</u>	2010-Spring (N, S), 2011-Spring (S)
T	2011- Autumn (N)	2011-Autumn (S)
W	<u>2011-Summer (N, S),</u> <u>2010-Summer (N)</u>	2010- Autumn (N, S), 2010-Summer (S)

Table 2.3. The Kruskal-Wallis test on differences in concentrations of zooplankton and fish between the more-oxygenated (MO) and less-oxygenated (LO) subgroups within the cool (C), temp (T), and warm (W) groups.

Zooplankton and fish concentration						
Species	Stage	Group	Sample size	d.f.	chi-square	p-value
<i>Acartia tonsa</i>	adult	C	103	1	15.1180	0.0001
		T	36	1	9.8108	0.0017
		W	127	1	1.6625	0.1973
<i>Acartia tonsa</i>	copepodite	C	107	1	8.5712	0.0034
		T	36	1	8.8460	0.0029
		W	127	1	25.785	<0.0001
<i>Anchoa mitchilli</i>	larval	C	60	1	6.5997	0.0102
		T	24	1	8.5792	0.0034
		W	58	1	0.5652	0.4522
	juvenile	C*	-	-	-	-
		T	24	1	0.1883	0.6643
		W	58	1	4.3211	0.0376
<i>Mnemiopsis leidyi</i>	adult	C	119	1	2.6121	0.1061
		T	48	1	35.225	< 0.0001
		W	116	1	17.545	< 0.0001
<i>Chrysaora chesapeakei</i>	medusa	C	0	-	-	-
		T	48	1	1	0.3171
		W	116	1	2.0241	0.1548

*Mid-water trawls were not conducted during the spring cruises, and thus, juvenile *A. mitchilli* were not sampled in the Cool group.

Table 2.4. The Kruskal-Wallis test on differences in *Acartia tonsa*'s non-predatory mortality between the more-oxygenated and less-oxygenated subgroups within the cool, temperate, and warm groups.

A. tonsa's non-predatory mortalities				
Group	Sample size	d.f.	chi-square	p-value
Cool	5	1	0.3333	0.5637
Temperate	6	1	2.3333	0.1266
Warm	18	1	6.9286	0.008

Figure 2.1. The study area of the Dead Zone Zooplankton research project. The square indicates the North Station (38.528° N, 76.418° W) and the circle indicates the South Station (37.738° N, 76.208° W), and the grey contouring indicates the water depth of Chesapeake Bay.

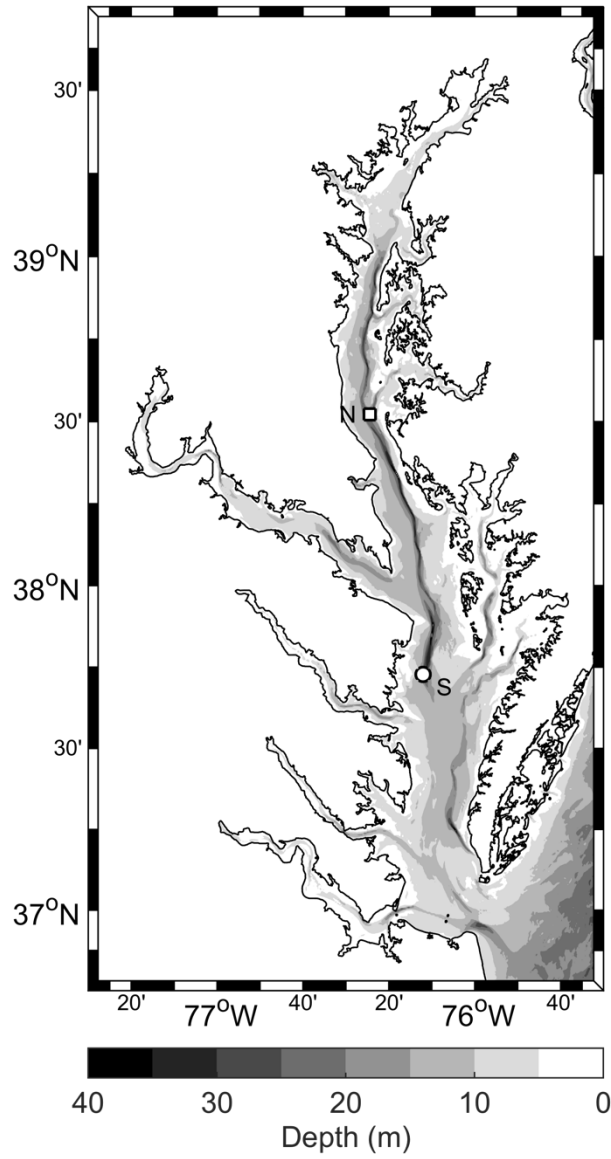


Figure 2.2. Average temperature ($^{\circ}\text{C}$, red) and salinity (blue) from the CTD casts taken at North (closed) and South (open) stations during 2010 and 2011 cruises. Symbols represent mean values in 0.5-m bins from all CTD measurements at each depth, and horizontal lines indicated standard deviations. Modified from (Pierson et al. 2017).

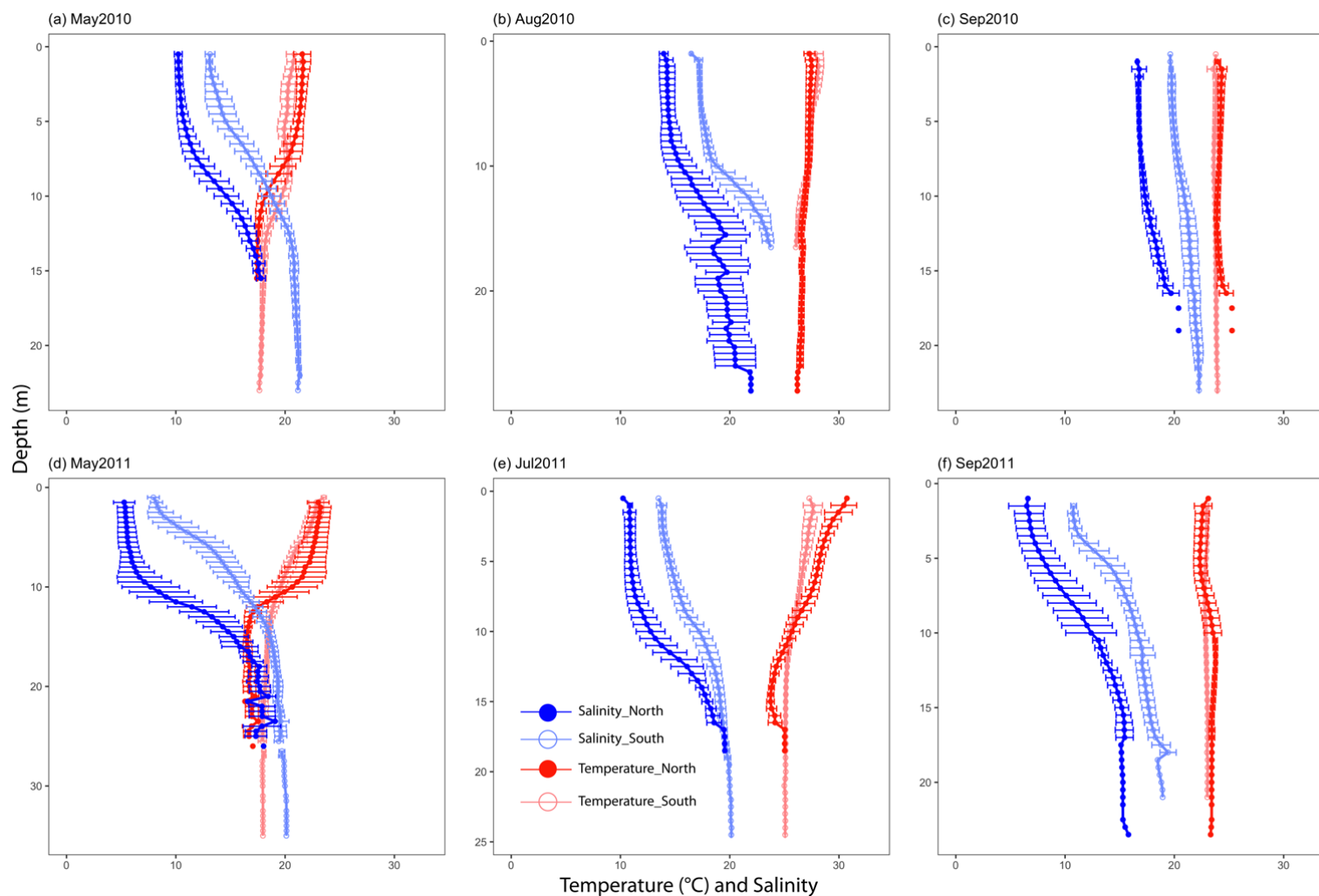


Figure 2.3. Average dissolved oxygen (diamonds, mg L^{-1}) from the CTD casts taken at North (closed) and South (open) stations during 2010 and 2011 cruises. Symbols represent mean values in 0.5 m bins from all CTD measurements at each depth, and horizontal lines indicated standard deviations. Color fillings represent partial pressure: above P_{crit} (green), between P_{crit} and P_{leth} (orange), and below P_{leth} (red). Dashed black lines indicated dissolved oxygen = 2 mg L^{-1} . Modified from (Pierson et al. 2017).

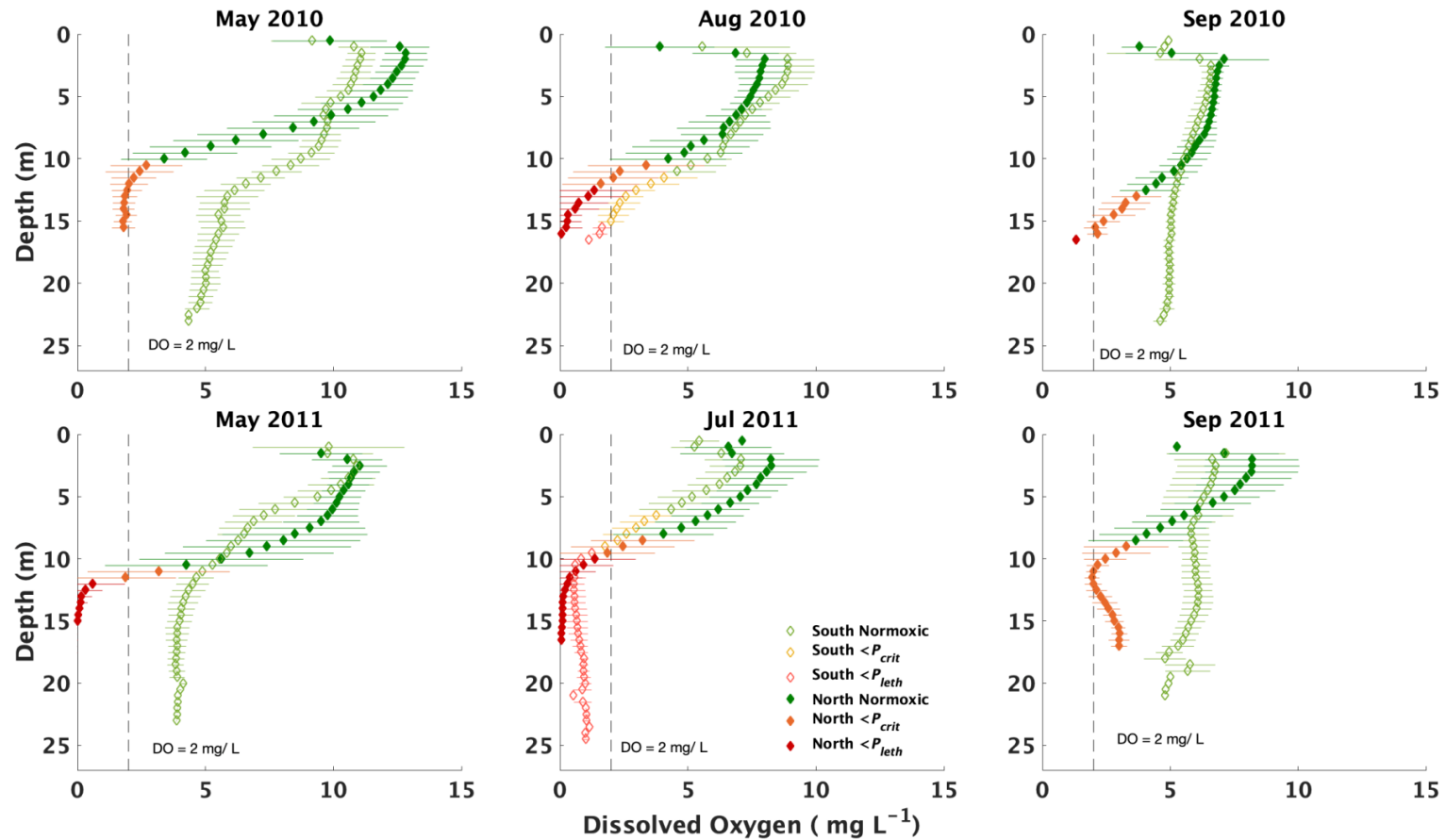


Figure 2.4. Concentrations of the copepod *Acartia tonsa* adults (a) and copepodites (b) collected at North (red) and South (green) station during the six research cruises from May, August/ July, September in 2010 and 2011. Bubble sizes indicate population sizes (ind. m⁻³).

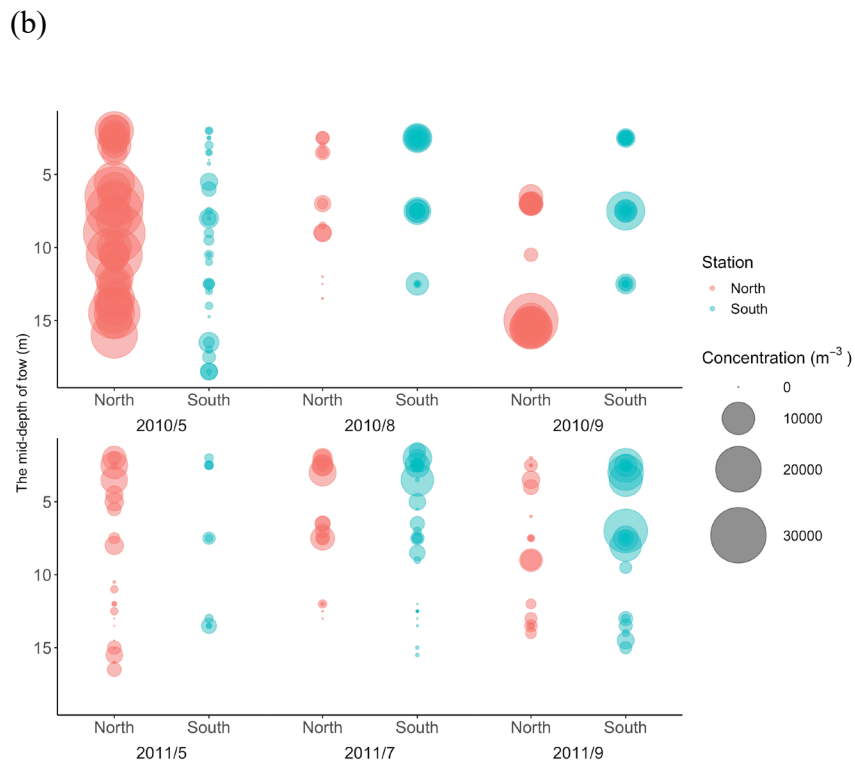
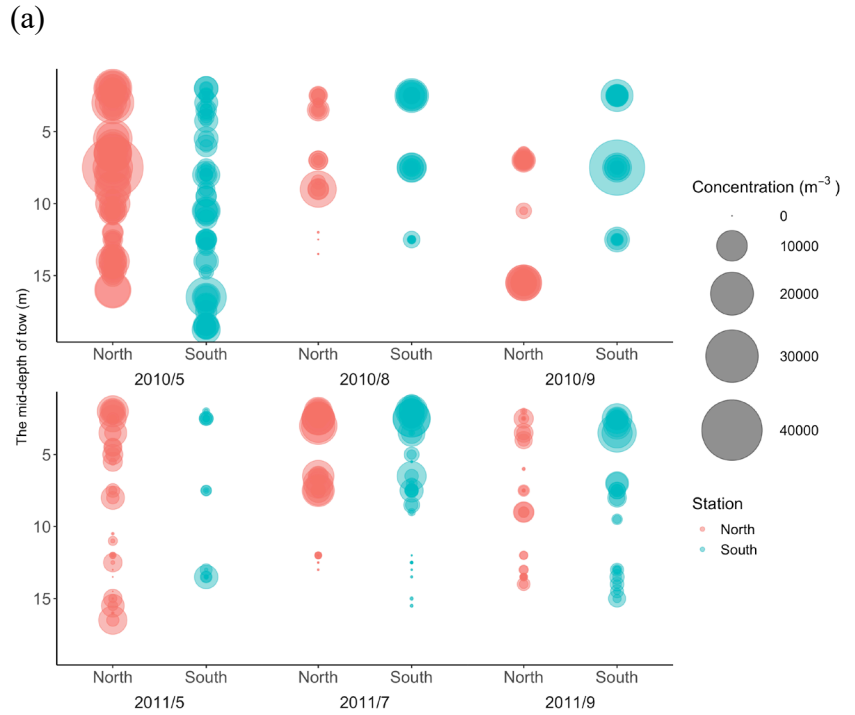


Figure 2.5. Concentrations of planktivorous fish, bay anchovy (*Anchoa mitchilli*) larvae (a) and juveniles (b) collected at North (red) and South (green) station during the six research cruises from May, August/July, September in 2010 and 2011. Bubble sizes indicate population sizes (ind. m^{-3}).

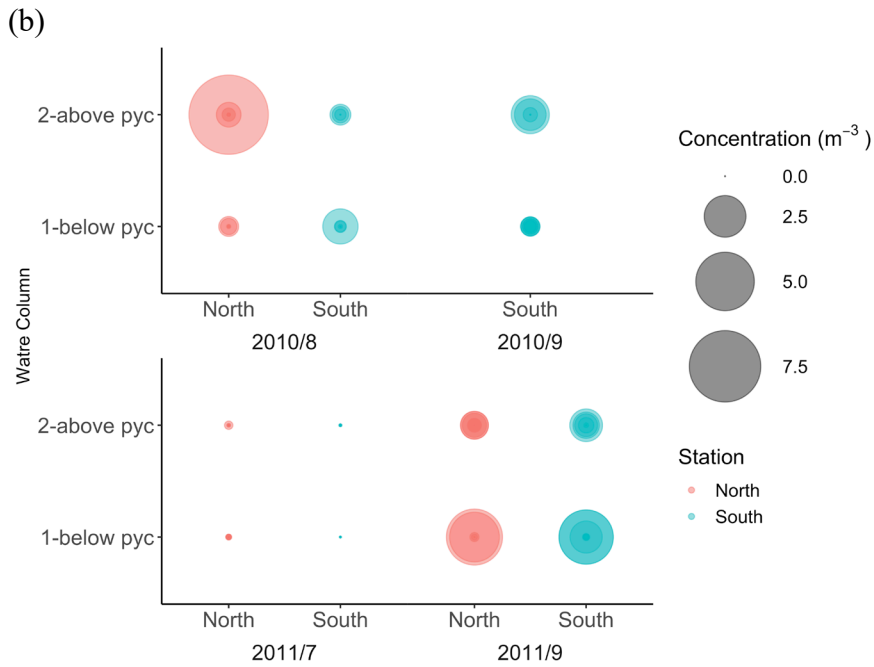
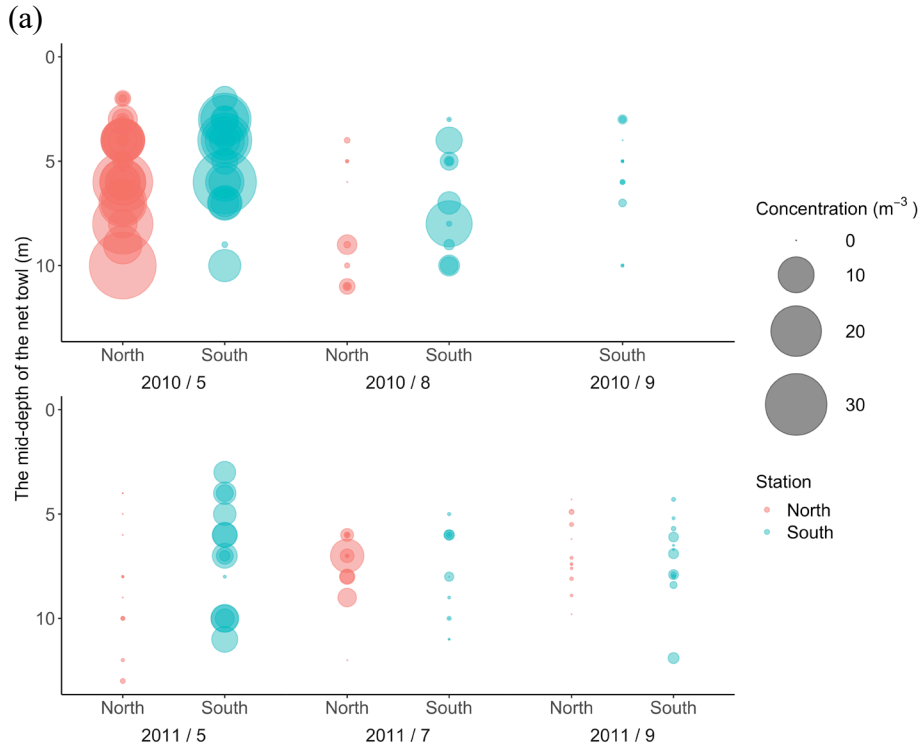


Figure 2.6. Concentrations of gelatinous zooplankton; comb jelly (*Mnemiopsis leidyi*, a) and bay nettle (*Chrysaora chesapeakei*, b) collected at North (red) and South (green) station during the six research cruises from May, August/July, September in 2010 and 2011. Bubble sizes indicate population sizes (ind. m⁻³).

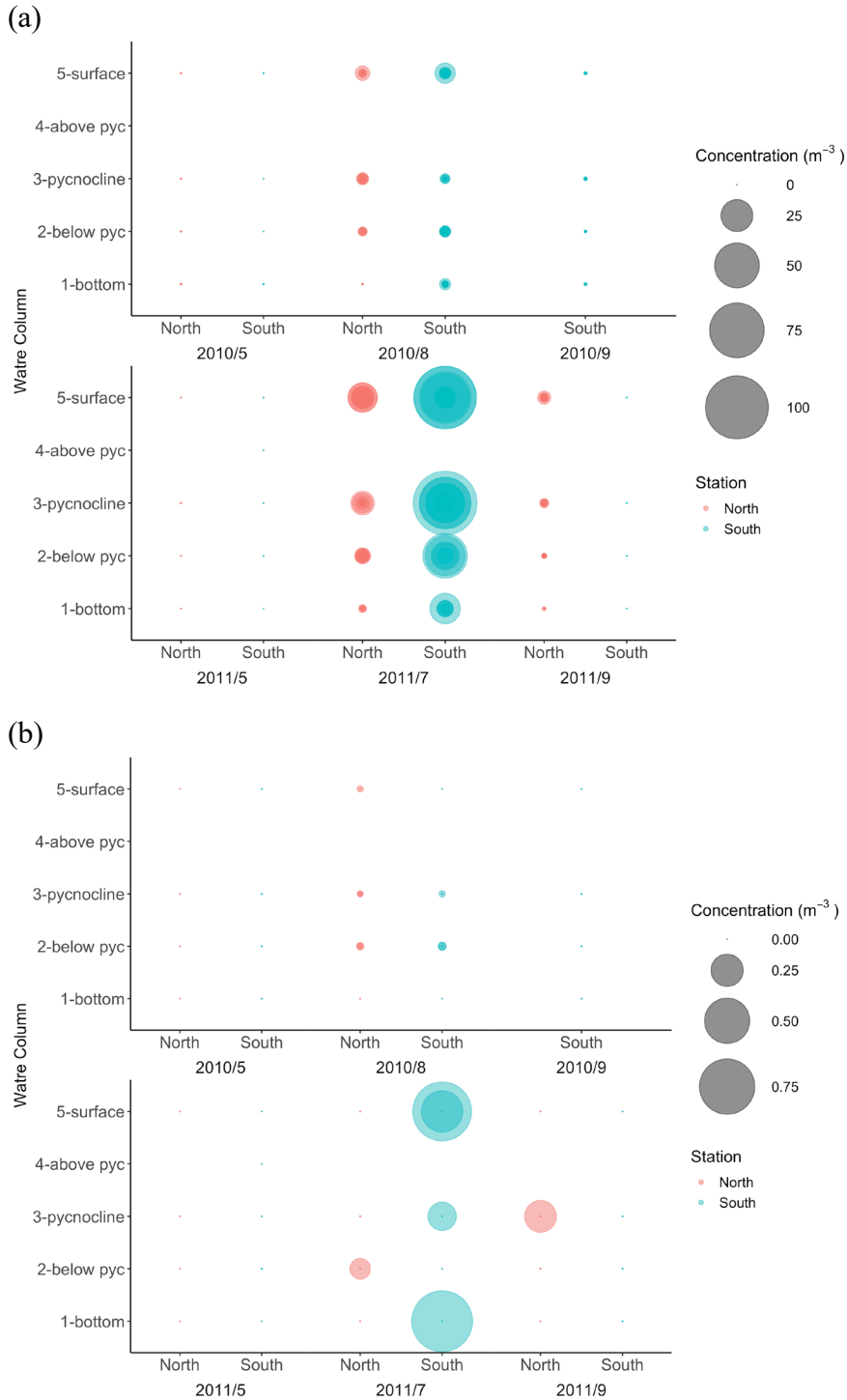


Figure 2.7. Principal component analysis of average temperature, salinity, and dissolved oxygen of the water above, at, and below pycnocline from each CTD cast at the North and South stations.

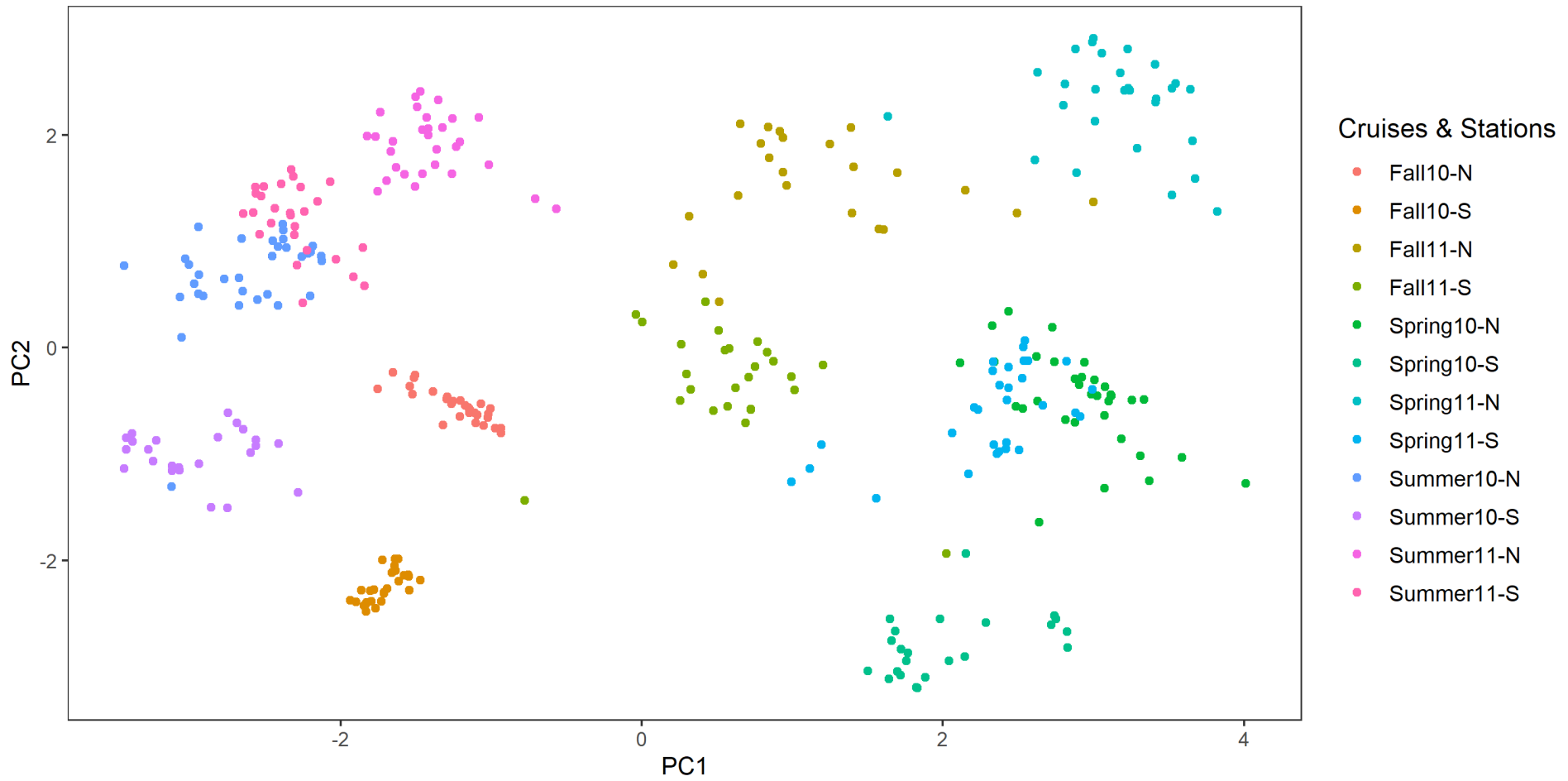


Figure 2.8. Temperature (a), salinity (b), and dissolved oxygen (c) from above, at, and below the pycnocline in the Cool, Temperate, and Warm groups. Circles with dots indicate medians, bars indicate 25 to 75 percentiles, lines indicate 5 to 95 percentile, and open circles indicate outliers.

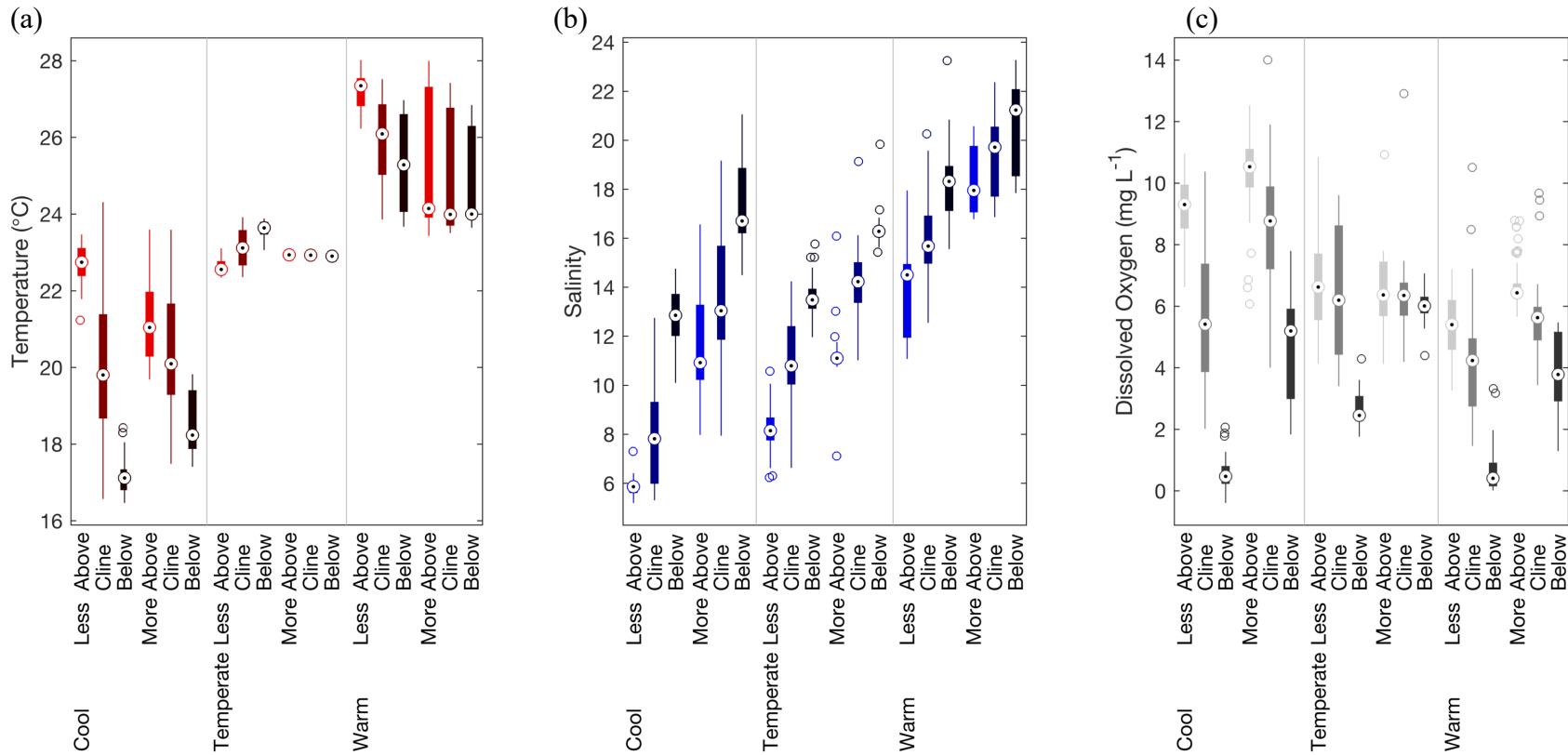
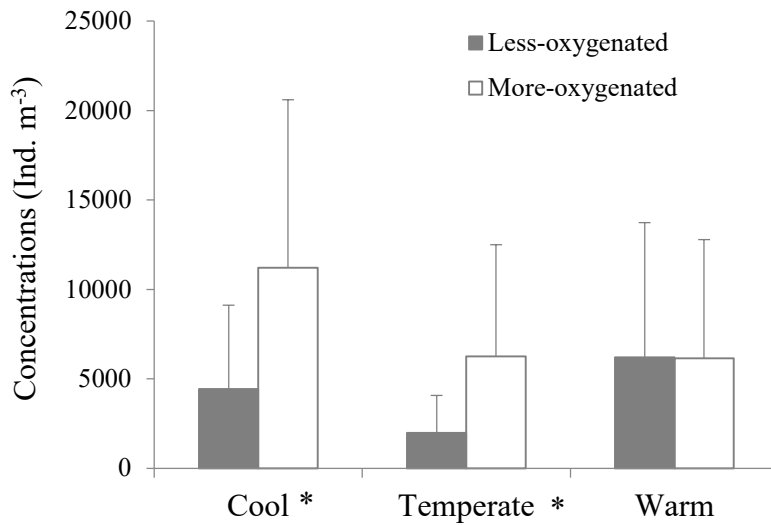


Figure 2.9. Comparison of copepod (*Acartia tonsa*) (a) adults and (b) copepodite concentrations between More-oxygenated (open bar) and Less-oxygenated (closed bar) subgroups within temperature groups (Cool, Temperate, Warm). Error bars indicate standard deviations and * indicates a significant difference in a Kruskal-Wallis test at $\alpha = 0.05$

(a)



(b)

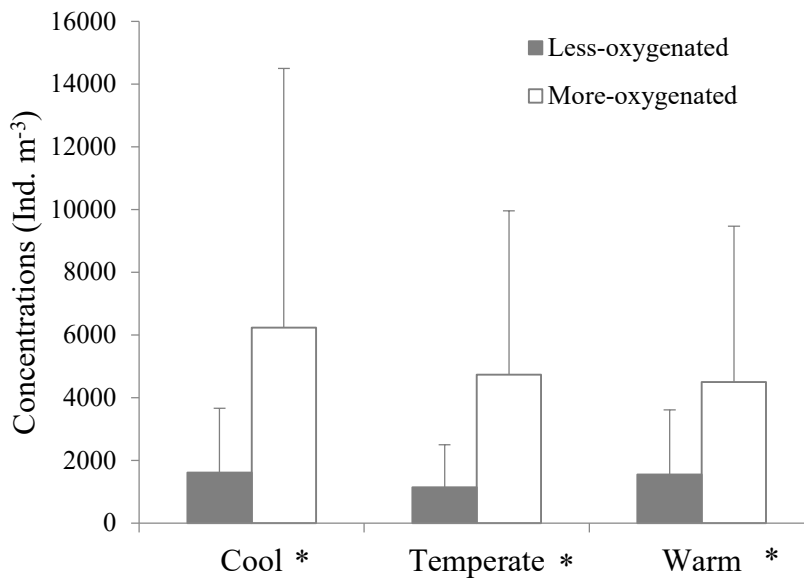
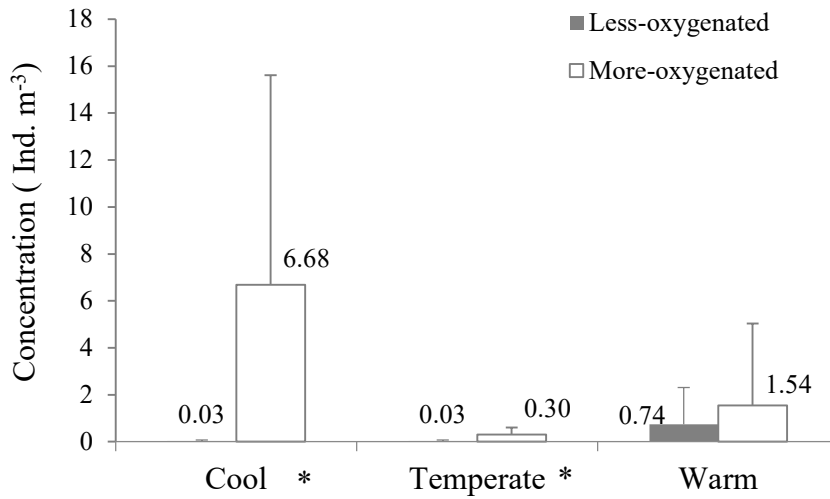


Figure 2.10. Comparison of (a) larval and (b) juvenile bay anchovy (*Anchoa mitchilli*) concentrations between More-oxygenated (open bar) and Less-oxygenated (closed bar) subgroups within temperature groups (Cool, Temp, Warm). Numbers indicate average concentrations, error bars indicate standard deviations, and * indicates significant difference in a Kruskal-Wallis test at $\alpha = 0.05$.

(a)



(b)

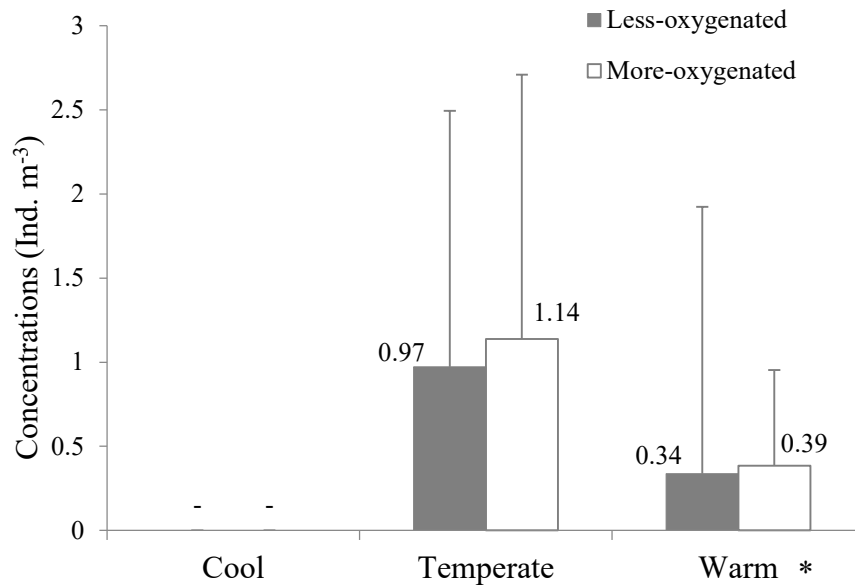


Figure 2.11. Comparison of (a) ctenophore (*Mnemiopsis leidyi*) and (b) bay nettle (*Chrysaora chesapeakei*) concentrations between More-oxygenated (open bar) and Less-oxygenated (closed bar) subgroups within temperature groups (Cool, Temperate, Warm). Numbers indicate average concentrations, error bars indicate standard deviations, and * indicates significant differences in a Kruskal-Wallis test at $\alpha = 0.05$

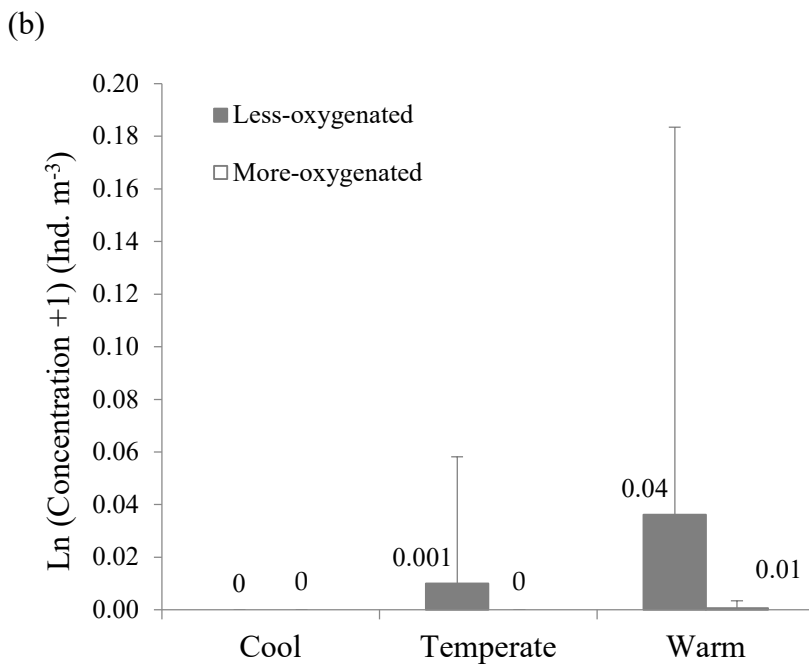
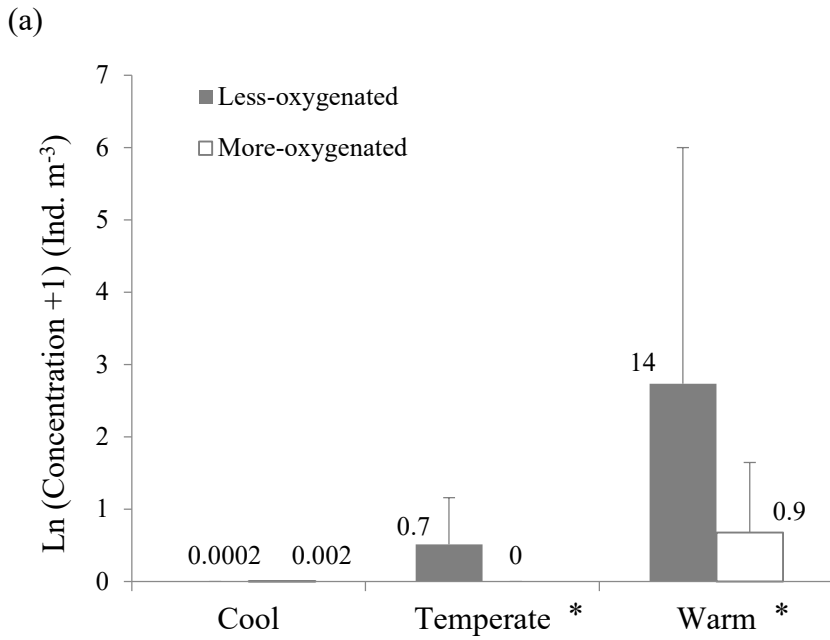
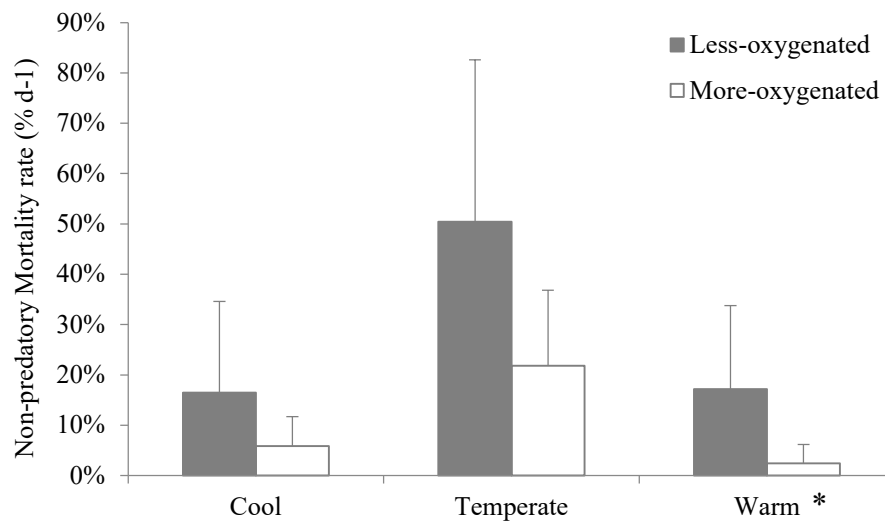


Figure 2.12. The average daily non-predatory mortality (% d⁻¹) of the copepod *Acartia tonsa* between More-oxygenated (M) and Less-oxygenated (L) subgroups within temperature groups (Cool, Temp, Warm). Error bars indicate standard deviations, and * indicates a significant difference in a Kruskal–Wallis test at $\alpha = 0.05$



Appendices

Appendix 2.1. The numbers of CTD casts deployed during each cruise.

Cruise	2010	2011
Season		
Spring	77	88
Summer	88	69
Autumn	64	66
Total Casts	229	223
		452

Appendix 2.2. The numbers of MOCNESS net tows, Tucker Trawls, and mid-water trawls conducted during each cruise.

Cruise	MOCNESS	Tucker Trawls	Mid-water trawls
2010			
Spring	11	18	0
Summer	11	11	11
Autumn	6	6	6
2011			
Spring	8	12	0
Summer	12	12	12
Autumn	12	12	12
Total	60	71	41

Appendix 2.3. Mean concentrations (\pm S.D.) (ind. m⁻³) of copepods (*Acartia tonsa*), bay anchovies (*Anchoa mitchilli*), ctenophore (*Mnemiopsis leidyi*), and bay nettles (*Chrysaora chesapeakei*) collected from the North and South Stations during the 2010 (a) and 2011(b) cruises

(a)

Species /Stage	<i>A. tonsa</i> (Adult female and male)	<i>A. tonsa</i> (Copepodite)	<i>A. mitchilli</i> (Larval)	<i>A. mitchilli</i> (Juvenile)	<i>M. leidyi</i> (Adult)	<i>C. chesapeakei</i> (Medusa)	
Nets	MOCNESS	MOCNESS	MOCNESS	Mid-water Trawl	Tucker Trawl	Tucker Trawl	
Station							
North	May	16232.39 \pm 10908.58	12656.34 \pm 8514.45	11.46 \pm 12.64	- ^c -	0.0027 \pm 0.0046	0 0
	Aug	4077.83 \pm 4882.37	981.92 \pm 1011.33	0.59 \pm 0.94	1.124 \pm 2.874	1.0951 \pm 1.3414	0.0019 \pm 0.0035
	Sep	5592.79 ^a \pm 5802.39	6244.62 ^a \pm 6126.24	- ^a -	- ^a -	- ^a -	- ^a -
South	May	7887.59 ^b \pm 4587.74	839.89 ^b \pm 1004.78	5.48 ^b 7.6	- ^c -	0.0007 \pm 0.0035	0 0
	Aug	6225.92 \pm 7010.20	3231.59 \pm 2624.41	2.95 \pm 4.60	0.269 0.505	1.8699 \pm 1.9468	0.0014 \pm 0.0039
	Sep	7028.05 \pm 7896.31	2595.67 \pm 3111.16	0.12 \pm 0.17	0.501 0.624	0.0671 \pm 0.0670	0 0

(b)

Species /Stage	<i>A. tonsa</i> (Adult female and male)	<i>A. tonsa</i> (Copepodite)	<i>A. mitchilli</i> (Larval)	<i>A. mitchilli</i> (Juvenile)	<i>M. leidyi</i> (Adult)	<i>C. chesapeakei</i> (Medusa)	
Nets	MOCNESS	MOCNESS	MOCNESS	Mid-water Trawl	Tucker Trawl	Tucker Trawl	
Station							
North	May	4426.36 \pm 4682.72	1605.72 \pm 2056.29	0.03 \pm 0.04	- ^c -	0.0002 \pm 0.0012	0 0
	Jul	9818.09 \pm 8922.12	2000.93 \pm 1977.54	1.42 \pm 2.39	0.016 \pm 0.023	5.3006 \pm 6.4913	0.0041 \pm 0.0203
	Sep	1978.11 \pm 2090.38	1139.02 \pm 1356.40	0.03 \pm 0.04	0.973 \pm 1.521	0.6708 \pm 0.9117	0.0101 \pm 0.0493
South	May	2521.99 \pm 2068.83	670.82 \pm 556.18	4.45 \pm 0.86	- ^c -	0.0008 \pm 0.0021	0 0
	Jul	4949.34 \pm 7132.56	1572.82 \pm 2481.06	0.19 \pm 0.28	0.001 \pm 0.002	34.6636 \pm 33.5756	0.0988 \pm 0.2581
	Sep	6258.11 \pm 6235.51	4734.49 \pm 5222.70	0.30 \pm 0.31	1.138 \pm 1.569	0 0	0 0

Note:

a. Due to issues with the ship's hydraulic winch in September 2010, *A. tonsa* concentrations at North Station were collected by Z-trap (Barba 2015), and anchovies and jellyfish were not collected.

b. *A. tonsa* and larval *A. mitchilli* concentrations were collected by Tucker Trawl at South Station in May 2010 due to mechanical issues with the MOCNESS

c. no Mid-water trawls were conducted during the May cruises.

Appendix 2.4. Mean (\pm S.D.) temperature, salinity, partial pressure of dissolved oxygen (pO_2) in three water layers (Surf. = above the pycnocline, Pyc. = within the pycnocline, Bot. = below the pycnocline), and the corresponding critical partial oxygen pressure (P_{crit}) and lethal oxygen partial pressure (P_{leth}) in each temperature (C = Cool, T = Temperate, and W = Warm) and dissolved oxygen subgroups (LO = less oxygenated, MO = more oxygenated). Sample sizes indicate the total numbers of CTD casts in each group. Bold pO_2 values indicate $pO_2 < P_{crit}$ (Biological hypoxia), and bold and italic values indicate $pO_2 < P_{leth}$.

Group	Sample Size		Layer	Temperature		Salinity		pO_2		P_{crit}		P_{leth}	
	LO	MO		LO	MO	LO	MO	LO	MO	LO	MO	LO	MO
C	28	87	Surf.	22.69 \pm 0.53	21.19 \pm 1.10	5.86 \pm 0.40	11.56 \pm 2.30	23.48 \pm 2.32	26.79 \pm 2.95	8.13	8.77	3.22	3.44
			Pyc.	19.95 \pm 1.81	20.39 \pm 1.55	8.06 \pm 2.22	13.57 \pm 2.92	13.80 \pm 5.39	21.87 \pm 5.06	8.26	8.74	3.26	3.43
			Bot.	17.18 \pm 0.50	18.51 \pm 0.75	12.76 \pm 1.14	17.44 \pm 1.75	1.48 \pm 1.36	11.79 \pm 4.33	7.88	8.27	3.13	3.27
T	23	26	Surf.	22.64 \pm 0.23	22.94 \pm 0.07	8.22 \pm 1.12	11.22 \pm 1.36	17.39 \pm 3.93	17.14 \pm 3.60	8.55	9.12	3.36	3.56
			Pyc.	23.14 \pm 0.49	22.91 \pm 0.07	11.06 \pm 1.92	14.30 \pm 1.52	16.92 \pm 5.65	17.33 \pm 4.17	9.13	9.62	3.57	3.74
			Bot.	23.61 \pm 0.22	22.90 \pm 0.06	13.61 \pm 0.93	16.42 \pm 0.79	7.36 \pm 1.68	16.37 \pm 1.36	9.73	9.95	3.78	3.85
W	87	86	Surf.	26.12 \pm 1.44	26.27 \pm 1.80	14.35 \pm 2.27	17.50 \pm 2.16	15.34 \pm 2.82	19.18 \pm 2.41	10.81	11.82	4.15	4.50
			Pyc.	24.87 \pm 0.89	25.95 \pm 1.62	15.99 \pm 1.51	19.05 \pm 1.94	11.82 \pm 4.59	15.68 \pm 3.74	10.72	12.09	4.12	4.60
			Bot.	24.39 \pm 0.60	25.69 \pm 1.34	17.85 \pm 0.93	20.85 \pm 1.53	4.06 \pm 4.34	8.34 \pm 5.61	10.91	12.41	4.19	4.71

Chapter Three. Hypoxia increases ctenophore and fish predation on copepods: a case study in the Chesapeake Bay

Abstract

The indirect impact of hypoxia on trophic interactions, particularly predator-prey relationships among crustacean zooplankton, gelatinous zooplankton, and planktivorous fish, was investigated in the Chesapeake Bay. Population data and gut content samples were collected with net tows at two stations in the mainstem of Chesapeake Bay during six research cruises from May to September in 2010 and 2011. Gut contents of the ctenophore (*Mnemiopsis leidyi*) and the larval and juvenile stages of bay anchovy (*Anchoa mitchilli*) were analyzed to estimate and compare their predation on the copepod *Acartia tonsa* under various dissolved oxygen conditions. The predatory impact was greater under hypoxia than under normoxic conditions. The importance of predatory mortality increased, and the primary predator shifted, with increasing severity of bottom-water hypoxia. Juvenile *A. mitchilli* contributed most to predatory mortality on *A. tonsa* under normoxic and mildly hypoxic conditions, but *M. leidyi* became the predominant predator under the warmest and most severely hypoxic conditions, suggesting that consumption by specific predators is also regulated by the hypoxia tolerance of the interacting species and not only predator seasonality. Two methods were applied to estimate predatory impact by *M. leidyi* on *A. tonsa*: 1) using gut contents and 2) applying an empirical relationship with tentacle bulb size. Results were generally similar except that estimated predation from tentacle

bulb size was larger than estimates from gut contents under the warmest and most hypoxic conditions. It was concluded that the total mortality of *A. tonsa* was higher under hypoxic conditions and the relative importance of predation increased with temperature (season) and hypoxia severity.

Introduction

A changing food web under eutrophication and hypoxia

While global warming is one of the major reasons for expanding oxygen minimum zones in the open ocean (Deutsch et al. 2015), nutrient enrichment from sewage discharges and agriculture runoff followed by algae blooms are directly associated with coastal hypoxia (reviewed in Breitburg et al., 2018). The excessive anthropogenic nutrients favor fast-growing phytoplankton species, shifting the primary producer community from perennial macroalgae and seagrasses to ephemeral macroalgae and pelagic microalgae (Borum 1996). This phenomenon was observed in the Chesapeake Bay, where seagrass decreased and the surface chlorophyll-a concentration has at least doubled from 1950s to 1980s (Kemp et al. 2005, Harding et al. 2019). However the enhanced spring bloom was shown to be decoupled from one of its principal grazers, the copepod *Acartia tonsa*, because the copepod's growth rate was limited by temperature (Heinle 1966), and so the unconsumed phytoplankton sank to the bottom. This depleted the bottom oxygen during its decomposition and fueled summer hypoxia.

During the seasonal hypoxia, mixotrophic phytoflagellates and dinoflagellates are often favored in the plankton community and microbial loops are enhanced (Baird

et al., 2004; Capriulo et al., 2002; Stoecker et al., 2017), altering the food web structure and favoring a smaller, zooplankton-dominated community that favors smaller planktivorous and filter-feeding consumers and, moreover, one in which production is directed toward microbial loops and gelatinous zooplankton more than finfish (Glibert & Burkholder, 2006; Glibert, 2010; Justić et al., 1995; Roman et al., 2019). For example, lab experiments found larval naked gobies (*Gobiosoma bosc*) are preyed upon more by bay nettles (*Chrysaora chesapeakei*) and less by juvenile striped bass (*Morone saxatilis*) in environments with low DO, leading to less energy flow to the economically valuable striped bass (Breitburg et al., 1997). When populations of the filter-feeding ctenophore *Mnemiopsis leidyi* increase in an eutrophic and microzooplankton-dominant ecosystem, there is a positive feedback of the *M. leidyi* bloom to the microzooplankton population through rich nitrogen excretion by the ctenophores (Purcell et al. 2001b, McNamara et al. 2013a b, 2014). Gelatinous zooplankton, as filter feeders and drifters with comparatively higher hypoxia-tolerance (reviewed in Ekau et al., 2010), have been hypothesized to exhibit increased population abundance in eutrophic and hypoxic areas (Parsons & Lalli 2002). Gelatinous zooplankton outbreaks also have been associated with fish stock declines resulting from hypothesized enhanced predation or competition (Lynam et al. 2005, 2006, Uye 2008, Dong et al. 2010, Robinson et al. 2014). Fishery scientists are increasingly urged to include gelatinous zooplankton in routine fishery surveys to enable a comprehensive understanding of food web dynamics and the effects of predation and competition (Brodeur et al., 2016).

Besides potentially increasing predation and competition, coastal hypoxia also affects fish population by decreasing habitat, reducing growth rates, and increasing mortality at young stages, resulting in declines of both the abundance and species diversity (Breitburg et al. 2001, Eby et al. 2005, Pollock et al. 2007). For example, the optimal habitat of striped bass *Morone saxatilis* in the Chesapeake Bay has shrunk during summer as the bottom waters have become hypoxic and the surface has become warmer (Coutant 1985, Coutant & Benson 1990). An individual-based model developed for Chesapeake Bay indicated that the mortality rate of *A. mitchilli* larvae would increase, as would spatial overlaps among *A. mitchilli* and its predators when bottom waters were hypoxic (Breitburg et al. 2001, Adamack et al. 2012). The impact of eutrophication-induced hypoxia on an ecosystem can be systemic, ranging from species to habitat to food web structure. Such an ecosystem is less resilient and is usually dominated by pelagic algae, microbial loops, smaller zooplankton, filter feeders, and smaller fish (McClelland & Valiela 1998, Wu 2002, Breitburg 2002, Kemp et al. 2005, Uye 2011, Kimmel et al. 2012).

The zooplankton food web in Chesapeake Bay

As the most abundant crustacean zooplankton in Chesapeake Bay, the copepod *Acartia tonsa* is the primary prey for many other planktivorous species, including fish and gelatinous zooplankton (Klebasko, 1991; Purcell & Decker, 2005). A major planktivorous fish in the Chesapeake Bay is Chesapeake Bay anchovy (*Anchoa mitchilli*). As an obligate planktivore in all of its life stages, *A. mitchilli* is a major consumer of mesozooplankton during summer and fall. The populations of larval and juvenile *A. mitchilli* are capable of consuming a substantial amount of

zooplankton. In turn, *A. mitchilli* is preyed upon by many piscivorous fishes, for example bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and striped bass (*Morone saxatilis*). Consumption by piscivorous fishes has been shown to be very high and at least 50% of the *A. mitchilli* annual production went to predation (Baird & Ulanowicz 1989, Jung & Houde 2004). Because of its significant roles as both a predator and prey, *A. mitchilli* is a key species for transferring production to higher trophic levels in the Chesapeake Bay and other estuaries (Baird & Ulanowicz 1989).

Another class of major predators on *A. tonsa* in Chesapeake Bay is gelatinous zooplankton (Breitburg & Burrell, 2014; Purcell, 1992). During summer the most commonly seen gelatinous zooplankton in the Chesapeake Bay are *C. chesapeakei* and *M. leidy*, and *C. chesapeakei* also preys on *M. leidy*. While both gelatinous zooplankton have high clearance rate on copepods ($> 70.3 \text{ L m}^{-3} \text{ d}^{-1}$, estimated by multiplying individual clearance rate and predator concentration), *M. leidy* has an especially large effect by consuming more copepods than *C. chesapeakei* does at equivalent sizes or weights (Purcell & Decker, 2005). As result, a field study in Chesapeake Bay indicated the average total clearance of copepods was three times higher in the years when *C. chesapeakei* were fewer and *M. leidy* was more pronounced than in the years that *M. leidy* were checked by *C. chesapeakei* predation (Purcell & Decker, 2005). Field observations in Chesapeake Bay indicated when *M. leidy* biovolumes were greater than $10\text{-}20 \text{ mL m}^{-3}$, they can hold the summer copepod population in check (Sellner & Sellner 2016). Considering *C. chesapeakei* abundance has been low in recent decades (Breitburg & Fulford, 2006; Kimmel et al.

2012), the importance of *M. leidy* as a copepod predator has been increasing. By consuming more *A. tonsa* than *C. chesapeakei*, *M. leidy* could be an important competitor of *A. mitchilli* for copepods (Purcell et al., 2001).

In addition to the direct predator-prey food chain among copepods, fish, and gelatinous zooplankton, there is also a predation relationship between jellyfish and fish in Chesapeake Bay. *M. leidy* has the potential to consume 10 to 65% of fish eggs d^{-1} and 20 to 40% d^{-1} fish larvae d^{-1} (Monteleone & Duguay 1988, Cowan & Houde 1992, 1993). There is also intraguild predation between *C. chesapeakei* and *M. leidy*; *C. chesapeakei* is the major predator of *M. leidy* in the Chesapeake Bay and can reduce *M. leidy* abundance when the concentration of *C. chesapeakei* is higher than $0.05 m^{-3}$ (Breitburg & Burrell, 2014). The predation pressure is strong enough to eradicate *M. leidy* in small tributaries (clearance rates up to $6180 L d^{-1}$ in mesocosms), but not in the mainstem of Chesapeake Bay (McNamara, 1955; Purcell & Cowan Jr, 1995). Due to the differences in life cycles, habitat preference, and their predation relationships, *C. chesapeakei* is often abundant in shallow tributaries with available hard substrate for the polyp stage and where salinity is 7-20, while the euryhaline holoplanktonic *M. leidy* is more abundant in the mainstem of Chesapeake Bay, where salinity ranges from 0.1-25.6 (Cargo & Schultz 1967). An *in situ* polyp settlement study, which distributed settlement plates in the upper and middle of Chesapeake Bay where salinity was 5-35, have observed *C. chesapeakei* polyps mostly in the estuaries of the northern Bay with (Shahrestani & Bi 2018), and another field reach also found *C. chesapeakei*'s medusa concentrations were seven times higher in creeks than in the mainstem Bay (18.6 and $2.4 medusae m^{-3}$, respectively,

Breitburg & Burrell, 2014). In contrast, *M. leidy* is much more abundant in the mainstream region (i.e., ~ 300 indiv. m^{-3} in June 1990, Breitburg & Burrell, 2014). My research focused on *M. leidy* because the study region was in the mainstem Bay where the abundance of *M. leidy* exceeded *C. chesapeakei* during research cruises (Slater et al. 2020)

Predation under hypoxia

Living in an oxygen-insufficient environment may induce stress responses and lead to behavior changes, which may in turn cause changes in predator-prey interactions. For example, many copepods exhibit diel vertical migration (DVM) to save energy and avoid visual predators during daytime (Lampert 1989, Cohen & Forward 2009), but low dissolved oxygen in the bottom water column can disrupt this behavior by shortening the DVM depth (Pierson et al., 2009; Pierson et al., 2017; Roman et al., 1993; Keister & Tuttle 2013). Decreasing excursion distance potentially may increase the vertical spatial overlap between copepods and their predators and increase predator-prey encounter rates and predatory mortality (Keister et al. 2000, Breitburg et al. 2003). As a result, some predators may benefit from the hypoxic environment, as it becomes easier for them to exploit prey species. Also, *A. tonsa*'s swimming speed and jumping frequency were shown to decrease under low DO, suggesting that the copepods may become more vulnerable to hypoxia-tolerant predators such as *M. leidy* and *C. chesapeakei*, whose clearance rates on copepods were maintained under hypoxic conditions (Decker et al. 2004, Kolesar et al. 2010). Since both the vertical distributions and the trophic interactions vary with oxygen

levels, hypoxia-sensitive species may be more vulnerable to hypoxia-tolerant predators.

To better understand the indirect effects of hypoxia on zooplankton, this chapter focuses on the trophic interactions among gelatinous zooplankton *M. leidy*, crustacean zooplankton *A. tonsa*, and planktivorous fish *A. mitchilli*. The objectives of this study are to: 1) analyze the distributions and concentrations of *M. leidy* and *A. mitchilli* under hypoxic and normoxic conditions, 2) estimate mortality of the *A. tonsa* from predation by *M. leidy* and *A. mitchilli* and the potential increase in mortality under hypoxic conditions, 3) compare *A. tonsa*'s predatory mortalities with nonpredatory mortality, and 4) understand how the *A. tonsa*'s mortality (non-predatory and predatory) is influenced by temperature and dissolved oxygen concentrations.

Methods

Six research cruises were conducted in May, July/ August, and September in 2010 and 2011 (Cruise details in Pierson et al. 2017), and during each cruise zooplankton, jellyfish, and fish were collected at the two stations (North and South) in the main stem of Chesapeake Bay. Hourly CTD casts were conducted at each station to collect temperature, salinity, and dissolved oxygen, and these data were later used in a PCA analysis. Briefly, samples were grouped by cruise and stations first according to their PC1 scores, for which the major loading was water temperature, and then each temperature group was divided into two subgroups according to their PC2 scores, for which the major loading was bottom dissolved

oxygen. Accordingly, all samples were grouped into three temperature groups (Cool, Temperate, and Warm) and two oxygenated subgroups (More or Less oxygenated) (Slater et al. 2020). Zooplankton concentrations, copepod nonpredatory (Slater et al. 2020), and predatory impact on copepods were compared within the same temperature group to isolate the effects of temperature.

Gut content analysis

A total of 240, 1138, and 145 gut content samples were collected from ctenophores *M. leidyi*, and larval and juvenile anchovy, *A. mitchilli*, respectively, during the six research cruises (Appendix 3.1). Gut samples were collected in a Reeve net, a MOCNESS, a Tucker Trawl, and a midwater trawl to evaluate ctenophore predation and planktivorous predation on copepods. To estimate ctenophore predation, *M. leidyi* were collected for gut content analysis with vertical tows (above, within, below pycnoclines) at dawn, noon, sunset, and midnight with a modified Reeve net (Reeve 1981). The net had a 1m-diameter mouth fitted with a 3m-long tapered, 5 mm mesh net, a belly band to close the net at depth and a 50 L non-filtering rigid cod-end (Sea Gear model 9000-BB). This design allowed us to collect fragile gelatinous zooplankton without damaging them as traditional zooplankton sampling methods would. During each sampling interval, up to ten individual ctenophore samples were collected (when possible) from the cod end of the Reeve net. Collected ctenophores were preserved individually in 220 ml jars with a 4% buffered formaldehyde and seawater solution, and ctenophore's gut contents were examined later in the lab with dissecting microscopes. The tentacle bulbs (B, mm) of each ctenophore were measured to estimate its wet weight (WW, g) using a

regression relationship (Equation 3.4, Purcell, 1988). Prey items were categorized as the copepod *A. tonsa* adults and copepodites, other copepods and copepodites, copepod nauplii, ciliates, barnacle nauplii, fish eggs, and others.

To estimate predation from planktivorous fish, *A. mitchilli* larvae and juveniles were collected from MOCNESS (200 μm) and midwater trawls, respectively, and preserved with 95% ethanol during the cruises. Gut contents of *A. mitchilli* larvae and juveniles were removed from the plankton samples in the lab and subsamples were analyzed with methods described in Auth (2003). Gut contents from up to five anchovies from each water layer were analyzed if sufficient numbers were present in the sample. All *A. mitchilli* larvae and juveniles used for gut content analyses were measured to the nearest 0.1 mm total length prior to dissection. The entire gut was removed from the body of a larva or juvenile with a fine-tipped wire probe, and the gut contents examined under 20X magnification. All prey items were enumerated, identified, and then preserved in 95% ethanol. Tucker Trawl (280 μm) was used on 2010 spring to collect larval *A. mitchilli*'s gut content due to mechanical issues.

Estimating predatory mortality

The gut contents were examined in the lab to estimate the *in situ* predatory mortality rates of *A. tonsa* adults and copepodites with methods described in Granhag, Moller, & Hansson (2011). Ingestion rates (I , prey predator⁻¹ time⁻¹, Equation 3.1) were estimated using the number of adult copepods and copepodites (G) in ctenophore or anchovy guts divided by the gut evacuation time (t). The gut evacuation time was estimated using empirical relationships and mean temperature

for specific groups of samples. Lab and field studies estimated it took 1h at 20°C or < 0.5h under 27°C for an adult *M. leidyi* to digest fewer than 10 adult *A. tonsa* (Granhag et al., 2011; Larson, 1987), accordingly a linear relationship between temperature and digestion time was approximated to estimate the *M. leidyi* digestion time (Equation 3.2). The temperature-dependent digestion time for *A. mitchilli* was estimated by applying (Equation 3.3, Vazquez 1989). Because ctenophores have fast digestion times, especially in a warm environment, the percentage of empty guts collected was high in the summer cruises and the resulting predatory mortality may be underestimated. Therefore, clearance rate (CR, liters cleared ctenophore⁻¹ day⁻¹) was also estimated from the estimated wet weight (WW) determined from measurements of ctenophore tentacle bulbs (B) (Equation 3.4 & 3.5; Purcell, 1988; Purcell, 2009). The product of clearance rates and prey concentration is ingestion rate, and the potential predatory impact could be estimated and compared with the estimates based on gut contents. Predatory mortality of copepods (M_p, % copepod standing stock consumed day⁻¹) was estimated by multiplying the ingestion rate of a given predator with abundance (P) of that predator and dividing by copepod abundance (C) (Equation 3.6). Copepod's predatory mortality was then compared with their non-predatory mortality (Elliott et al., 2013; Elliott, 2010) under various oxygen conditions to determine the mortality factor that caused a larger portion of copepod population decreased under more hypoxic conditions.

$$I = \frac{I}{t} \quad \text{(Equation 3.1)}$$

$$D_j = -0.0714\text{temp} + 2.4286 \quad (\text{Equation 3.2})$$

$$D_a = 472.53\text{temp}^{-1.836} \quad (\text{Equation 3.3})$$

$$\text{WW} = 0.81B^{1.913} \quad (\text{Equation 3.4})$$

$$\text{Log CR} = 0.766\text{LogWW} + 0.423 \quad (\text{Equation 3.5})$$

$$M_p = \frac{I \times P}{C} \times 100\% \quad (\text{Equation 3.6})$$

Note:

D_j : digestion time for *M. leidyi*

D_a : digestion time for *A. mitchilli*

WW: *M. leidyi* wet weight (g)

B: Tentacle bulb length (mm)

I: ingestion rate (prey predator⁻¹ h⁻¹)

G: gut content (number)

t: digestion time (h)

M_p : predatory mortality (copepod standing stock consumed day⁻¹)

P: predator concentration (numbers L⁻¹)

C: prey (copepod) concentration (numbers L⁻¹)

CR: clearance rate (liters cleared predator⁻¹ day⁻¹)

Results

Ctenophore predation

The *M. leidyi* collected with the Reeve net for diet analysis were all adults and their mean wet weight was 13.2 ± 10.8 g (sample size = 240). The majority of the samples were collected from the surface layers during summer cruises, except for some were collected from the depth of the pycnocline, and only a few were taken from the bottom water layer (Table 3.1). No ctenophores occurred in the Reeve net during the spring cruises and only a few occurred in the Reeve net at the south station during the autumn cruises. Regardless of collection location or time, the gut contents of *M. leidyi* were primarily *A. tonsa* (adults and copepodites) and copepod nauplii, with some microzooplankton (ciliates and tintinnids) and invertebrate eggs (Table 3.1).

More ctenophore samples were collected during the Warm - Less Oxygenated (W - LO) cruises (i.e., N, S - 2011 summer and N - 2010 summer) than during the W - More Oxygenated (W - MO) cruises (i.e., S - 2010 summer and N, S - autumn). Empty guts were common among ctenophore samples. However, there were fewer ctenophores had empty guts during the W - LO cruises (approximately 25% empty) compared to the samples collected from the W - MO cruises (approximately 65% empty). No ctenophore gut samples were collected from the T - MO cruise (S - 2011

autumn), however, similar to the Warm group, a low proportion of empty guts (15%) was observed in the T - LO group. Among those ctenophore gut samples with prey items in the Warm group, copepods (adults, copepodites, and nauplii) were the dominant prey type (> 80%), and the percentage of nauplii among the prey increased from 6% under more oxygenated conditions to 24% under less oxygenated conditions (Figure 3.1). Ctenophore diets in the Temperate group, collected during the 2011-autumn cruise after Hurricane Irene and Tropical Storm Lee, were very different compared with the Warm group. Instead of being dominated by copepods, the gut contents in the Temperate group were dominated instead by invertebrate eggs (51%, Figure 3.1).

In addition to gut-content estimates of ctenophore predation on *A. tonsa* (Adults and copepodites), clearance rates (liters cleared ctenophore⁻¹ day⁻¹) of *A. tonsa* were also estimated from the ctenophore wet weights. Ctenophore predation was found to be highest during the July 2011 cruise (55% and 49% from guts and wet weights, respectively) and lowest during autumn cruises (approximately 1% using both methods) (Table 3.2). Predation pressure upon *A. tonsa* was much higher under W - LO than W - MO —14% d⁻¹ vs. <1% d⁻¹ from gut contents (Figure 3.2a) and 31% d⁻¹ vs. 2% d⁻¹ as calculated from wet weights (Figure 3.2b). Although estimates determined by ctenophore wet weight were higher than those from gut contents, the relatively higher consumption impact under less oxygenated conditions was consistent between the two methods.

Larval anchovy predation

A total of 432 small (TL < 10 mm) and 467 large (10 < TL < 32 mm) larval *A. mitchilli* were collected during the six cruises and their gut contents were examined (Table 3.3 & 3.4). More anchovy larvae were sampled from the surface layers during summer cruises than from other depths and seasons. Many specimens had empty guts, especially among the small larval *A. mitchilli*. The empty-gut rate dropped with increased body lengths, from 93% among the small larval *A. mitchilli* to 56% among large larval *A. mitchilli* (Table 3.5). In general, gut contents of small larval *A. mitchilli* consisted of primary copepods and invertebrate eggs (Table 3.3), while many other crustaceans, including cladocerans, barnacle nauplii, and microzooplankton, were also observed in large larval *A. mitchilli* (Table 3.4). The proportion of copepods (both adults and copepodites) in the guts increased with larval size as well, from 52% in small larval *A. mitchilli* to 87% in large larval *A. mitchilli*.

Diets of larval *A. mitchilli* varied under the different oxygenated conditions. Copepods dominated in the larval gut contents under MO conditions, but invertebrate larvae and eggs predominated under LO conditions (Figure 3.3 & 3.4). However, this was not the case for large larval *A. mitchilli* in the Warm group, whose guts contained mostly copepods under both MO and LO conditions (> 90 %, Figure 3.4). The estimated predatory impact of larval *A. mitchilli* on *A. tonsa*, small and large larvae combined, was minimal during all cruises (< 1% of *A. tonsa*'s mortality, Table 3.9). Larval *A. mitchilli* predation upon *A. tonsa* was observed higher under LO conditions: 0.22% d⁻¹ vs 0.1% d⁻¹ under LO and MO conditions in the Temperate group and 0.08% d⁻¹ vs 0.07% d⁻¹ in the Warm group (Figure 3.2). Although the predatory

impact of *A. mitchilli* larvae was likely underestimated due to the high percentage of empty gut samples, the predatory impact was observed higher in LO conditions relative to MO conditions

Juvenile anchovy predation

A total 39 small ($32 < TL < 40$ mm) and 60 large ($40 < TL < 60$ mm) juvenile *A. mitchilli* were examined during the six cruises (Table 3.6 & 3.7). In contrast to the high ratio of empty guts in larval *A. mitchilli*, all juvenile *A. mitchilli* examined guts contained food (Table 3.8). These gut samples contained a higher diversity of prey items, including items such as tunicate larvae, crab larvae, and oyster veligers, which was not observed in the larval *A. mitchilli* diets (Table 3.6 & 3.7). Copepods (adults and copepodites) remained a common prey of juvenile *A. mitchilli*, comprising 23% and 30% of the prey items to small and large juvenile *A. mitchilli* diets, respectively. In addition, invertebrate eggs (26% in small and 19% in large juveniles) and phytoplankton (mostly diatoms, 10% in small and 15% in large juveniles) occupied substantial proportion of juvenile *A. mitchilli* diets.

The proportion of invertebrate eggs in small juvenile *A. mitchilli* guts was often larger under LO conditions relative to those under MO conditions. Invertebrate eggs on average accounted for 44% and 55% of the items in small juvenile *A. mitchilli* guts collected during T - LO (N - 2011 autumn) and W-LO cruises (N - 2010 summer and N, S- 2011 summer), respectively, but only 36% and 20% of the prey items in guts collected during the T-MO (S - 2011 autumn) and W-MO (S - 2010 Summer, N, S - 2010 autumn) cruises, respectively (Figure 3.5). On the contrary, copepod adults and copepodites were present in similar proportions in small juvenile

A. mitchilli diets under both LO and MO conditions; approximately 35% in the Temperate group and 20% in the Warm group (Figure 3.5). Copepod adults and copepodites contributed larger percentages to large juvenile *A. mitchilli* gut contents, and there were higher percentages of copepods under LO than MO conditions in both the Temperate and Warm groups (37% vs 15% and 59% vs 36%, respectively) (Figure 3.6).

Predation by juvenile *A. mitchilli* on *A. tonsa* was highest during the September 2011 cruise at the North station ($12\% \text{ d}^{-1}$). Less than $5\% \text{ d}^{-1}$ predation was observed on all other cruises (Table 3.10). In the Temperate group, juvenile *A. mitchilli* predation of *A. tonsa* was elevated under LO conditions. In the Warm group, in which both LO and MO subgroups were hypoxic, but differed in severity, the predation pressure decreased from $17\% \text{ d}^{-1}$ under MO conditions (moderate hypoxia) to $1.3\% \text{ d}^{-1}$ under LO conditions (severe hypoxia) (Figure 3.2). Compared with larval *A. mitchilli* and the ctenophore *M. leidyi*, predation by juvenile *A. mitchilli* was higher and responsible for more predatory mortality of *A. tonsa* under most temperatures and oxygenated combinations, with the exception of warm and extremely hypoxic conditions, when *M. leidyi*'s predation was higher than that of juvenile *A. mitchilli* (Figure 3.2).

Discussion

The goal of this study was to understand the influence of oxygen deficiency on the trophic interactions among copepods, fish, and gelatinous zooplankton in Chesapeake Bay. Copepods, ctenophores, and larval and juvenile bay anchovies were

collected from two stations during six cruises from spring to autumn in 2010 and 2011. Their gut contents were examined and their predatory impact on copepods was estimated based on *in situ* predator concentrations. Using a PCA analysis to statistically group samples, comparisons were made under different oxygenated conditions but otherwise similar temperature and salinity environments. The results indicated both juvenile bay anchovy and ctenophore predation upon *A. tonsa* were often higher under hypoxic conditions. While the seasonality and phenology of predators had an effect on the patterns of mortality, non-predatory factors also contributed largely to *A. tonsa* mortality under hypoxic conditions. However, the importance of predatory factors increased under warmer and more hypoxic conditions.

Predation under hypoxia

Among larval and juvenile *A. mitchilli*, and *M. leidy*, the greatest predatory pressure on *A. tonsa* was caused by juvenile *A. mitchilli* in autumn, followed by *M. leidy*'s in summer. For both of these predators, *A. tonsa* consumption increased as dissolved oxygen concentrations decreased (Figure 3.2). This Hypoxia-enhanced predation has also been observed in other planktivores. For example, the Atlantic Bumper, *Chloroscombrus chrysurus*, consumed more shrimp larvae in the hypoxic area than in normoxic areas of the northern Gulf of Mexico (Glaspie et al. 2018). Because we observed increased predation under hypoxic conditions in two very different planktivores (a fish and ctenophore) and in different seasons (summer and autumn), and also because consumption comparisons were made within the same temperature group, we interpret these findings to not be simply due to species

differences or seasonality. That is, our results indicate that hypoxia contributed to the elevated predation impact.

The phenology and seasonality of *M. leidyi* and *A. mitchilli* did play a role in the observed predation patterns. *M. leidyi* abundance peaks in summer when hypoxia is also the most pronounced, and juvenile *A. mitchilli* reach high abundance levels in late summer and autumn. Peak ctenophore predation occurred primarily in the Warm group (i.e., summer), and juvenile anchovy predation was highest in the Temperate group (i.e., autumn cruises). On the contrary, predator abundance is low in spring, and minimum predatory mortality observed in the Cool temperature group. However, seasonality alone could not explain the observation of higher predatory impact under hypoxia. For example, juvenile *A. mitchilli* concentration was similar between MO and LO in the Temperature group (Slater et al. 2020), but their predatory impact was three times larger under hypoxia (LO group) than in normoxia (MO group) (Figure 3.2). Similarly, *M. leidyi* concentrations were similar during the 2010 summer cruise (i.e., 1.1 m^{-3} at the North and 1.9 m^{-3} at the South stations, Slater et al. 2020), but their predation impact was three times larger at the North station where oxygen was lower than at the South station (Table 3.2).

The decoupling of predator concentration and their predatory impact indicates that something more than the presence of predator plays a role in Chesapeake Bay planktonic trophic dynamics. Because samples were statistically grouped according to the PCA analysis, and comparisons were made between oxygenated levels within otherwise statistically similar conditions, showing enhanced predatory impact with increasing hypoxia. This observation was seen repeatedly in multiple temperature

groups and with different predators, indicating that hypoxia led to higher predatory impacts on *A. tonsa*.

There are two hypothesized explanations for this hypoxia-enhanced predation phenomenon that we observed: 1) changes in trophic interactions due to differences in hypoxia tolerance between predator and prey, and 2) behavioral and distributional changes due to hypoxia-avoidance behaviors (Brodeur et al, 2008; Diaz & Rosenberg, 2008; Purcell et al., 2001). Differences in hypoxia tolerance may play a role in higher ctenophore predation on copepods under hypoxic conditions because they in general are better oxyregulators and have lower oxygen demand than crustaceans and fish at the same temperature (Purcell et al. 2001a, Thuesen et al. 2005). Furthermore, Richardson et al. (2009) hypothesized that eutrophication-induced hypoxia can promote non-visual predators and hypoxia-tolerant species like gelatinous zooplankton blooms in some estuaries and coastal areas. Because our results indicate that both *M. leidy* abundances (Slater et al. 2020) and their predation was enhanced under hypoxic conditions during the six cruises, our observations support the hypothesis that gelatinous zooplankton populations could be favored under hypoxic conditions.

However, for juvenile *A. mitchilli*, it seems more likely that behavioral changes resulted in increased predation on *A. tonsa* under hypoxia, rather than predator-prey differences in hypoxia tolerance. Crustacean zooplankton are typically more tolerant of hypoxia than fish (summarized in Ekau et al., 2010). Both lab experiments and field studies found the behavior of *A. tonsa* changes under hypoxic conditions. *A. tonsa* exhibited decreased jumping frequency with decreasing

dissolved oxygen concentrations (Decker et al. 2004), which may make them more vulnerable to capture in hypoxic conditions. Decreased diel vertical migration (DVM) depths and reduced access to bottom water have also been observed for *A. tonsa* when a significant proportion of the bottom water column was hypoxic (Ludsin et al., 2009; Pierson et al., 2009; Roman et al., 2012), which resulted in increased predator-prey spatial overlap under hypoxic conditions. Habitat compression could be especially significant in a shallow estuary like the Chesapeake Bay, where the vertical volume of hypoxic water can exceed 70% in the summer (Pierson et al., 2017). Increased *A. mitchilli* predation on *A. tonsa* under hypoxic conditions implies that behavioral changes could also lead to higher mortality of *A. tonsa* under hypoxic conditions. The relative low-oxygen tolerance of predator and prey, together with behavioral changes, may determine whether predation rates increase under hypoxia (Breitburg 1994, Breitburg et al. 1997)

In addition to enhanced predation impact under hypoxia, we also observed changes in the predators that cause the most predatory mortality on *A. tonsa*. The predator that consumed the most *A. tonsa* standing stock shifted from juvenile *A. mitchilli* under normoxic (T - MO) and mildly hypoxic conditions (T - LO & W - MO) to *M. leidy* under warm and severely hypoxic conditions (W - LO). This in part is a consequence of the natural succession of *M. leidy* blooming in summer and juvenile *A. mitchilli* increasing in autumn, along with hypoxia development reaching its peak in summer. The peak seasonalities of juvenile *A. mitchilli* and *M. leidy*, are different, so there was not sufficient direct evidence to distinguish between the effects of seasonality and hypoxia. However, *M. leidy* tolerates severe hypoxia better than *A.*

mitchilli, and other studies have also observed food web structural changes under hypoxia, in addition to eutrophication, overfishing, and climate change, which together resulted in more primary production going to filter feeders, like gelatinous zooplankton, and have directly more net energy flows into microbes instead of finfish (Diaz & Rosenberg 2008, Ekau et al. 2010, Uye 2011, Condon et al. 2011). A time-series analysis of the Chesapeake Bay also indicated that the abundances of anchovies and copepods decreased and ctenophores increased as hypoxia in Chesapeake Bay increased over many decades (Kimmel et al. 2012). Although this studies did not fully examine the microzooplankton communities under hypoxia, similar cascading effects have been observed in mesocosm studies in the Great South Bay of New York (McNamara et al. 2013b, 2014). Both predator species and predation pressure in this study changed with temperature (due to seasonal changes in predator abundance) and dissolved oxygen concentrations. Our results support the hypothesis that predation of crustacean zooplankton is enhanced under hypoxic conditions, but more research is required to examine how hypoxia further affects other components of the food web.

Estimates of predatory impact

The predatory impact estimated from gut contents with predator and prey densities in the whole water column could be overestimated by carcasses consumption. Meanwhile, the predation impact could also be underestimated by ctenophore's short digestion time in summer, larval anchovies' gut voiding behavior, and by aggregating the whole water column especially under severely hypoxic conditions. However, the general conclusion remained the same with considerations with potential adjustments.

Some of the copepods enumerated in the gut contents could have been captured as carcasses, therefore the predatory impact estimated with gut contents could be overestimated with carcasses consumption. Although live or dead copepods were indistinguishable in the gut samples, carcass consumption may not be a large portion of ctenophore diets because the vertical distribution of ctenophores did not overlap as much with carcasses as with live copepods. Dead copepods sink, resulting in more carcasses present in the bottom water layer (Elliott et al., 2013). However, *M. leidy* gut samples were primarily collected from the surface water layers especially when the bottom was hypoxic (Table 3.1), and thus, the likelihood of the ctenophore guts containing a large portion of dead copepods is low. In addition, ctenophore consumption estimated by wet weight also showed similar results, and this estimate was not influenced by the possibility of carcass consumption. On the other hand, there were juvenile *A. mitchilli* collected from below the whole water column (Table 3.6 Table 3.7), and studies have not examined whether *A. mitchilli* is selective with respect to living or dead prey. However, since larval *A. mitchilli* eat relatively fewer copepods compared with juvenile *A. mitchilli* and *M. leidy*, the consumption of carcasses vs live copepods might not be important for larval anchovy. Approximately one-third of the copepods collected from the bottom layer were carcasses (Elliott et al., 2013), If carcasses and live copepods were evenly mixed in the water column and juvenile *A. mitchilli* consume carcasses and live copepods unselectively, then the estimated predatory impact from juvenile *A. mitchilli* on live copepods could be overestimated by maximum 1/3, and then the comparative importance of ctenophore predation would increase under warm and severely hypoxic conditions.

On the other hand, the impacts of ctenophore predation may have been underestimated in this study. Gelatinous zooplankton, such as *M. leidyi*, are known for their fast clearance rates and short digestion times. Granhag et al. (2011) found the digestion time of *M. leidyi* that had consumed 1-10 *A. tonsa* was approximately 1 h at 20 °C. *M. leidyi* digest prey quickly at warmer temperatures (i.e., < 30 min to digest 2-10 *A. tonsa* at 27 °C, Rowshantabari et al., 2012). Surface water temperature during our summer cruises was 24 - 26 °C (Slater et al. 2020), and thus, the *in-situ* digestion time of *M. leidyi* was likely close to 30 min during its peak season. Since prey distributions are patchy and *M. leidyi*'s capture rate is approximately 50% of the copepods they encountered (Waggett & Buskey 2006a), it is possible that our gut-content sampling may have collected some *M. leidyi* that were in between prey encounters and after they had cleared their guts. This would have resulted in empty gut samples, and thus, the predation stress estimated by gut contents would be an underestimate. On the other hand, clearance estimates determined from ctenophore wet weights, which were based on lab experiments (Purcell 1988), were an independent measure of “potential” predation capacity. These weight-based values were higher than the predation impact estimated from gut contents (Figure 3.2). In fact, *M. leidyi* predation estimated from wet weights indicated that *M. leidyi* is capable of consuming 30% of the *A. tonsa* standing stock per day under W - LO conditions. W - LO was the only group in which *A. tonsa* predatory mortality was higher than non-predatory mortality, and *M. leidyi* was the primary predator (Figure 3.2). Although the actual ctenophore predation pressure likely falls somewhere in

between these two measures, both methods indicate a similar trend of high ctenophore predation under the most hypoxic conditions.

Larval *A. mitchilli* predatory impact could be underestimated in this study because of gut avoiding behavior and also experimental design. Large proportions of empty guts especially in small larval *A. mitchilli* (Total length < 10 mm, Table 3.5a), and the low percentage of feeding anchovy larvae may be an artifact of gut voiding by the larvae upon capture in nets which was also observed in the lab (Detwyler & Houde 1970). In addition, our cruise schedule (May - Aug/Jul -Sep) was designed to study the development of hypoxia, and thus it may miss *A. mitchilli*'s typical peak spawning time in July, which usually requires more frequent sampling to capture (Zastrow et al. 1991). Considering the *A. tonsa* and *A. mitchilli* concentrations during our cruises (Slater et al. 2020), even if each larval *A. mitchilli* had at least one *A. tonsa* in their guts, their predatory impact would not be substantial (ranged 0 - 1.44% d⁻¹). It took at least 10 *A. tonsa* in each larval *A. mitchilli*'s gut to make their predatory impact larger than 10% d⁻¹ if the densities of larval *A. mitchilli* and *A. tonsa* remained the same. Nevertheless, the lab observations did find that larval *A. mitchilli* feed actively at high, for example, >100% of body weight daily (Detwyler & Houde 1970, Houde & Schekter 1981, Chesney 2008), and thus the actual predatory impact on *A. tonsa* by larval *A. mitchilli* might be higher when the abundance of larval *A. mitchilli* was higher during its peak spawning season.

The *in situ* predatory impact could be underestimated above pycnoclines and overestimated below pycnoclines with whole water column predator and prey concentrations especially during summertime when more zooplankton and

planktivores were above pycnoclines (Slater et al. 2020). The depth-specific predatory impact was not used in this study because the goal to compare predatory impact across *M. leidyi*, larval *A. mitchilli*, and juvenile *A. mitchilli*, which were collected with various nets at different depth intervals. In addition, our desire to compare *A. tonsa*'s predatory mortality with nonpredatory mortality, which was aggregated into whole water column because carcasses sink and no means to distinguish which depth when the mortality happened with current methods. Similarly, for very active swimming predators like juvenile *A. mitchilli*, it was hard to tell if the depths of predation and the depth of sample collection were the same. It would take higher sampling frequency, ideally shorter than digestion time, and finer vertical sampling scale, to more precisely estimate the depth-specific *in situ* predatory impact.

The day-night effect on predation efficiency and net efficiency could be a source of underestimation for *A. mitchilli*'s predation on *A. tonsa* with current estimations. As a visual predator, larval *A. mitchilli* feeds more during daytime, but their night feeding ability grow with age, and a juvenile *A. mitchilli* could utilize dim light during sunrise, sunset, and moonlight, eventually, an adult *A. mitchilli* could feed through night (Din & Gunter 1986, Vazquez 1989, Johnson et al. 1990). In addition, *A. mitchilli*'s abilities to avoid net capture are better during daytime and thus more *A. mitchilli* would be captured during night time (North & Houde 2004). Therefore we might collect more gut samples during nighttime, the non-feeding time for most larval *A. mitchilli* and some juvenile *A. mitchilli*, than daytime. The reason to still include night samples and estimate the predatory impact as standing stock per

day is the study goal to compare with *M. leidy*'s predation, which was less influenced by ambient light intensity, and also the study objective to compare predatory impact with nonpredatory mortality, which happened both day and night.

To understand the overall pattern, we made some generalization to enable comparisons across different mortality sources, including nonpredatory sources and three predatory sources, which were often not all covered in one study. Although the exact values of predatory impact may be different from our comparatively conservative estimations, with consideration of potential adjustments, the conclusion remained as the nonpredatory and predatory mortality increased under hypoxic conditions, the relative importance of predatory mortality increased with hypoxia severity, and the leading predator shifted from juvenile *A. mitchilli* under moderately hypoxic conditions to *M. leidy* under warm and severely hypoxic conditions.

The relative importance of non-predatory and predatory mortality

High total *A. tonsa* mortality was observed in the less-oxygenated subgroups in all temperature conditions, and both non-predatory mortalities and predator mortality were higher in the less oxygenated subgroup compared to the more-oxygenated subgroup. Non-predatory mortalities were at least two times higher in the less oxygenated subgroups relative to more oxygenated subgroup, suggesting that hypoxia directly contributed to high *A. tonsa* mortality and resulted in lower *A. tonsa* abundances (Figure 3.2). Non-predatory mortality played a comparatively important role in lower-temperature environments; non-predatory mortality contributed to > 99% of the total *A. tonsa* mortality in the cool groups, a contribution that decreased to >70% in the temperate group, and dropped even further, to > 5%, in the warm groups.

This may be in part due to that neither juvenile *A. mitchilli* nor *M. leidy* were abundant in the spring cruises (the Cool group), and larval *A. mitchilli* predation might have been relatively small even though gut evacuation could be a source of underestimation. On the contrary, all major predators were abundant in the warmer groups (i.e., summer and the autumn without weather events). As a result, the importance of predation on copepod populations increased with temperature, when the predators became abundant. In the Cool group, less than 1% of *A. tonsa* mortality was due to predation. By contrast, *M. leidy* and *A. mitchilli* together consumed > 15% of the copepod standing stocks in warm conditions (Figure 3.2a) and potentially could have consumed > 30% (Figure 3.2b). High predatory impact under low oxygen conditions compared was observed at all temperatures. Juvenile *A. mitchilli* predation on *A. tonsa* was three times higher in the T - LO subgroup than in the T - MO subgroup, and *M. leidy* predation on *A. tonsa* occurred primarily in the W - LO subgroup. Since our comparisons were made within the same temperature group, the effects of seasonality were isolated. Our results indicate that the relative importance of these mortality sources and the dominant predators differed with the season and environmental conditions.

Prey competition and temporal and spatial overlaps

A. tonsa was the dominant prey for both *M. leidy* and *A. mitchilli*, and the predation pressure of both these planktivores on *A. tonsa* increased in hypoxic conditions, and thus, competition for prey could potentially be enhanced under lower dissolved oxygen conditions. However, in our study these planktivores were dominant at different times: larval *A. mitchilli* was the only predator present in the

spring, *M. leidy* was abundant in summer, and juvenile *A. mitchilli* dominated in autumn. As a result, although these predators all consume *A. tonsa* and they all consumed more *A. tonsa* under more hypoxic conditions, the timing of their respective periods of maximum consumption did not overlap, and therefore competition might not have been substantial.

Our field study design, which was designed to examine various degrees of hypoxia at two stations in two or three water layers, did not aim to study habitat overlaps. The gut samples were collected with a Reeve net, a Tucker trawl, and a midwater trawl, which are not precise samplers of specific depth strata. Although *M. leidy* did not avoid lightly hypoxic bottom environments (Keister et al. 2000, Kolesar et al. 2010), they appear slightly preferred locations above pycnoclines in summer when the bottom was hypoxic during our research. In our study larger portion of *A. tonsa* was collected from the upper water column during summer cruises (Slater et al. 2020), suggesting potential more vertical overlaps between *M. leidy* and *A. tonsa* under hypoxic conditions. In a shallower tributary like the Patuxent River, scientists observed that the vertical overlap between ctenophores and copepods and between larval bay anchovies and copepods decreased with decreasing bottom DO (Kolesar et al. 2010). However, in the deeper mid-Chesapeake Bay, several studies with stratified tows or fine-scale vertical tows observed *M. leidy*, *A. mitchilli*, and copepod aggregation near pycnoclines when the bottom water column was hypoxic, resulting in increasing habitat overlapped and higher predatory impact around pycnoclines (North & Houde 2004, Purcell et al. 2014). The vertical overlapped under hypoxic condition might be depending on location.

Information on whether or not *A. tonsa* perform diel vertical migration in Chesapeake Bay is inconclusive. Minimal DVM of zooplankton may occur in this estuary for a variety of reasons: Chesapeake Bay is shallow (Cuker & Watson 2002), and food is widely distributed vertically, and so are predators, thus DVM may be disadvantageous to *A. tonsa* in this setting. However, other study conducted in the Bay's main channel of Chesapeake documented the sex-specific DVM, in which male *A. tonsa* utilized deeper water than female *A. tonsa* and both temperature and bottom hypoxia influenced their vertical distributions and migration patterns (Pierson et al., 2017). Thus, changes in zooplankton vertical distribution due to hypoxia in Chesapeake Bay is still uncertain, both location and diel cycle seem to matter, and more research is required to evaluate how vertical distributions changes among predators and *A. tonsa* influence trophic interactions.

Conclusion

Copepod mortality, both non-predatory and predatory mortalities, increased with hypoxia in the mid-Chesapeake Bay. Factors like the severity of hypoxia, predation intensity, and significant weather events all influenced copepod's mortality, yet the relative importance of these impacts varied with environmental conditions. The direct effect of low dissolved oxygen concentrations (i.e., non-predatory mortality), was generally a significant determinant of total mortality. However, predatory mortality became more influential with warmer temperature and hypoxia severity, indicating that there are interactions among dissolved oxygen concentration, temperature (season), and predation. An important predator in the Chesapeake Bay is

juvenile anchovy, and their predation impact on copepods is strengthened under moderately hypoxic conditions. When the environment is warm and severely hypoxic, ctenophore predation becomes prominent, suggesting that predation by specific predators is regulated by the hypoxia tolerance of both predator and prey species. Combined with the findings of Slater et al. (2020), these results support the hypothesis that combined hypoxia and predation contributed to the copepod population decline during summer, and the relative importance of factors contributing to copepod mortality shift from primarily the direct effects of hypoxia in cooler conditions to a combination of non-predatory and predatory impacts in warmer conditions.

Reference

- Adamack A, Rose K, Breitburg D, Nice A, Lung W (2012) Simulating the effect of hypoxia on bay anchovy egg and larval mortality using coupled watershed, water quality, and individual-based predation models. *Mar Ecol Prog Ser* 445:141–160.
- Auth TD (2003) Interannual and Regional Patterns of Abundance, Growth, and Feeding Ecology of Larval Bay Anchovy (*Anchoa Mitchilli*) in Chesapeake Bay. University of Maryland, College Park
- Baird D, Christian RR, Peterson CH, Johnson GA (2004) Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecol Appl* 14:805–822.
- Baird D, Ulanowicz RE (1989) The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol Monogr* 59:329–364.
- Borum J (1996) Shallow waters and land/sea boundaries. *Eutrophication Coast Mar Ecosyst* 52:179–203.
- Breitburg D (2002) Effects of Hypoxia, and the Balance between Hypoxia and Enrichment, on Coastal Fishes and Fisheries. *Estuaries* 25:767–781.
- Breitburg D, Burrell R (2014) Predator-mediated landscape structure: seasonal patterns of spatial expansion and prey control by *Chrysaora quinquecirrha* and *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 510:183–200.
- Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240.
- Breitburg DL (1994) Behavioral response of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Mar Biol* 120:615–625.
- Breitburg DL, Adamack A, Rose KA, Kolesar SE, Decker B, Purcell JE, Keister JE, Cowan JH (2003) The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. *Estuaries* 26:280–297.
- Breitburg DL, Fulford RS (2006) Oyster-sea nettle interdependence and altered control within the Chesapeake Bay ecosystem. *Estuaries Coasts* 29:776–784.
- Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecol Monogr* 67:489–507.
- Breitburg DL, Pihl L, Kolesar SE (2001) Effects of low dissolved oxygen on the behavior, ecology and harvest of fishes: a comparison of the Chesapeake Bay

- and Baltic Kattegat systems. *Coast Hypoxia Consequences Living Resour Ecosyst*:241–267.
- Brodeur RD, Link JS, Smith BE, Ford MD, Kobayashi DR, Jones TT (2016) Ecological and economic consequences of ignoring jellyfish: a plea for increased monitoring of ecosystems. *Fisheries* 41:630–637.
- Brodeur RD, Suchman CL, Reese DC, Miller TW, Daly EA (2008) Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. *Mar Biol* 154:649–659.
- Capriulo GM, Smith G, Troy R, Wikfors GH, Pellet J, Yarish C (2002) The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. In: *Nutrients and Eutrophication in Estuaries and Coastal Waters*. Orive E, Elliott M, de Jonge VN (eds) Springer Netherlands, Dordrecht, p 263–333
- Cargo DG, Schultz LP (1967) Further observations on the biology of the sea nettle and jellyfishes in Chesapeake Bay. *Chesap Sci* 8:209–220.
- Chesney EJ (2008) Foraging behavior of bay anchovy larvae, *Anchoa mitchilli*. *J Exp Mar Biol Ecol* 362:117–124.
- Cohen JH, Forward RB (2009) Zooplankton diel vertical migration - a review of proximate control. *Oceanogr Mar Biol* 47:77–110.
- Condon RH, Steinberg DK, del Giorgio PA, Bouvier TC, Bronk DA, Graham WM, Ducklow HW (2011) Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proc Natl Acad Sci* 108:10225–10230.
- Coutant CC (1985) Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. *Trans Am Fish Soc* 114:31–61.
- Coutant CC, Benson DL (1990) Summer habitat suitability for striped bass in Chesapeake Bay: reflections on a population decline. *Trans Am Fish Soc* 119:757–778.
- Cowan JH, Houde ED (1993) Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. *Mar Ecol-Prog Ser* 95:55–55.
- Cowan JH, Houde ED (1992) Size-dependent predation on marine fish larvae by Ctenophores, Scyphomedusae, and Planktivorous fish. *Fish Oceanogr* 1:113–126.
- Cuker B, Watson M (2002) Diel vertical migration of zooplankton in contrasting habitats of the Chesapeake Bay. *Estuaries Coasts* 25:296–307.
- Decker MB, Breitburg D, Purcell JE (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 280:163–72.

- Detwyler R, Houde ED (1970) Food selection by laboratory-reared larvae of the scaled sardine *Harengula pensacolae* (Pisces, Clupeidae) and the bay anchovy *Anchoa mitchilli* (Pisces, Engraulidae). *Mar Biol* 7:214–222.
- Deutsch C, Ferrel A, Seibel B, Portner H-O, Huey RB (2015) Climate change tightens a metabolic constraint on marine habitats. *Science* 348:1132–1135.
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *science* 321:926–929.
- Din B, Gunter G (1986) The food and feeding habits of the common bay anchovy, *Anchoa mitchilli* (Valenciennes). *Pertanika* 9:99–108.
- Dong Z, Liu D, Keesing JK (2010) Jellyfish blooms in China: dominant species, causes and consequences. *Mar Pollut Bull* 60:954–963.
- Eby LA, Crowder LB, McClellan CM, Peterson CH, Powers MJ (2005) Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Mar Ecol Prog Ser* 291:249–262.
- Ekau W, Auel H, Poertner H, Gilbert D (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7:1669–1699.
- Elliott DT (2010) Copepod carcasses, mortality and population dynamics in the tributaries of the Lower Chesapeake Bay. The College of William and Mary
- Elliott DT, Pierson JJ, Roman MR (2013) Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. *J Plankton Res* 35:1027–1034.
- Glaspie CN, Clouse MA, Adamack AT, Cha Y, Ludsin SA, Mason DM, Roman MR, Stow CA, Brandt SB (2018) Effect of Hypoxia on Diet of Atlantic Bumpers in the Northern Gulf of Mexico. *Trans Am Fish Soc.*
- Glibert PM (2010) Long-Term Changes in Nutrient Loading and Stoichiometry and Their Relationships with Changes in the Food Web and Dominant Pelagic Fish Species in the San Francisco Estuary, California. *Rev Fish Sci* 18:211–232.
- Glibert PM, Burkholder JM (2006) The complex relationships between increases in fertilization of the earth, coastal eutrophication and proliferation of harmful algal blooms. *Ecol Harmful Algae*:341–354.
- Granhag L, Moller LF, Hansson LJ (2011) Size-specific clearance rates of the ctenophore *Mnemiopsis leidyi* based on in situ gut content analyses. *J Plankton Res* 33:1043–1052.
- Harding LW, Mallonee ME, Perry ES, Miller WD, Adolf JE, Gallegos CL, Paerl HW (2019) Long-term trends, current status, and transitions of water quality in Chesapeake Bay. *Sci Rep* 9.
- Heinle DR (1966) Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River estuary. *Chesap Sci* 7:59–74.

- Houde ED, Schekter RC (1981) Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. *Rapp Proces-Ver- Baux Reun Cons Int Pour Explora- Tion Mer*:441–453.
- Johnson W, Allen D, Ogburn M, Stancyk S (1990) Short-term predation responses of adult bay anchovies *Anchoa mitchilli* to estuarine zooplankton availability. *Mar Ecol Prog Ser* 64:55–68.
- Jung S, Houde ED (2004) Recruitment and spawning-stock biomass distribution of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay. *Fish Bull* 102:63–77.
- Justić D, Rabalais NN, Turner RE, Dortch Q (1995) Changes in nutrient structure of river-dominated coastal waters: stoichiometric nutrient balance and its consequences. *Estuar Coast Shelf Sci* 40:339–356.
- Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. *Mar Ecol Prog Ser* 205:43–59.
- Kemp WM, Boynton WR, Adolf JE, Boesch DF, Boicourt WC, Brush G, Cornwell JC, Fisher TR, Glibert PM, Hagy JD, others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Mar Ecol Prog Ser* 303:1–29.
- Kimmel DG, Boynton WR, Roman MR (2012) Long-term decline in the calanoid copepod *Acartia tonsa* in central Chesapeake Bay, USA: An indirect effect of eutrophication? *Estuar Coast Shelf Sci* 101:76–85.
- Klebasko MJ (1991) Feeding ecology and daily ration of bay anchovy (*Anchoa mitchilli*) in the mid-Chesapeake Bay. University of Maryland at College Park
- Kolesar S, Breitburg D, Purcell J, Decker M (2010) Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: clearance rates and vertical habitat overlap. *Mar Ecol Prog Ser* 411:173–188.
- Lampert W (1989) The adaptive significance of diel vertical migration of zooplankton. *Funct Ecol* 3:21.
- Ludsin SA, Zhang X, Brandt SB, Roman MR, Boicourt WC, Mason DM, Costantini M (2009) Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implications for food web interactions and fish recruitment. *J Exp Mar Biol Ecol* 381:S121–S131.
- Lynam CP, Gibbons MJ, Axelsen BE, Sparks CA, Coetzee J, Heywood BG, Brierley AS (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Curr Biol* 16:R492.
- Lynam CP, Heath MR, Hay SJ, Brierley AS (2005) Evidence for impacts by jellyfish on North Sea herring recruitment. *Mar Ecol Prog Ser* 298:157–167.
- McClelland JW, Valiela I (1998) Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. *Mar Ecol Prog Ser*:259–271.

- McNamara M, Lonsdale D, Cerrato R (2014) Role of eutrophication in structuring planktonic communities in the presence of the ctenophore *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 510:151–165.
- McNamara ME, Lonsdale DJ, Aller RC (2013a) Elemental Composition of *Mnemiopsis leidyi* A. Agassiz 1865 and Its Implications for Nutrient Recycling in a Long Island Estuary. *Estuaries Coasts* 36:1253–1264.
- McNamara ME, Lonsdale DJ, Cerrato RM (2013b) Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores. *Estuar Coast Shelf Sci* 133:2–10.
- McNamara P (1955) Sea nettles observed to feed on sea walnuts in laboratory. *Md Tidewater News* 12:3–3.
- Monteleone DM, Duguay LE (1988) Laboratory studies of predation by the ctenophore *Mnemiopsis leidyi* on the early stages in the life history of the bay anchovy, *Anchoa mitchilli*. *J Plankton Res* 10:359–372.
- North EW, Houde ED (2004) Distribution and transport of bay anchovy (*Anchoa mitchilli*) eggs and larvae in Chesapeake Bay. *Estuar Coast Shelf Sci* 60:409–429.
- Parsons TR, Lalli CM (2002) Jellyfish population explosions: revisiting a hypothesis of possible causes. *La mer* 40:111–121.
- Pierson J, Slater W, Elliott D, Roman M (2017) Synergistic effects of seasonal deoxygenation and temperature truncate copepod vertical migration and distribution. *Mar Ecol Prog Ser* 575:57–68.
- Pierson JJ, Roman MR, Kimmel DG, Boicourt WC, Zhang X (2009) Quantifying changes in the vertical distribution of mesozooplankton in response to hypoxic bottom waters. *J Exp Mar Biol Ecol* 381:S74–S79.
- Pollock MS, Clarke LMJ, Dubé MG (2007) The effects of hypoxia on fishes: from ecological relevance to physiological effects. *Environ Rev* 15:1–14.
- Purcell J, Decker M, Breitbart D, Broughton K (2014) Fine-scale vertical distributions of *Mnemiopsis leidyi* ctenophores: predation on copepods relative to stratification and hypoxia. *Mar Ecol Prog Ser* 500:103–120.
- Purcell JE (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. *Mar Ecol-Prog Ser* 87:65–76.
- Purcell JE (2009) Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* 616:23–50.
- Purcell JE (1988) Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. *Mar Ecol Prog Ser Oldendorf* 45:197–200.

- Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ, Raskoff KA (2001a) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: *Coastal and Estuarine Studies*. p 77–100
- Purcell JE, Cowan Jr JH (1995) Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores. *Mar Ecol Prog Ser*:63–70.
- Purcell JE, Decker MB (2005) Effects of Climate on Relative Predation by Scyphomedusae and Ctenophores on Copepods in Chesapeake Bay during 1987-2000. *Limnol Oceanogr* 50:376–387.
- Purcell JE, Shiganova TA, Decker MB, Houde ED (2001b) The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. *Hydrobiologia* 451:145–176.
- Reeve MR (1981) Large cod-end reservoirs as an aid to the live collection of delicate zooplankton. *Limnol Oceanogr* 26:577–580.
- Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol Evol* 24:312–322.
- Robinson K, Ruzicka J, Decker MB, Brodeur R, Hernandez F, Quiñones J, Acha M, Uye S, Mianzan H, Graham W (2014) Jellyfish, Forage Fish, and the World's Major Fisheries. *Oceanography* 27:104–115.
- Roman MR, Brandt SB, Houde ED, Pierson JJ (2019) Interactive Effects of Hypoxia and Temperature on Coastal Pelagic Zooplankton and Fish. *Front Mar Sci* 6.
- Roman MR, Gauzens AL, Rhinehart WK, White JR (1993) Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnol Oceanogr* 38:1603–1614.
- Roman MR, Pierson JJ, Kimmel DG, Boicourt WC, Zhang X (2012) Impacts of hypoxia on zooplankton spatial distributions in the northern Gulf of Mexico. *Estuaries Coasts* 35:1261–1269.
- Rowshantabari M, Finenko GA, Kideys AE, Kiabi B (2012) Effect of temperature on clearance rate, daily ration and digestion time of *Mnemiopsis leidyi* from the southern Caspian Sea. *Casp J Env Sci* 10:157–167.
- Sellner KG, Sellner SG (2016) Copepod, Ctenophore, and Scyphomedusae Control in Structuring the Chesapeake Bay Summer Mesohaline Planktonic Food Web. In: *Aquatic Microbial Ecology and Biogeochemistry: A Dual Perspective*. Glibert PM, Kana TM (eds) Springer International Publishing, Cham, p 273–283
- Shahrestani S, Bi H (2018) Settlement and survival of *Chrysaora chesapeakei* polyps: implications for adult abundance. *Mar Ecol Prog Ser* 601:139–151.
- Slater WL, Pierson JJ, Decker MB, Houde ED, Lozano C, Seuberling J (2020) Fewer copepods, fewer anchovies, and more jellyfish: how does hypoxia impact the Chesapeake Bay zooplankton community? *Diversity* 12:35.

- Stoecker DK, Hansen PJ, Caron DA, Mitra A (2017) Mixotrophy in the Marine Plankton. *Annu Rev Mar Sci* 9:311–335.
- Thuesen EV, Rutherford LD, Brommer PL (2005) The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. *J Mar Biol Assoc U K* 85:627–633.
- Uye S (2008) Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas. *Plankton Benthos Res* 3:125–131.
- Uye S (2011) Human forcing of the copepod–fish–jellyfish triangular trophic relationship. *Hydrobiologia* 666:71–83.
- Vazquez AV (1989) Energetics, trophic relationships and chemical composition of bay anchovy, *Anchoa mitchilli*, in the Chesapeake Bay. University of Maryland, College Park
- Waggett R, Buskey E (2006) Copepod sensitivity to flow fields: detection by copepods of predatory ctenophores. *Mar Ecol Prog Ser* 323:205–211.
- Wu RS (2002) Hypoxia: from molecular responses to ecosystem responses. *Mar Pollut Bull* 45:35–45.
- Zastrow CE, Houde ED, Morin LG (1991) Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy *Anchoa mitchilli* in mid-Chesapeake Bay. *Mar Ecol Prog Ser*:161–171.

Tables and figures

Table 3.1. *Mnemiopsis leidyi* gut content sample sizes, mean wet weight and number of prey items. Ctenophores were collected from the surface (Surf), pycnocline (Pyc) and bottom (Bot) water layers with a Reeve net at the North (N) and South (S) stations during the six cruises in 2010 and 2011.

Year	2010	2010	2010	2010	2010	2010	2010	2010	2010	2010	2010	2011	2011	2011	2011	2011
Month	Aug	Aug	Aug	Aug	Aug	Aug	Sep	Sep	Sep	Sep	Sep	Jul	Jul	Jul	Sep	Sep
Station	N	N	N	S	S	S	N	N	N	S	S	S	S	S	N	N
Depth	Bot	Pyc	Surf	Bot	Pyc	Surf	Bot	Pyc	Surf	Surf	Surf	Bot	Pyc	Surf	Bot	Surf
Sample size	2	22	24	3	11	46	2	11	19	4	17	34	30	1	14	
Wet weight (g)	31.51	31.73	17.45	8.95	11.36	15.13	12.96	11.07	8.09	5.73	5.97	9.89	8.75	5.96	7.93	
Copepod adults & Copepodites	1.50	0.18	0.63	0.33	0.09	0.13	0.50	0.55	1.58	2.00	1.18	1.97	3.70	0.00	2.14	
Copepod nauplii	0.00	0.00	0.00	0.33	0.00	0.02	0.00	0.00	0.11	0.00	1.76	0.82	0.77	6.00	0.14	
Tintinnids & ciliates	0.00	0.09	0.04	0.33	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.09	0.33	0.00	0.07	
Invertebrate eggs	0.00	0.32	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.12	0.15	0.00	0.00	3.07	
Other crustaceans	0.00	0.09	0.04	0.00	0.00	0.02	0.00	0.09	0.00	0.00	0.00	0.00	0.03	0.00	0.14	
Invertebrate larvae	0.50	0.14	0.00	0.00	0.00	0.07	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	

Table 3.2. Daily predation of *M. leidyi* on *A. tonsa* (adults & copepodites) estimated by gut contents (M_j , d^{-1}) and by ctenophore wet weights (WW) (M_j , d^{-1}) at the North (N) and South (S) stations in 2010 and 2011.

		2010				2011	
		Aug		Sep		Jul	Sep
		N	S	N	S	S	N
Environmental Conditions	Mean ctenophore concentration (L^{-1})	0.0011	0.0019	- ⁱⁱ	0.0001	0.0347	0.0007
	Mean copepod and copepodite concentration (L^{-1})	5.1	9.5	11.8	9.6	6.5	3.1
	Mean water column temperature (C)	27.1	27.1	24.1	23.7	26	23.1
Predation effects estimated with gut contents	Copepod & copepodites in ctenophore guts	0.46	0.13	1.16	2	2.44	2
	Estimated gut evacuation time (h)	0.5	0.5	0.71	0.73	0.57	0.78
	Clearance Rate ($L \text{ ind}^{-1} \text{ h}^{-1}$)	0.18	0.03	0.14	0.28	0.66	0.83
	Ingestion by gut content ($\# \text{ ind}^{-1} \text{ h}^{-1}$)	0.93	0.26	1.63	2.73	4.27	2.57
	M_j ($\% d^{-1}$)	0.48%	0.13%	-	0.07%	54.66%	1.39%
Clearance rates estimated from wet weight	Mean ctenophore WW (g)	24.58	14.13	9.42	5.73	8.65	7.8
	Estimated CR by WW ($L \text{ ind}^{-1} \text{ d}^{-1}$)	31.78	20.67	15.1	10.26	14.13	13.04
	Ingestion by WW ($\# \text{ ind}^{-1} \text{ h}^{-1}$)	6.75	8.18	7.42	4.1	3.83	1.68
	M_j ' ($\% d^{-1}$)	3.5%	3.93%	-	0.1%	49.03%	0.91%

Note:

i. No *M. leidyi* gut contents were collected by the Reeve net at the North station in July 2011 and at the South Station in September 2011

ii. Tucker Trawl sampling was not conducted at the North station during the September 2010 cruise due to shipboard mechanical issues

Table 3.3. Small larval *A. mitchilli* (total length ≤ 10 mm) gut content sample sizes, mean total length and number of prey items. Larvae were collected from the surface to pycnocline layer (Surf) and from the pycnocline to bottom layer (Bot) with a Tucker Trawl at the North (N) and South (S) stations during the six cruises in 2010 and 2011.

Year	2010	2010	2010	2010	2010	2010	2010	2011	2011	2011	2011	2011	2011	2011
Month	5	5	8	8	8	9	9	5	7	7	7	7	9	9
Station	North	North	North	South	South	South	South	North	North	North	South	South	South	South
Depth	Bot	Surf	Surf	Bot	Surf	Bot	Surf	Surf	Bot	Surf	Bot	Surf	Bot	Surf
Sample Sizes	38	78	28	61	104	5	9	10	18	22	2	23	10	24
Total length (mm)	4.36	5.72	5.78	6.44	6.59	8.52	9.18	4.20	6.00	6.80	7.65	6.97	8.25	8.43
Copepod adults	0	0.03	0	0.03	0.04	0.40	0.11	0	0	0	0	0	0	0
Copepod nauplii	0	0.01	0.04	0	0	0	0	0	0	0	0	0	0	0
Copepodites	0.03	0.03	0.04	0	0.01	0	0	0	0	0	0	0	0	0
Cladocera daphnia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tintinnids	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barnacle nauplii	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustacean nauplii	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diatoms	0	0	0	0.02	0.02	0	0	0	0	0	0	0	0	0
Amphipods	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rotifers	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decapods	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Invertebrate eggs	0	0.03	0.11	0.02	0	0	0	0.10	0	0	0	0.04	0	0
Others	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4. Medium larval *A. mitchilli* (total length 10 - 32mm) gut content sample sizes, mean total length and number of prey items. Larvae were collected from the surface to pycnocline layer (Surf) and from the pycnocline to bottom layer (Bot) with a Tucker Trawl at the North (N) and South (S) stations during the six cruises in 2010 and 2011.

Year	2010	2010	2010	2010	2010	2010	2010	2011	2011	2011	2011	2011	2011	2011	2011
Month	5	8	8	8	8	9	9	7	7	7	7	9	9	9	9
Station	North	North	North	South	South	South	South	North	North	South	South	North	North	South	South
Depth	Surf	Bot	Surf	Bot	Surf	Bot	Surf	Bot	Surf	Bot	Surf	Bot	Surf	Bot	Surf
Sample Sizes	2	8	78	28	46	18	24	5	78	7	62	1	6	52	52
Total length (mm)	13.10	21.36	18.22	15.21	14.81	11.68	11.64	15.53	17.48	14.05	13.82	28.98	19.51	16.06	14.07
Copepod adults	0	2.25	0.32	1.14	0.61	0.89	0.50	0.80	0.69	0.00	0.35	25.00	7.33	3.58	1.42
Copepod nauplii	0	0	0	0	0	0	0	0	0	0	0	0	0	0.67	0.04
Copepodites	0	0	0.01	0.04	0.11	0	0	0	0	0	0	0	0	0.17	0
Cladocera daphnia	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0
Mollusca	0	0	0	0.11	0	0	0	0	0	0	0	0	0	0	0
Tintinnids	0	0	0	0	0	0	0.04	0	0	0	0	0	0	0	0
Barnacle nauplii	0	0	0	0.04	0	0	0	0	0.03	0	0	0	0	0.02	0
Crustacea larvae	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0.02	0
Crustacean nauplii	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0
Polychaeta larvae	0	0.13	0	0	0	0	0	0	0	0	0	0	0	0	0
Diatoms	0	0	0	0	0	0	0	0	0	0	0	0	1.17	0	0
Amphipods	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rotifers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decapods	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Invertebrate eggs	0	0	0	0	0	0	0.08	0	0.01	0.29	0.03	0	1.17	0.15	0.04
Others	0.5	0	0	0	0.04	0	0	0	0	0	0	0	0	0.10	0.02

Table 3.5. Larval *A. mitchilli* (total length (a) < 10mm < (b) < 32mm) gut content sample sizes, mean number of prey items, and percentage of guts containing prey. Samples were collected with the Tucker Trawl under different temperature (warm, temperate, and cool) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).

(a)

PCA group		Sample size	Mean prey items	Guts with prey (%)
Cool	LO	10	0.10	10%
	MO	116	0.08	8%
Temperate	LO	-	-	-
	MO	34	0	0%
Warm	LO	93	0.08	10%
	MO	179	0.08	8%

(b)

PCA group		Sample size	Mean prey items	Guts with prey (%)
Cool	LO	2	0.5	50%
	MO	7	11.9	43%
Temperate	LO	-	-	-
	MO	104	3.1	63%
Warm	LO	238	0.6	34%
	MO	116	0.9	53%

Table 3.6. Small juvenile *A. mitchilli* (Total length 32 - 40 mm) gut content sample sizes, mean total length and number of prey items. Juveniles were collected from the surface to pycnocline layer (Surf) and from the pycnocline to bottom layer (Bot) with mid-water trawls at the North (N) and South (S) stations during the six cruises in 2010 and 2011.

Year	2010	2010	2010	2010	2010	2011	2011
Month	Aug	Aug	Aug	Aug	Sep	Sep	Sep
Station	North	North	South	South	South	North	South
Layer	Bot	Surf	Bot	Surf	Bot	Bot	Bot
Sample size	5	1	1	2	10	10	10
Mean total length (mm)	31.8	38.7	39.7	38.5	35.1	34.1	31.8
Mean count	9.6	11	129	140.5	55.9	59.1	18.6
Copepod adults	0.4	2	25	15	6.7	11.1	3.2
Copepodites	1	1	27	0	2.4	3.3	0.5
Copepod nauplii	1.2	0	0	50	0.2	7.2	0
Other copepods	0.6	0	0	0	1.3	0.5	2.2
Invertebrate eggs	4.8	6	0	23	12.4	21.3	5.6
Oyster veligers	0	0	0	9	7.6	1.1	0.2
Barnacle cyprid larvae	0.2	0	2	0.5	1.1	0.2	0
Tunicate larvae	0	0	0	0	0	0	0.5
Tintinnids	0	0	0	0	10.3	0	0
Oligochaeta larvae	0.4	0	0	1.5	1.3	0.8	2.2
Gastropods	0	0	0	0	0.2	0	0
Diatoms	0.6	0	50	26.5	4.5	2.4	0.9
Mysid adults	0	0	0	0	0	0.1	0
Cladocera	0	0	0	0	0.4	0	0
Amphipods	0	0	0	0	0.1	0	0
Polychaete	0	0	0	0	0	0	0.1
Ctenophores	0	0	0	0	0.4	0	0
Fish eggs	0	0	0	0	0.1	0	0
Others	0	0	0	0	0.1	0	0

Table 3.7. Large juvenile/adult *A. mitchilli* (total length 40 - 60 mm) gut content sample sizes, mean total length and number of prey items. Larvae were collected from the surface to pycnocline layer (Surf) and from the pycnocline to bottom layer (Bot) with mid-water trawls at the North (N) and South (S) stations during the six cruises in 2010 and 2011.

Year	2010	2010	2010	2010	2011	2011	2011	2011	2011
Month	Aug	Aug	Aug	Sep	Jul	Jul	Jul	Sep	Sep
Occupation	North	South	South	South	North	North	South	North	South
Layer	Surf	Bot	Surf	Bot	Bot	Surf	Bot	Bot	Bot
Sample size	5	5	10	10	5	5	1	10	10
Mean length (mm)	48.2	46.9	47.9	52.7	49.9	52.1	52.6	53.5	53.2
Mean count	32.8	334.8	133.8	85.7	44	45.4	46	109.2	27.9
Copepod adults	5	136.6	12.8	9	12	14.4	15	21.2	2.2
Copepodites	1.2	15	0.6	2.7	2.8	3.2	10	7.5	0.3
Copepod nauplii	3.2	0	0.2	0.1	0.8	0.4	0	3	0
Other copepods	0.6	2.2	5.3	1	6	7	0	3.7	1.3
Invertebrate eggs	6.2	0	54.2	13.7	5.6	2.6	2	30.7	8.2
Oyster veligers	0	3.4	4.9	10.8	0.2	0.2	0	2.4	0.5
Barnacle cyprid larvae	0.4	3.8	2.2	2.7	0	0	0	0.8	0.5
Barnacle nauplii	0	0	0	0	0	0	0	0	0
Tunicate larvae	2.4	0	0.4	0.2	2.6	1	0	1.6	0.9
Tintinnids	1.2	0	0	20.8	0	0	0	0	0.1
Oligochaeta larvae	2	1	1.3	0.7	1.6	0.6	2	2	7.8
Gastropods	0	0.6	0.3	0.1	0	0	0	0	0.1
Diatoms	3.8	32.2	38.4	14.4	0.4	0.6	2	14.6	2.9
Mysid adults	0	0	0	0.1	0	0	0	0	0.3
Mysid statocysts	0	0	0	0	0	0	0	0.2	0
Oyster spat	0	0	0	0	0	0	0	0	0
Crab zoea	0	0.2	0.1	0	0	0	0	0	0
Crab megalopae	0	0	0	0	0	0	0	0	0
Foraminifera	0	0	0	0	0	0	0	0	0
Ostracods	0	2	0	0	0	0.4	0	0	0
Cladocera	0	0.4	0	0.2	0	0	0	0	0
Planulae	0	0	0	0	0	0.2	0	0	0.1
Polychaete	1.8	0.2	0	0.1	0	0.2	0	0.1	0
Polychaete larvae	0	0	0.1	0	0	0	0	0	0
Hydroids	0	0	0	0	0	0	0	0	0
Ctenophores	0	0	0	0.1	0	0	0	0	0
Fish eggs	0	0	0	0	0	0	0	0	0.1
Trochophore larvae	0	0	0	0	0	0	0	0	0.1
Other	0	0.6	0.2	0	0	0	0	0	0.1

Table 3.8. Juvenile *A. mitchilli* (Total length 32mm < (a) < 40mm < (b) < 60mm) gut content sample sizes, mean number of prey items, and percentage of guts containing prey. Samples were collect with the Tucker Trawl under different temperature (warm, temperate, and cool) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).

(a)

PCA group		Sample size	Mean prey items	Guts with prey (%)
Cool	LO	-		
	MO	-		
Temperate	LO	10	60	100%
	MO	10	19	100%
Warm	LO	6	10	100%
	MO	13	95	100%

(b)

PCA group		Sample size	Mean prey items	Guts with prey (%)
Cool	LO	-		
	MO	-		
Temperate	LO	10	109	100%
	MO	10	28	100%
Warm	LO	16	42	100%
	MO	25	155	100%

Table 3.9. Daily predation of larval *A. mitchilli* (M_{LA}) upon *A. tonsa* (adults & copepodites) estimated by gut contents collected at the North (N) and South (S) stations in 2010 and 2011.

	2010					2011					
	May		Aug		Sep	May		Jul	Sep		
	N	S	N	S	S	N	S	N	S	N	S
Mean <i>A. tonsa</i> in guts	0.04	0.07	0.39	0.31	0.55	0.00	0.05	0.47	0.23	9.86	1.95
Mean larval <i>A. mitchilli</i> concentration (L^{-1})	0.00985	0.01046	0.00059	0.00295	0.00012	0.00003	0.00350	0.00142	0.00019	0.00003	0.00030
Mean <i>A. tonsa</i> adults and copepods concentration (L^{-1})	29.2	8.7	5.1	9.5	9.6	5.8	3.4	11.8	6.5	3.1	11.0
Mean water temperature ($^{\circ}C$)	19.8	19.3	27.1	27.3	23.8	20.4	19.9	26.6	26.0	23.2	22.9
Estimated gut evacuation time (h)	2.0	2.1	1.1	1.1	1.4	1.9	1.9	1.1	1.2	1.5	1.5
Clearance rate ($L \text{ ind}^{-1} \text{ h}^{-1}$)	0.0007	0.0037	0.0705	0.0296	0.0409	0.0000	0.0072	0.0349	0.0300	2.1451	0.1180
Ingestion ($\# \text{ ind}^{-1} \text{ h}^{-1}$)	0.0196	0.0319	0.3567	0.2802	0.3932	0.0000	0.0243	0.4123	0.1959	6.6866	1.2968
M_{LA} (d^{-1})	0.02%	0.09%	0.10%	0.21%	0.01%	0.00%	0.06%	0.12%	0.01%	0.16%	0.09%

Table 3.10. Daily predation of juvenile *A. mitchilli* (M_{JA}) upon *A. tonsa* (adults & copepodites) estimated by gut contents collected at the North (N) and South (S) stations in 2010 and 2011.

	2010		2011				
	Aug		Sep	Jul		Sep	
	N	S	S	N	S	N	S
Copepod & copepodites in anchovy guts	4.3	57.7	11.6	22.7	25	23.65	4.85
Mean juvenile Anchovy Concentration (L^{-1})	0.0011	0.0003	0.0005	0.000016	0.000001	0.001	0.0011
Mean <i>A. tonsa</i> adult and copepodites concentration (L^{-1})	5.1	9.5	9.6	11.8	6.5	3.1	11
Average water column temperature ($^{\circ}C$)	27.1	27.3	23.8	16.6	26.0	23.2	22.9
Estimated gut evacuation time (h)	1.1	1.1	1.4	1.1	1.2	1.5	1.5
Clearance rate ($L\ ind^{-1}\ h^{-1}$)	0.8	5.6	0.9	1.7	3.2	5.1	0.3
Ingestion ($\#\ ind^{-1}\ h^{-1}$)	3.9	52.9	8.2	19.8	20.9	16.0	3.2
M_{JA} (d^{-1})	2.1%	3.6%	1.0%	0.1%	0.0%	12.0%	0.8%

Figure 3.1. The composition of *M. leidyi* prey under different temperature (Warm, Temperate (T)) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).

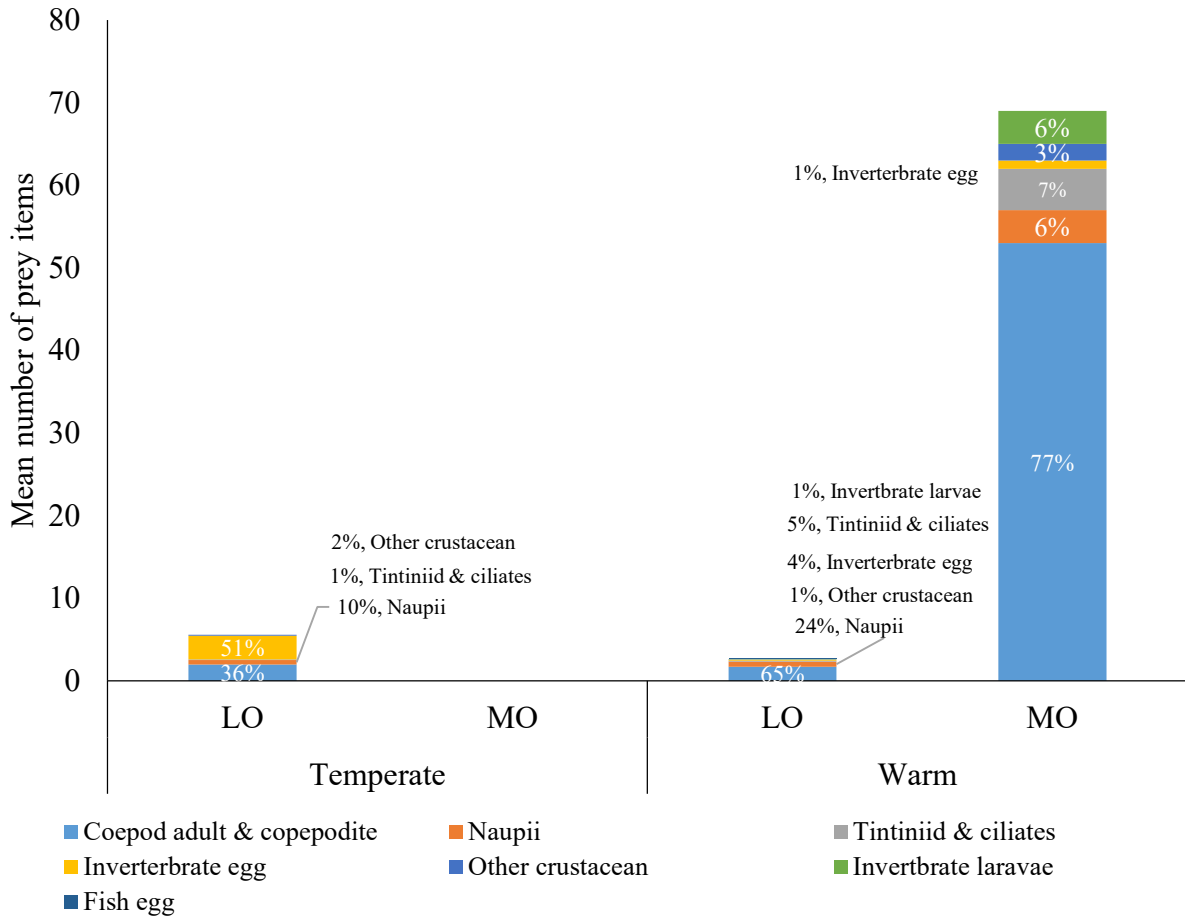
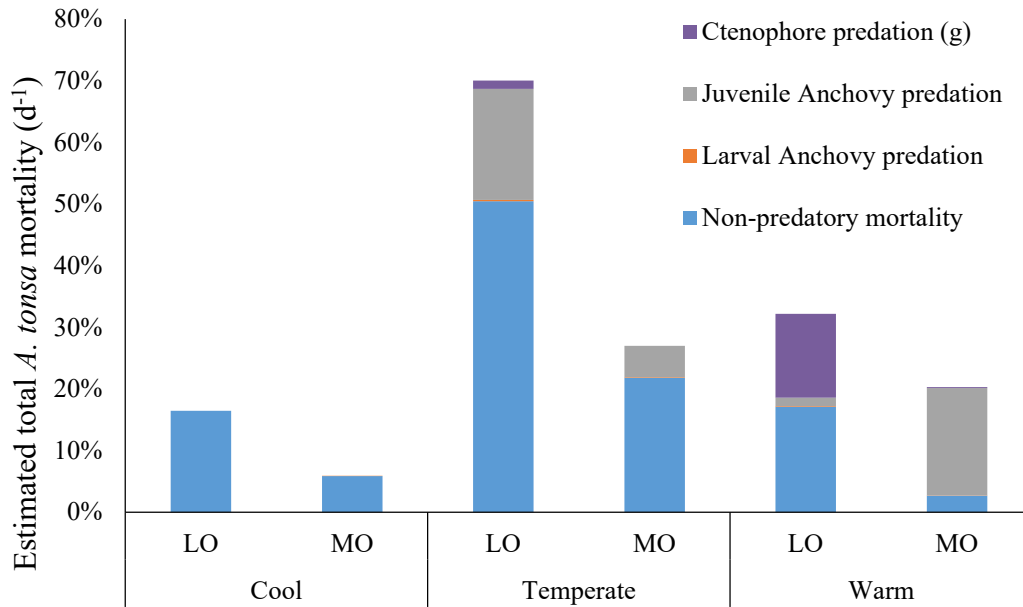


Figure 3.2. Predatory and non-predatory mortality (% d⁻¹) of *A. tonsa* by larval *A. mitchilli*, juvenile *A. mitchilli*, and *M. leidy*. *M. leidy* predation was made from (a) gut contents and (b) wet weights under different temperature (Cool, Temperate, Warm) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).

(a)



(b)

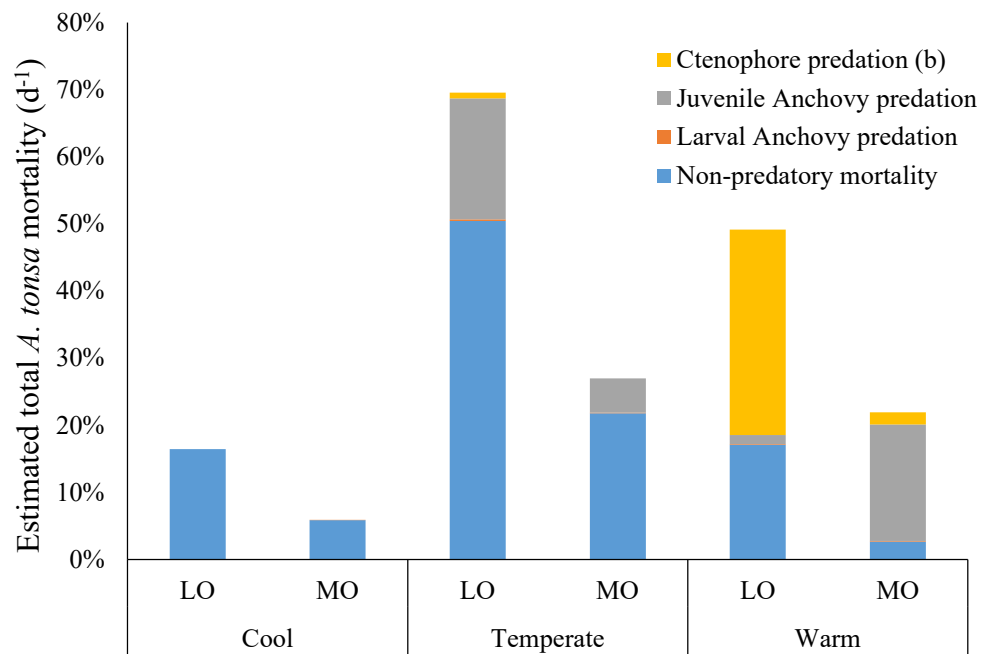
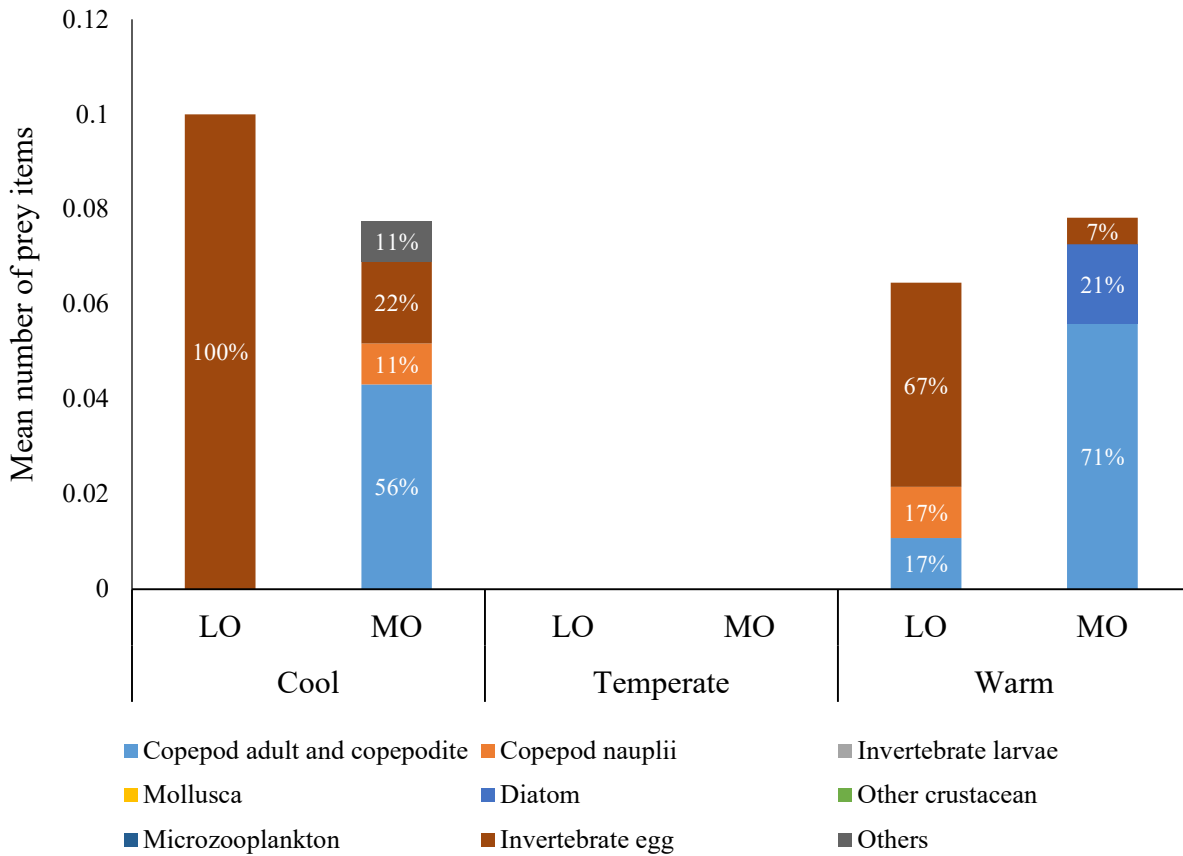
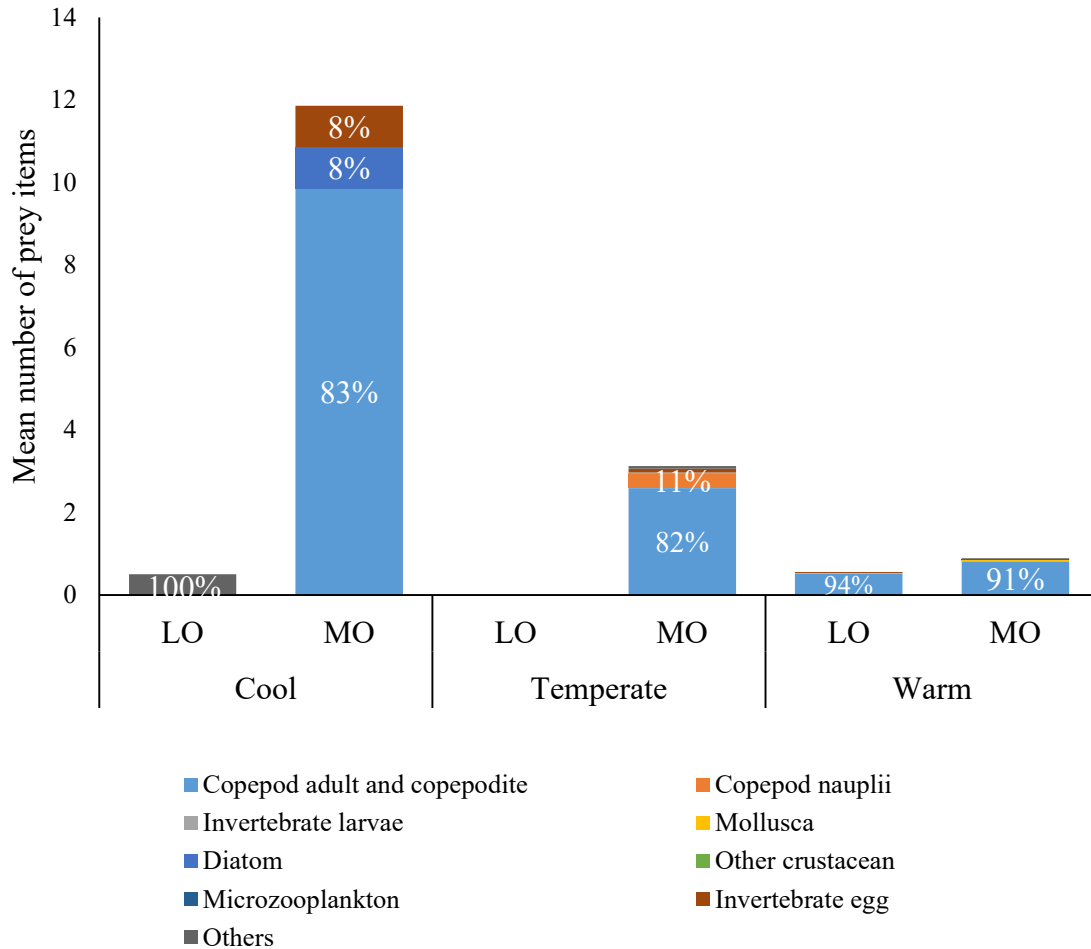


Figure 3.3. Prey composition of larval *A. mitchilli* (< 10mm) under different temperature (Cool, Warm) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).



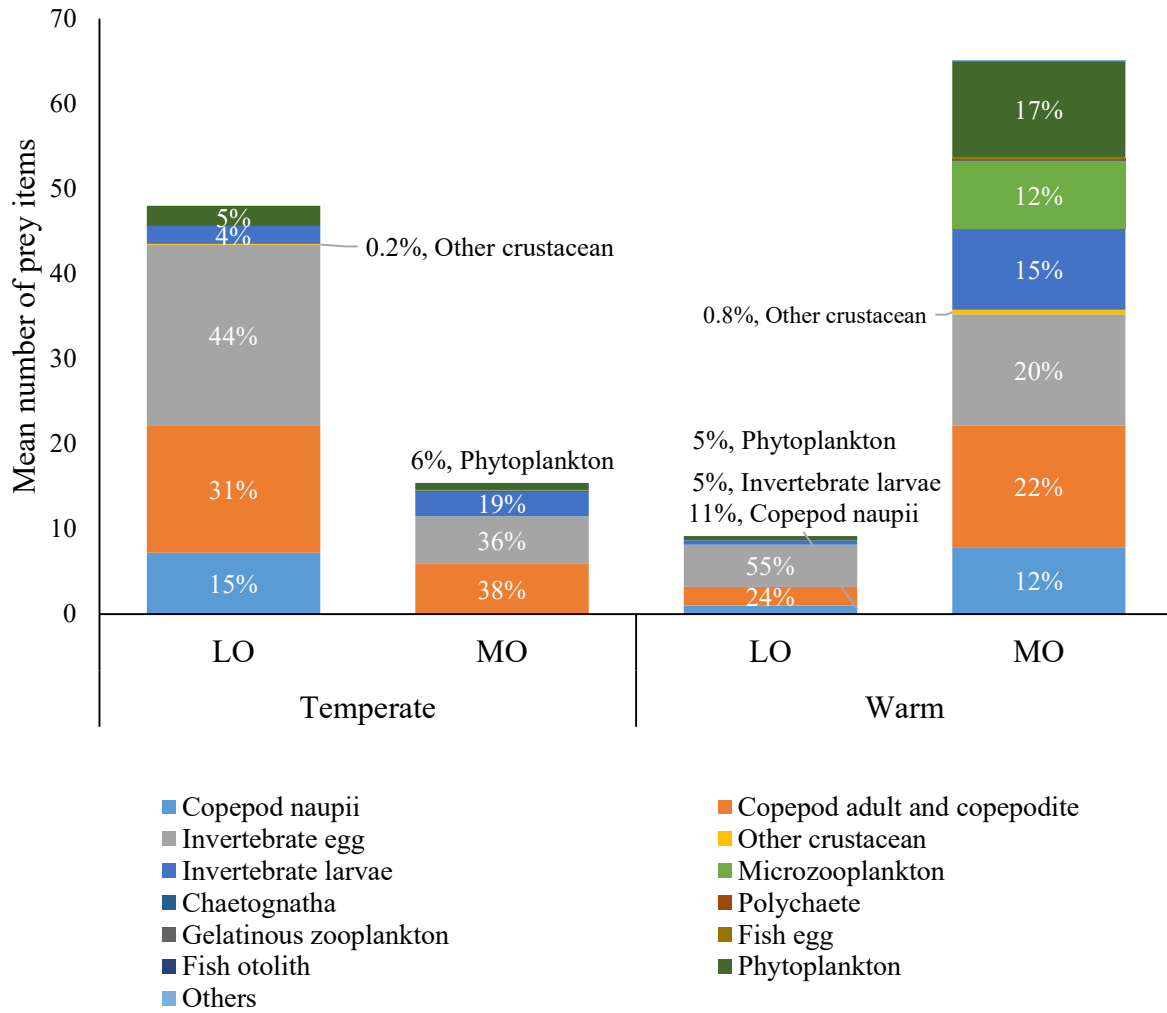
Note: There were no larval bay anchovy < 10mm caught during 2011–September cruise at the North station (the T–LO group), and all the larval bay anchovy in this size category collected during 2011–September cruise at the South station (the T–MO group) had empty guts

Figure 3.4. Prey composition of larval *A. mitchilli* (10 – 32 mm) gut contents under different temperature (Cool, Temperate, Warm) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).



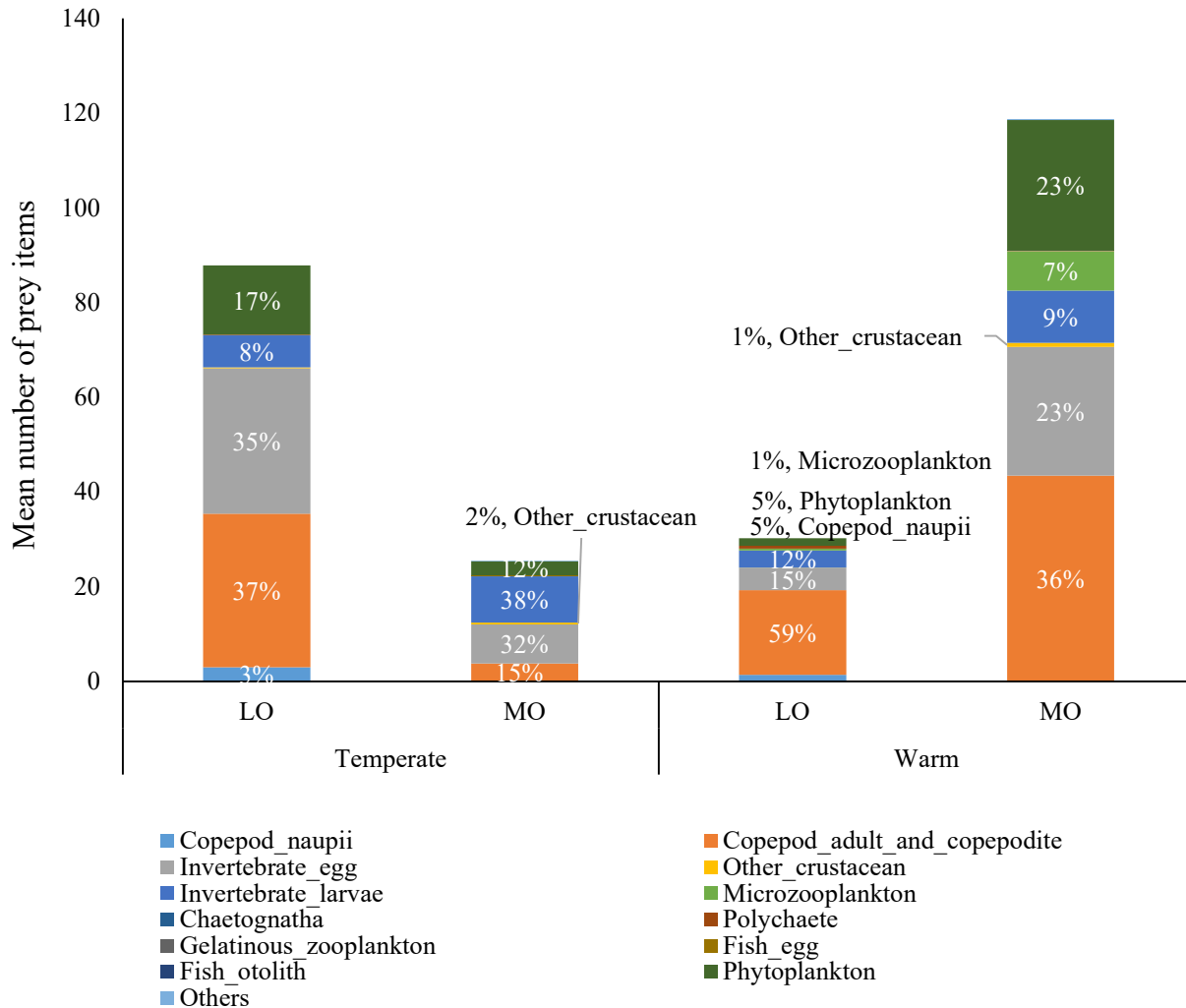
Note: There were no larval bay anchovy in this size category caught during 2011–September cruise at North station (the T–LO group).

Figure 3.5. Prey composition of juvenile *A. mitchilli* (32 – 40mm) gut contents collected with the mid-water trawl under different temperature (Temperate (T)/ Warm (W)) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).



Note: Mid-water trawls were not conducted during the spring cruises (the cool group).

Figure 3.6. Prey composition of juvenile *A. mitchilli* (40 – 60mm) gut contents collected with the mid–water trawl under different temperature (Temperate (T)/ Warm (W)) and oxygen conditions (less oxygenated (LO), more oxygenated (MO)).



Note: Mid–water trawls were not conducted during the spring cruises (the cool group).

Appendix 3.1. Numbers of *Mnemiopsis leidyi*, larval and juvenile *Anchoa mitchilli* gut content samples collected with Reeve net, Tucker Trawl, and mid-water trawl during the six research cruises

Cruise	Stations	<i>M. leidyi</i>	Larval <i>A. mitchilli</i>	Juvenile <i>A. mitchilli</i>
Net		Reeve net	Tucker Trawl	Mid-water trawl
2010 - May	North	0	118	-
	South	0	0	-
2010 - Aug	North	48	114	12
	South	60	239	19
2010 - Sep	North	32	-	-
	South	4	56	30
2011 - May	North	0	10	-
	South	0	0	-
2012 - Aug	North	0	123	20
	South	81	94	11
2013 - Sep	North	15	7	23
	South	0	138	30

Chapter Four: Avoiding hypoxia and escaping predators: Examining behavior trade-offs with an individual-based model

Abstract

Zooplankton face multiple stressors including low dissolved oxygen (hypoxia) and predation in many coastal systems. The objective of this study was to evaluate whether the avoidance of hypoxia affects the risk of predation, and how different behavioral responses the copepods may alter that impact using an individual-based behavior model. The weighted mean depths of the copepods and their time spent in both hypoxia and predation patches under three different scenarios (no hypoxia, moderate, and severe hypoxia) were used as metrics to test the effects of hypoxia on the vertical distribution of simulated copepods and to assess the tradeoff between avoiding hypoxia and predation. With similar amounts of predation stress, the predation risk was highest under the severe hypoxia scenario, followed by the moderate hypoxia scenario, and finally by the no hypoxia scenario. Sensitivity analysis indicated that increasing swimming speed when individuals encountered stressors was the most influential variable which allowed copepods to quickly leave an undesirable area, but also increased the risk of predation from ambush predators. Increasing sinking rate was important for aggregating copepods in deeper depths, and increased turning angle was critical for keeping vertical position at a specific layer. In a region with the most severe hypoxia at bottom and the most predators at the surface,

avoiding hypoxic bottom water by swimming faster, jumping more, sinking less, and turning smaller angles resulted in shallower weighted mean depth and more aggregation between the layers of stressors, which also resulted in spending more time in predation patches and potentially increasing predation risk. These findings suggest a tradeoff between avoiding hypoxia stress and predation stress. The simulation results reflected the field observation that copepod predation mortality was higher under hypoxic conditions and supported the hypothesis that copepod behavior changes under hypoxic conditions could contribute to enhanced predatory mortality.

Introduction

Summer hypoxia, jellyfish blooms, and a decrease in the copepod population are often concurrent phenomena in coastal ecosystems. For example, the moon jellyfish, *Aurelia aurita*, often blooms in Hiroshima Bay during summer, the season of peak hypoxia (Shoji et al., 2010). Similarly, *A. aurita*, ghost jellyfish *Cyanea nozakii*, and the giant jellyfish *Nemopilema nomurai* frequently form large blooms in Chinese seas in the same period as hypoxia, resulting in fishery collapses (Dong et al. 2010). In the Chesapeake Bay, the population of the copepod *Acartia tonsa* has been observed to decrease in summer, when the bottom hypoxia is most pronounced (Pierson et al., 2017; Roman et al., 2005) and jellyfish (the bay nettle *Chrysaora chesapeakei* and the comb jellyfish, *Mnemiopsis leidyi*), are often abundant at the same time (Purcell, White, & Roman, 1994). Because the peaks in hypoxia which coincide with decreases in copepods and increases in jellyfish has been observed in multiple ecosystems, it is likely these are not independent phenomena.

Many studies have suggested that hypoxia and jellyfish blooms directly lead to a decrease in the copepod population by increasing mortality and/or predation, respectively (Elliott, Pierson, & Roman, 2013; Olesen, 1995; Purcell & Decker, 2005; Roman et al., 2005). However, more research is still needed to explain the indirect effects and interactions between hypoxia and predation. For example, does hypoxia intensify predation on copepods, and if so, how? Using field sampling and gut analysis, Slater et al. (Ch. 3) confirmed both non-predatory and predatory mortality of the copepod *A. tonsa* (from juvenile anchovy *Anchoa mitchilli* and ctenophore *M. leidyi*) increased under hypoxic conditions in the Chesapeake Bay, and the dominant predator transitioned from fish to jellyfish as moderate hypoxia developed into severe hypoxia. By comparing predatory and non-predatory mortalities under a variety of environmental conditions, Slater et al. (2020 & Ch. 3) showed that the impact of predation was enhanced under hypoxia and that this effect was not solely due to the seasonal change in predator populations that is coincident with changing hypoxia conditions.

Two hypotheses have been put forward to explain why predation may be increased under hypoxic conditions. The first invokes differences in hypoxia tolerance. The tolerance gap hypothesis states jellyfish are often more tolerant to hypoxia than their prey, and therefore may have advantages in hypoxic environments (Decker, Breitburg, & Purcell, 2004; Ekau et al., 2010; Purcell et al., 2001). For example, the critical partial pressures of oxygen (P_{CO_2}), which is the partial pressure necessary to maintain base metabolism at 25 °C, for *M. leidyi* and *C. chesapeakei* ($P_{CO_2} = 7.2$ and 12.3 kPa, respectively) are lower than that of *A. tonsa* ($P_{CO_2} = 13.0$

kPa) (Elliott et al., 2013; Thuesen, Rutherford, & Brommer, 2005; Thuesen et al., 2005). While it is true that gelatinous zooplankton are in general more tolerant to hypoxia than other taxa, this hypothesis does not explain why fish predation on copepods also is exacerbated under hypoxia (Ch. 3). Highly mobile species like fish have a higher metabolism and require more oxygen than drifting species, and therefore are usually more sensitive to low dissolved oxygen than plankton species like copepods (reviewed in Ekau et al., 2010).

Another common explanation is the theory of behavioral change. The amount of suitable habitat decreases when the bottom water column is hypoxic; hence, aerobic animals may avoid the hypoxic bottom water and congregate in the water column above. This may increase the encounter rates between predators and prey, potentially resulting in higher predatory mortality (Breitburg, 1994; Breitburg et al., 1994; Kolesar et al., 2010; Roman et al., 2019). In support of this hypothesis, a mesocosm experiment suggested that hypoxia influenced food web interactions more through altered habitat use and encounter rates than by directly affecting predation (Kolesar et al. 2010). Field observations also have shown that *M. leidy* aggregated above pycnoclines in the Chesapeake Bay when the bottom of the water column was moderately hypoxic, and below pycnoclines when the bottom of the water column was severely hypoxic, resulting in the strongest predation on copepods near pycnoclines, where both species were concentrated (Purcell et al., 2014).

While mesocosm studies and field sampling have provided important snapshots of the interactions between copepods and their predators under hypoxia, the spatial and temporal scales of these studies (meters and hours) are large compared to

the size and response time of individual copepods reacting to a stressor (millimeters and microseconds) as has been observed in the laboratory. Lab studies using high-speed cameras have revealed copepods exhibit sophisticated behaviors when encountering predators, including sequences of turns, jumps and fast swimming with variation among sexes, stages, and species. For example, the average total body length of *A. tonsa* is 1 mm, its average swimming speed is 1.4 mm s^{-1} , but its escape speed can reach $> 370 \text{ mm s}^{-1}$ within microseconds and for short bursts (acceleration $> 100 \text{ mm s}^{-2}$) when encountering predators. When escaping, male *A. tonsa* swim faster and female *A. tonsa* jump longer (Buskey, Lenz, & Hartline, 2002; Waggett & Buskey, 2006). Lab studies have also found that the jumping frequency and swimming speed of copepods decreases with decreasing dissolved oxygen (Decker et al., 2004; Svetlichny et al., 2000). There are geographical differences in behavioral responses to hypoxia, as *A. tonsa* from the Chesapeake Bay avoid hypoxic water, while *A. tonsa* from Florida do not (Decker et al. 2003). This may be partly because of the genetic differences within *A. tonsa*. For example, phylogenetic analyses revealed *A. tonsa* adapting to fine-scale salinity features, with two reproductive isolated cryptic species in the Chesapeake Bay (Chen & Hare, 2008; Plough et al., 2018). These multiple clades within a species may be the reasons for varied responses toward similar stressor in different regions, and thus the result from one region may not be applicable for other regions even if the “species” is the same.

However, with these fine spatial and temporal scales, the lab environment is comparatively simple compared with that observed in mesocosm or field studies. To better understand the effects of behavioral changes under multiple stressors, and the

potential consequences for non-predatory and predatory mortality, we built an idealized individual-based model to simulate copepod avoidance behavior toward two stressors, hypoxia and predation. The scenarios that were tested included two controls – no hypoxia (environmental control) and no hypoxia avoidance (behavioral control) – and two treatments: moderate hypoxia with hypoxia avoidance and severe hypoxia with hypoxia avoidance. We evaluated how changing avoidance behaviors, including swimming speed, turning angle, jumping, and sinking, may affect copepod vertical distributions, risks of suffocation from bottom hypoxia, or being eaten by nonmobile surface predators.

Methods

Overall environment

An idealized 3D individual-based model, modified from a copepod foraging model (Leising 2001), was built in MATLAB® ver. R2019a to simulate copepod stress avoidance behaviors in the Chesapeake Bay. Model parameters were summarized in Table 4.1a. The model dimensions were $1 \times 1 \times 20$ m, representing a 20 m^3 vertical water column in the main channel of the Chesapeake Bay. The grid size was 1 cm^3 , and the time step was 1 s. One thousand copepods were randomly placed in the model at the beginning of each simulation. The body length of a copepod was modeled as 1 mm, approximately the average total body length of adult female (1.03 ± 0.02 mm) and male (and 0.96 ± 0.05) *A. tonsa* (Buskey et al., 2002) (Table 4.1). *A. tonsa* display a “hop and sink” behavior, swimming rapidly upwards and then sinking slowly (Buskey, 1994). The “hop” behavior was simulated as

individual copepods moving twice their body length each time step, an approximation from the free-swimming behavior of *A. clausi* (moving 1.5 ± 0.1 mm during 100 ms, Saiz & Alcaraz, 1992). The “sink” behavior was simulated as moving half their body length each second, approximated from the published mean sinking velocity of *A. tonsa* (0.58 ± 0.1 mm s⁻¹, Jonsson & Tiselius, 1990).

Stimulants were placed in the model to simulate stressors in the Chesapeake Bay during summer that cause responses in the copepods (Table 4.1). Stimulants above mid-depth (10 m) represented ctenophore predators and stimulants below the mid-depth represented hypoxia. The stimulation strength was measured in relative intensity from 0 to 1, with 0 representing an absence of stressors (“safe zone”), and 1 representing an anoxic area or where ctenophore predation occurred. Hypoxic stress increased with depth from the mid-depth to the bottom, reflecting the observations made during research cruises in summer 2010 and 2011, that dissolved oxygen levels were lower below pycnoclines (Pierson et al. 2017). In keeping with the data from summer 2010 in the Chesapeake Bay, the intensity of hypoxia stress was gradually increased from 0 to 1 from the mid-depth to the bottom (20 m) in the moderate hypoxia scenario (Figure 4.1a). For the severe hypoxia scenario, the intensity of hypoxia was simulated with a marked increase in relative intensity from 0 to 0.8 over 5 m, from the mid-depth to 15 m, and then slowly increased from 0.8 to 1 from 15 m to the bottom, representing the hypoxic conditions during 2011 summer cruise (Figure 4.1b).

In contrast with how hypoxia was parameterized, predation stress was maximal at the surface with a relative intensity of 1 and decreased to 0 at the mid-

depth, reflecting field observations that ctenophores were mostly concentrated above the pycnocline during summer (North & Houde 2004, Slater et al. 2020). Predation was modeled as increasing from the mid-depth to the surface and included a random component to simulate patchiness in predators. To create the trend and patchiness, stress in each horizontal cell was linearly interpolated from intensity = 0 to 1 from mid-depth to the surface, and then this intensity was multiplied by a random number between 0 and 1, so the maximum predation stress increased in both mean and variance from mid-depth to the surface (Figure 4.2). As a result, when a simulated copepod swam up from mid-depth (10 m) toward the surface, its risk of being preyed upon increased, yet there are places without predation stress at each depth. The combined stress field (hypoxia + predation) was then summed as the total stress field (Figure 4.3). Although the final stress field was simpler than reality, because the two stressors did not overlap, the general real-world pattern of more predators above pycnoclines and less dissolved oxygen below pycnoclines was reflected in the model.

Model equations and parameters

The model can be broken down into two major behavioral components: (1) stress avoidance and (2) impairment under hypoxia.

Stress avoidance

This stress avoidance component was modified from a copepod spatial foraging model (Leising & Franks, 2000; Leising et al, 2005), in which copepods respond to stimuli (food) with an “area-restricted search” behavior. In this behavior, copepods swim more slowly and with a more tortuous path in order to stay in a food patch (Tinbergen et al. 1967), with the opposite true when searching for food. The

model showed this spatial foraging strategy provided better “fitness” (defined as the ratio of total ingestion over mortality) than a random walk (Leising et al, 2005). Our stress-avoidance model adopted this spatial foraging so that simulated copepods would move more quickly away from an undesirable area and stay longer in a favorable zone. In our model, the stimuli represented stressors, either hypoxia stress or predation stress, depending on the depth of individual copepods in the model. When encountering a stressor, copepods in the model swam faster and straighter to escape and to search for safe zones (defined as $I = 0$); upon arriving in a safe zone, copepods swam more slowly and made bigger turns to remain near that location. Similarly, copepods jumped more and sunk less in a stress patch ($I > 0.5$), approximating responses toward a predator or hydrodynamic disturbance (Burdick et al., 2007; Waggett & Buskey, 2006, 2007; Waggett & Buskey, 2006). The opposite was true for copepods trying to stay in a safe zone longer, as approximated from Tiselius's (1992) description of aggregation behavior in food patches.

Copepod behavioral responses in the model were a linear function of the stimulant intensity (Table 4.2). These linear relationships were based on studies with high-speed cameras in which copepod responses increased with proximity to the source of a hydrodynamic disturbance, and thus the probability of an escape response can be described as a function of distance from the stimulus (Burdick, Hartline, & Lenz, 2007; Buskey et al., 2002; Gilbert & Buskey, 2005). In our model, when there was no stressor (stress intensity = 0) copepods swam at a resting swimming speed (sw) of 1.5 mm s^{-1} as approximated from the mean observed adult *A. tonsa* swimming speed ($1.4 \pm 0.18 \text{ mm s}^{-1}$, Waggett & Buskey, 2006). The standard deviation of

copepods' turning angle (τ) was 90, assigned to generate the most torturous path. The jumping percentage (jp) was parameterized so that 5% of the population at any given time was jumping, based on lab observations that *Acartia* sp. only hop intermittently and spend most of their time sinking (Buskey et al., 2002; Tiselius & Jonsson, 1990). The sink percentage (sp) was arbitrarily assigned to be 50% of copepods in the top half layer and 10% in the bottom half layer at any given time step, to simulate in general more sinking than jumping and less sinking in the bottom under hypoxic conditions.

The overall escape strategy was swimming faster and straighter, jumping more, and sinking less. Accordingly, when the comparative stress intensity changed from 0 to 1 (i.e., the maximum, such as under anoxia or at the mouth of a ctenophore), the following changes occurred: the swimming speed increased to 4.5 mm s⁻¹ (Equation 4.1), the standard deviation of turning angle range decreased to 5 degrees (Equation 4.2), the jumping percentage increased to 60% (Equation 4.3), and the sinking percentage decreased to 1% in the bottom-half layer and 5% in the top-half layer (Equation 4.1 & 4.2). These values were scaled linearly with the stress intensity. The largest swimming speed when a copepod encountered maximum stress (4.5 mm s⁻¹, Equation 4.1) was based on the observed average jump distance (4.2/4.6 mm in male/female *A. tonsa*, Buskey et al., 2002). The minimum standard deviation of copepods' turning angle was arbitrarily assigned as 5 for a straighter path when encountering stressors (Equation 4.2). The maximum jump percentage (60%) was based on lab observations of the percentage of escape responses of *Acartia* sp. next to a disturbance source (Burdick et al., 2007; Buskey et al., 2002) (Equation 4.3).

Minimum sinking (5% for the top layer copepods and 1% for the bottom layer copepods) was arbitrarily assigned for improving escape efficiency. The equations were:

$$\frac{\Delta sw}{\Delta t} = 0.15 + 0.3 I \quad (\text{Equation 4.1})$$

$$\frac{\Delta \tau}{\Delta t} = 90 - 85I \quad (\text{Equation 4.2})$$

$$\frac{\Delta jp}{\Delta t} = 0.05 + 0.55I \quad (\text{Equation 4.3})$$

$$\frac{\Delta sp}{\Delta t} = 0.5 - 0.45I, \text{ if depth} \leq 10 \text{ m} \quad (\text{Equation 4.4})$$

$$\frac{\Delta sp}{\Delta t} = 0.1 - 0.09I, \text{ if depth} > 10 \text{ m} \quad (\text{Equation 4.5})$$

Impairment under hypoxia

When a simulated copepod was in hypoxic conditions (below 10 m), the swimming and jumping responses were impaired based on the hypoxia stress intensity by multiplying the behavior function by an impairment factor (IF, Equation 4.6). This factor was intended to simulate the effects of decreasing dissolved oxygen on copepods' ability to escape (Decker et al. 2004). Under the maximum stress scenario (intensity = 1, simulating anoxia), the slope of swimming and jumping was reduced by half, making the simulated copepods less responsive to the stimuli and less capable of escaping hypoxia.

$$IF = 1 - 0.5I \text{ if depth} > 10, \text{ else } IF = 1 \quad (\text{Equation 4.6})$$

Scenarios and assumptions

Three scenarios were tested with the model: 1) no hypoxia (a control scenario with only predation); 2) moderate hypoxia; and 3) severe hypoxia. Each scenario simulated 6-hours in the copepods' life. Each scenario was repeated three times, with the locations of the 1000 copepods randomly selected and the predation field generated at the beginning of each run. After each set of three simulations was complete, the average and standard deviation of weighted mean depth (WMD), and the total time spent in stressor patches ($I > 0.5$) were calculated for each individual in the simulation to evaluate the tradeoff between avoiding hypoxia and avoiding predation.

To focus on the stress avoidance behaviors, copepod growth, feeding, and mortality were neglected, and copepod prey chasing behavior was suppressed as well. The distributions of predation stress were fixed within each simulation. Because the study sought to simulate predation stress from ctenophores, which are a drifting species, and because our simulation time was comparatively short, a fixed predation stress field was used for the duration of each model run to decrease the model's complexity. These parameterizations allowed the modeling effort to focus directly on the consequences of behavioral changes under multiple stressors.

Sensitivity analysis

To determine the sensitivity of the model results to the parameterization of the escape responses, a series of model sensitivity runs were completed by varying the magnitude of individual escape behaviors. In general, for these runs, the slope of copepod response toward stimulants was varied by $\pm 50\%$, except for the standard deviations, which were varied by $\pm 5\%$, and the sinking percentages which were

varied by $\pm 10\%$, to avoid values below 0 (Table 4.2). For example, for Equation 4.1 in the sensitive analysis, the slope of the stress response was elevated or lowered by 50%, resulting in $0.15 + 0.45 I$ in the more responsive scenario and $0.15 + 0.15 I$ in the less responsive scenario. A series of model runs using the severe hypoxia scenario were then completed, with the behavioral parameters varied in each run to examine how the results changed. The mean weighted depth, copepod concentrations in the top half, middle, and bottom layer (0-10, 10-15, 15-20m), and the time spent in the hypoxia or predation stress zone ($I > 0.5$) were calculated as percentage changes for each parameter from the default response.

Results

Vertical distribution and time spent in stress patch

The vertical distribution of copepods was strongly influenced by stress related to dissolved oxygen. In the case of no hypoxia (control scenario), copepods gradually sank to the bottom (Figure 4.3a, Figure 4.4a) because there was no motivation to swim upward (e.g., for feeding) built into the model. However, when bottom hypoxia was present, copepods in the bottom layer quickly moved upward in both moderate and severe hypoxia scenarios. It took approximately 1 hour for copepods to completely escape the hypoxic zone (depth = 18 – 20 m) in the moderate hypoxia scenario (Figure 4.3b), and it took twice as long under the severe hypoxia scenario when the hypoxia zone ($I > 0.8$, depth = 15 – 20 m) was bigger and they were more impaired (Figure 4.3c). It took longer for copepods to move away from the predation stress in the surface layer when hypoxia stress also was present. During the 6-hr

simulation, the copepod relative concentration (% of total abundance) in the top-half of the water column constantly decreased by 5% every 30 min under the no hypoxia scenario (Figure 4.3a), but the changes in abundance were < 3% after 3 hrs of simulation in both hypoxia scenarios (Figure 4.3b, c).

The mean weighted depth (MWD) of copepods also was strongly influenced by hypoxia. After 6-hrs of simulation, MWD was shallowest under severe hypoxia (Figure 4.6a). The MWD was 12.83 ± 0.04 m and 11.97 ± 0.07 m in the moderate and severe hypoxia scenario, respectively, and both were shallower than the MWD in the control scenario (19.15 m). Copepods aggregated below the stress-free mid-depth region (found at 10 – 12 m) and above the stress zone where $I > 0.5$ when hypoxia was present, which was markedly different from the aggregations near bottom in the control scenario (Figure 4.7).

Aggregation was more pronounced under severely hypoxic conditions than under moderately hypoxic conditions. More than three times more copepods aggregated at depths of 10 – 12 m ($z = 1000 - 800$ cm) in the severe hypoxia scenario (number of copepods = 708) than in the moderate hypoxia scenario (number of copepods = 209), compared with only 100 copepods in the no hypoxia scenario (Figure 4.7). Hence, avoiding bottom hypoxia resulted in shallower vertical distributions and aggregation in a comparatively stress-free zone. Increasing the severity of hypoxia further increased the shoaling of the copepods' vertical distributions and increased aggregation.

Copepods on average spent 37% more time in the hypoxia patch ($I > 0.5$) in the severe hypoxia scenario (38 ± 0.6 min) than in the moderate hypoxia scenario (27 ± 0.4 min) (Figure 4.6b). By avoiding bottom hypoxia and moving upward, copepods also spent 19% more time in predation stress patch ($I > 0.5$) in the severe hypoxia scenario (19.2 ± 0.7 min) than in the moderate hypoxia scenario (16.9 ± 1.7 min) (Figure 4.6c). The altered vertical distribution resulted in more time spent in predation stress patches, supporting the idea that predation risk increased under more hypoxic conditions.

Sensitivity analysis

Results of the sensitivity analysis indicated that simulated stress avoidance strategies enhanced copepod escape from bottom hypoxia, including swimming faster, turning less, jumping more, and sinking less. Swimming faster was the most effective way to escape bottom hypoxia. By increasing the slope of swimming speed by 50% and increasing the maximum speed to 60 mm s^{-1} , the time spent in hypoxia patch (TIH) decreased by 16%, and the WMD was 6% shallower than the default parameter settings with 7% more copepods concentrated in the upper half of the water column. Smaller turning angles were also very effective at enhancing escape from hypoxia. By increasing the slope of turning responses by 5% and decreasing the minimum turning angle to 0.75 degrees, the TIH decreased by 8%, and the WMD was 2% shallower than default with 6% more copepods concentrated in the upper half of the water column. Jumping more was less effective than swimming faster and straighter. By increasing the slope of jump percentage by 50% and increasing the maximum jumping to 87.5%, the TIH decreased by 6%, and the WMD was 4%

shallower than default with 6% more copepods concentrated in the upper half of the water column. Comparatively, sinking less was the least effective way to escape bottom hypoxia. By increasing the sinking responses by 10% and minimizing the sinking to 0.1% when copepods encountered stress, the TIH decreased by 2%, and the WMD was similar to the default scenario with only 1% more copepods concentrated in the upper half of the water column.

In contrast, decreasing the magnitude of escape responses resulted in copepods remaining in the hypoxic zone for a longer amount of time, and their escape responses were impaired more severely. Although the final WMD was similar to the default scenario, it took longer for copepods to get to the safe zone and they spent more time in hypoxia patches during the 6-hr simulation. For example, decreasing swimming speed by 50%, which reduced maximum swimming speed to 30 mm s^{-1} , increased TIH by 44%. Overall, increasing the magnitude of the response to stressors decreased the amount of time copepods spent in all stress patches by 3 – 9%, and decreased the stressor responses which created negative feedbacks that resulted in increased time spent in stress patches by 13 – 28% (Table 4.3).

Although swimming faster and straighter, jumping more, and sinking less enhanced copepod escape from bottom hypoxia, not all of the behaviors helped to decrease time spent in predation stress. For example, swimming faster made the MWD shallower and increased concentrations in the upper half of the water column, thus also increasing the time spent in predation patches by 8% (Table 4.3), suggesting a tradeoff between avoiding hypoxia stress and avoiding predation stress. When comparing the time spent in hypoxia and predation patches with $I > 0.5$, the behaviors

of swimming faster, straighter and jumping more slightly increased time spent in predation patches (Figure 4.8). The effects of changing sinking rates were not as pronounced, and the tradeoff between avoiding hypoxia and avoiding predation were bigger for some behaviors (i.e., swimming faster) than the others (i.e., sinking less).

Discussion

This study focused on the dilemma of avoiding two different stressors by employing an individual-based model to test if avoiding hypoxia could increase predation risk for copepods. By swimming faster, turning with smaller angles, jumping more and sinking less when encountering stressors, simulated copepods were able to escape stressors (either predator or hypoxia) and eventually aggregate around the mid-depth (the “safe zone”) in scenarios with both hypoxia and predators. However, avoiding bottom hypoxia also resulted in shallower vertical depth distributions, which increased predation risks by forcing copepods to spend more time in predation stress patches.

Cue hierarchy

The tradeoff between avoiding hypoxia and predation was observed in this model. Aggregating at shallower depths, swimming faster, and jumping more, decreased the time spent in hypoxia zone, but these behaviors also increased time spent in predation patches and thus increased predation risk (Figure 4.8). In this model, both hypoxia and predation stress were equally weighted, and copepods responded toward them in the same manner which was scaled to the intensity of the stressor. However, hypoxia and predation are fundamentally distinct stressors.

Predators present acute stresses; once met, escape responses are an immediate necessity otherwise the consequence is irreversible. Hypoxia, on the other hand, is a more chronic stress; it will not kill copepods immediately when encountered, but it eventually will reduce growth and reproduction (Sedlacek 2003, Marcus et al. 2004) before mortality happens which would take a longer time compared with a predator encounter.

In addition to having different time scales of influence on individual copepods, hypoxia and predation stress also have dissimilarities in the field. Hypoxia usually takes some time to establish near the bottom and there is often a declining oxygen gradient with stratification above it (Kemp et al. 2005). Because zooplankton could react to slight changes ($\leq 1\%$) in oxygen (Wishner et al. 2013) and some copepods change their vertical distribution accordingly (Tinson & Laybourn-Parry 1985), copepods may be able to use oxyclines or stratification as a warning sign. In contrast, the distribution of predators is comparatively less predictable. Because the force of predation selection is very strong and often alter animal's behavior when present (Lima & Dill 1990), it is likely copepods weigh predation and hypoxia differently and have different strategies for coping with these two stressors.

For the hypoxia, swimming up was an effective choice to escape because the stressor was evenly distributed in the bottom layer. However, the distribution of predation stress was random, so there were small safe zones in the upper half of the water column, and thus copepods did not have to move toward a specific direction to be safe. In the laboratory, copepods have escaped predators by rapid reorientation (30° s^{-1} , Buskey et al. 2002), opposite of the stress responses in my model. A test was

conducted to see what happens if copepods were turning bigger angles (30 ° - 90°) when encountering stress (Figure 4.11). The results indicated that copepods overall stayed in hypoxia zones twice as long (84 min vs 40 min), but the time spent in predation patches was also decreased to approximately 14 min (compared with ~35 min in default), indicating that larger turning angles could effectively help copepods avoid ambush predators with low risk of jumping into another predator (which is what increased swimming speed would do). Considering the optimal escape direction for avoiding bottom hypoxia (moving up) and avoiding predators (moving away) are not the same, a good strategy for escaping uniform stress (like hypoxia) may not be as good for escaping a randomly distributed stress (like predation).

Swimming faster also increased the encounter rate with ambush predators (Buskey 1994), and jumping more increased the chance of being detected by predators (Wong et al. 1986); both of these tradeoffs were observed in this model (Figure 4.8). Copepod behavior studies have focused on the cue hierarchy between feeding and predation (Woodson et al. 2007), but not on the tradeoffs between hypoxia and predation. A study on fish did find predation seems outweigh hypoxia: the dwarf gourami (*Colisa lalia*) spent more time in extreme hypoxia (DO < 1 mg L⁻¹) rather than leave vegetation cover when their predator snakeheads (*Channa micropeltes*) were present compared to the treatment when no snakeheads were present (Wolf & Kramer 1987). In the same study, snakeheads' predation success was higher when the water was hypoxic because dwarf gourami left cover more often compared with normoxic (Wolf & Kramer 1987). This may explain why copepods have been found in hypoxic bottom waters (Taylor 2003, Pierson et al. 2017).

Because the model captures trade-offs related to stressors and copepod behaviors, this model provides a novel tool to understand the mechanisms of copepod responses toward stressors and how that will affect their vertical distributions. It can also help evaluate the effectiveness of different stress avoidance strategies and the tradeoff between avoiding different types of stressors (hypoxia and predation in this study) by analyzing the time spent in different stress patches. Although the model does not yet replicate a copepod's response to a full range of stressors, the comparison among the different stressor types and distributions could provide insight on copepod behaviors which maximize survival and minimize mortality in many different ecosystems.

Predator responses

Aggregation within the stress-free zone was observed, and severe bottom hypoxia increased the concentration of copepods in the safe zone (Figure 4.7). This model focused on copepod stress avoidance strategies, and thus the predation stress was simplified. In the model, simulated predation stress was non-mobile, and the distribution of predation stress was fixed throughout the entire simulation (but differed in space among simulations), with the goal of simulating ctenophore predation risk. The largest predation stress was at the surface, reflecting field observations that ctenophores were more abundant above pycnoclines when the bottom was hypoxic (North & Houde 2004, Slater et al. 2020) . However, this created a mismatch with the depth of copepod aggregation, potentially underestimating predation risks if ctenophores are distributed more evenly above the pycnocline.

Evidence exists related to the distribution and abundance of jellyfish which can inform individual-based modeling efforts. A fine-scale (1 m resolution) vertical sampling study indicated that *M. leidyi* aggregated around the pycnoclines where the maximum predation impact occurred (Purcell et al. 2014). In addition, gelatinous zooplankton can respond to prey patchiness. For example, an analysis of tagged-jellyfish (*Rhizostoma octopus*) in Carmarthen Bay indicated that jellyfish searched the water column (Hays et al. 2011). Lab observations on bay nettle also found that they swam faster and pulsed less frequently when prey was available (Matanoski et al. 2001). Field observations showed that different ctenophores have different foraging behavior (Matsumoto & Harbison 1993), and *M. leidyi* altered the positions of their oral lobe to increase capture efficiency (Costello et al. 1999, Waggett & Costello 1999). If the largest predation stress occurred near mid-depth and predators responded by moving toward prey aggregations, then even slight increases in the time spent in predation patches under hypoxia due to the shallower vertical distributions of the copepod could lead to a significant increase in predation risk.

The magnitude of the tradeoffs between avoiding hypoxia and avoiding predation were different among the different escape behaviors tested in this modeling study. For example, swimming faster was very effective for escaping the hypoxic bottom water, but it also increased the time spent in the predation patches. The time spent in these two different stressors should not be weighed equally, as one minute longer in hypoxia is potentially lethal, but one minute longer in the mouth of a predator is mortal. The tradeoff for sinking less was comparatively lower. Part of the reason for the different tradeoffs among the behaviors was because the predation

stress in the model was patchy and at fixed locations (more like an ambush predator), and increasing copepod swimming speed can increase the predator-prey encounter rates (Buskey 1994, Kiørboe 2011). This creates a tradeoff between effectively escaping from bottom hypoxia and avoiding patchy ctenophores near the surface. If the predation stress were moving fast or actively chasing after copepods, then swimming faster would be critical for successfully escaping from predators as the relative speed between predator and prey plays an influential role on encounter rates (Gerritsen & Strickler 1977, Evans 1989, Huse & Fiksen 2010). In the model, the predation stress was not mobile, and the simulated predators did not take advantage of prey aggregations as a real predator would, and thus the predator impact was likely underestimated in the model. However, by comparing among the different scenarios we can see how the general encounter rates of copepods and patches of predation are impacted by different hypoxia conditions and behavioral responses.

Sinking and survival

The hop and sink behavior, instead of constantly swimming, is a behavior that can allow copepods to save energy (Haury & Weihs 1976). Laboratory studies indicate that *A. tonsa* can spend around 80% of the time sinking (Buskey et al., 2002; Tiselius & Jonsson, 1990), but a lower sinking ratio (5 – 50% in the surface layer, 1 – 10% in the bottom layer, Table 4.2) was adopted in the model to compensate for the absence of upward swimming behavior (feeding) and to expedite copepods movement away from hypoxic bottom waters. Changing the sinking rate to 10 – 80% caused all copepods to aggregate below the “stress clines” and sit right above the hypoxic layer ($I > 0.8$, Figure 4.9), resulting in a deeper MWD. On the contrary, very small sinking

rates (1 – 5 %) increased the amount of time it took copepods to leave the surface layer, and resulted in copepods being more spread out over the water column instead of concentrated in the “safe zone” (Figure 4.10). Thus, the simulation results indicated that the sinking rate plays an important role in plankton aggregation and vertical distribution, and potential tradeoffs between avoiding hypoxia and saving energy.

To better understand how foraging prey, escaping predators, and avoiding hypoxia will affect copepod vertical distribution and mortality, foraging behavior should be incorporated in future model development and sinking rates should be closer to 80% when there is no stressor. Nevertheless, in the current study, the model results highlight the influence of sinking rates, in which sinking less helped copepods escape stressors and decreased aggregation.

Future research

Understanding zooplankton behavior is an important aspect of understanding how they adapt to different environments, cope with various adversities, and interact with other species (Schmitt & Seuront 2001, Schmitt et al. 2006). Copepods have developed sophisticated strategies to optimize their foraging opportunities while minimizing energy spent or encounters with predators, including the classic “hop and sink” behavior (Haury & Weihs 1976), instantaneously fast swimming ($> 100 \text{ mm s}^{-2}$ acceleration within few microseconds) with sequences of big turns when predators are encountered (Buskey et al. 2002), or conducting several vertical migrations at night to maximize feeding and minimize encounters with predators and save energy (Leising & Franks 2000, Leising et al. 2005). Some research has focused on how

copepods handle the dilemma of simultaneously foraging for prey and avoiding visual predators (Kiorboe & Jiang 2012, Kiorboe 2013), but few focus on the dilemma between avoiding bottom hypoxia and predators. Considering that actual copepod escape responses are comparatively more complex than other crustacean zooplankton such as cladocerans or crab zoea (Singarajah 1969, Ohman 1988), more research is still needed to understand how these taxa react within microseconds toward multiple cues that often contradict to each other.

Recent developments in computing technology can provide a powerful tool to fill the gap between field research and lab experiments (as predicted by Lima & Dill 1990). As with the model simulations presented here, it is useful to test various hypothesized behaviors and responses that are hard to manipulate in field or laboratory settings. Although the current model is much simplified from reality, for example the simulated copepods do not eat and the simulated predators do not pursue prey, this model does represent a step toward understanding how different behaviors may not only affect the efficiency of escaping from stressors but also may affect copepod vertical distributions and interactions with predators. This study represents a beginning to understand how copepods handle the dilemma of avoiding hypoxia and predators with an individual-based model, and the model results suggest tradeoffs in mortality risk when avoiding multiple stressors. Coupling prey feeding behaviors and adding predator chasing behavior could be the next steps toward increased understanding of how different individual responses toward surrounding micro-environments and specific stressors may further affect the population's distribution and interactions.

References

- Breitburg DL (1994) Behavioral response of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Mar Biol* 120:615–625.
- Breitburg DL, Steinberg N, DuBean S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar Ecol Prog Ser* 104:235–246.
- Burdick DS, Hartline DK, Lenz PH (2007) Escape strategies in co-occurring calanoid copepods. *Limnol Oceanogr* 52:2373–2385.
- Burdick, DS, Hartline, DK and Lenz PH (2007). Escape strategies in co-occurring calanoid copepods. *Limnology and Oceanography*, 52(6), pp.2373-2385.
- Buskey E, Lenz P, Hartline D (2002) Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. *Mar Ecol Prog Ser* 235:135–146.
- Buskey EJ (1994) Factors affecting feeding selectivity of visual predators on the copepod *Acartia tonsa*: locomotion, visibility and escape responses. *Hydrobiologia* 292:447–453.
- Chen G, Hare MP (2008) Cryptic ecological diversification of a planktonic estuarine copepod, *Acartia tonsa*. *Mol Ecol* 17:1451–1468.
- Costello J, Loftus R, Waggett R (1999) Influence of prey detection on capture success for the ctenophore *Mnemiopsis leidyi* feeding upon adult *Acartia tonsa* and *Oithona colcarva* copepods. *Mar Ecol Prog Ser* 191:207–216.
- Decker MB, Breitburg D, Purcell JE (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 280:163–72.
- Decker MB, Breitburg DL, Marcus NH (2003) Geographical differences in behavioral responses to hypoxia: Local adaptation to an anthropogenic stressor? *Ecol Appl* 13:1104–1109.
- Dong Z, Liu D, Keesing JK (2010) Jellyfish blooms in China: dominant species, causes and consequences. *Mar Pollut Bull* 60:954–963.
- Ekau W, Auel H, Poertner H, Gilbert D (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7:1669–1699.
- Elliott DT, Pierson JJ, Roman MR (2013a) Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. *J Plankton Res* 35:1027–1034.
- Elliott DT, Pierson JJ, Roman MR (2013b) Predicting the Effects of Coastal Hypoxia on Vital Rates of the Planktonic Copepod *Acartia tonsa* Dana. *PLoS ONE* 8:e63987.

- Evans GT (1989) The encounter speed of moving predator and prey. *J Plankton Res* 11:415–417.
- Gerritsen J, Strickler JR (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *J Fish Board Can* 34:73–82.
- Gilbert OM, Buskey EJ (2005) Turbulence decreases the hydrodynamic predator sensing ability of the calanoid copepod *Acartia tonsa*. *J Plankton Res* 27:1067–1071.
- Haury L, Weihs D (1976) Energetically efficient swimming behavior of negatively buoyant zooplankton: Zooplankton swimming behavior. *Limnol Oceanogr* 21:797–803.
- Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW (2011) High activity and Levy searches: jellyfish can search the water column like fish. *Proc R Soc B Biol Sci* 279:465–473.
- Huse G, Fiksen Ø (2010) Modelling encounter rates and distribution of mobile predators and prey. *Prog Oceanogr* 84:93–104.
- Jonsson P, Tiselius P (1990) Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Mar Ecol Prog Ser* 60:35–44.
- Kemp WM, Boynton WR, Adolf JE, Boesch DF, Boicourt WC, Brush G, Cornwell JC, Fisher TR, Glibert PM, Hagy JD, others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Mar Ecol Prog Ser* 303:1–29.
- Kiorboe T (2013) Attack or Attacked: The Sensory and Fluid Mechanical Constraints of Copepods' Predator-Prey Interactions. *Integr Comp Biol* 53:821–831.
- Kiørboe T (2011) How zooplankton feed: mechanisms, traits and trade-offs. *Biol Rev* 86:311–339.
- Kiorboe T, Jiang H (2012) To eat and not be eaten: optimal foraging behaviour in suspension feeding copepods. *J R Soc Interface* 10:20120693–20120693.
- Kolesar S, Breitbart D, Purcell J, Decker M (2010) Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: clearance rates and vertical habitat overlap. *Mar Ecol Prog Ser* 411:173–188.
- Leising A (2001) Copepod foraging in patchy habitats and thin layers using a 2-D individual-based model. *Mar Ecol Prog Ser* 216:167–179.
- Leising AW, Franks PJ (2000) Copepod vertical distribution within a spatially variable food source: A simple foraging-strategy model. *J Plankton Res* 22:999–1024.
- Leising AW, Pierson JJ, Cary S, Frost BW (2005) Copepod foraging and predation risk within the surface layer during night-time feeding forays. *J Plankton Res* 27:987–1001.

- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Marcus NH, Richmond C, Sedlacek C, Miller GA, Oppert C (2004) Impact of hypoxia on the survival, egg production and population dynamics of *Acartia tonsa* Dana. *J Exp Mar Biol Ecol* 301:111–128.
- Matanoski J, Hood R, Purcell J (2001) Characterizing the effect of prey on swimming and feeding efficiency of the scyphomedusa *Chrysaora quinquecirrha*. *Mar Biol* 139:191–200.
- Matsumoto GI, Harbison GR (1993) In situ observations of foraging, feeding, and escape behavior in three orders of oceanic ctenophores: Lobata, Cestida, and Beroida. *Mar Biol* 117:279–287.
- North EW, Houde ED (2004) Distribution and transport of bay anchovy (*Anchoa mitchilli*) eggs and larvae in Chesapeake Bay. *Estuar Coast Shelf Sci* 60:409–429.
- Ohman MD (1988) Behavioral responses of zooplankton to predation. *Bull Mar Sci* 43:530–550.
- Olesen NJ (1995) Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. *Mar Ecol Prog Ser Oldendorf* 124:63–72.
- Pierson J, Slater W, Elliott D, Roman M (2017) Synergistic effects of seasonal deoxygenation and temperature truncate copepod vertical migration and distribution. *Mar Ecol Prog Ser* 575:57–68.
- Plough LV, Fitzgerald C, Plummer A, Pierson JJ (2018) Reproductive isolation and morphological divergence between cryptic lineages of the copepod *Acartia tonsa* in Chesapeake Bay. *Mar Ecol Prog Ser* in press.
- Purcell J, Decker M, Breitburg D, Broughton K (2014) Fine-scale vertical distributions of *Mnemiopsis leidyi* ctenophores: predation on copepods relative to stratification and hypoxia. *Mar Ecol Prog Ser* 500:103–120.
- Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ, Raskoff KA (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: *Coastal and Estuarine Studies*. p 77–100
- Purcell JE, Decker MB (2005) Effects of Climate on Relative Predation by Scyphomedusae and Ctenophores on Copepods in Chesapeake Bay during 1987–2000. *Limnol Oceanogr* 50:376–387.
- Purcell JE, White JR, Roman MR (1994) Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. *Limnol Oceanogr* 39:263–278.
- Roman M, Zhang X, McGilliard C, Boicourt W (2005a) Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. *Limnol Oceanogr*:480–492.

- Roman MR, Boicourt WC, Kimmel DG, Miller WD, Adolf JE, Bichy J, Harding LW, Houde ED, Jung S, Zhang X (2005b) Chesapeake Bay plankton and fish abundance enhanced by Hurricane Isabel. *Eos Trans Am Geophys Union* 86:261.
- Roman MR, Brandt SB, Houde ED, Pierson JJ (2019) Interactive effects of hypoxia and temperature on coastal pelagic zooplankton and fish. *Front Mar Sci* 6.
- Saiz E, Alcaraz M (1992) Free-swimming behaviour of *Acartia clausi* (Copepoda: Calanoida) under turbulent water movement. *Mar Ecol Prog Ser* 80:229–236.
- Schmitt FG, Seuront L (2001) Multifractal random walk in copepod behavior. *Phys Stat Mech Its Appl* 301:375–396.
- Schmitt FG, Seuront L, Hwang J-S, Souissi S, Tseng L-C (2006) Scaling of swimming sequences in copepod behavior: Data analysis and simulation. *Phys Stat Mech Its Appl* 364:287–296.
- Sedlacek C (2003) Effect hypoxia has on feeding and egg production rates of *Acartia tonsa* Dana 1849 (Copepoda: Calanoida).
- Shoji J, Kudoh T, Takatsuji H, Kawaguchi O, Kasai A (2010) Distribution of moon jellyfish *Aurelia aurita* in relation to summer hypoxia in Hiroshima Bay, Seto Inland Sea. *Estuar Coast Shelf Sci* 86:485–490.
- Singarajah KV (1969) Escape reactions of zooplankton: the avoidance of a pursuing siphon tube. *J Exp Mar Biol Ecol* 3:171–178.

Tables and Figures

Table 4.1. Summary model environment setting (a) and stressor distribution (b) of the copepod's stress avoidance model

Parameter	Abbreviation	Value	Unit
Domain Width	x	1	m
Domain Length	y	1	m
Domain Depth	z	20	m
Grid size		1	cm ³
Timestep	t	1	second
Copepod numbers	n	1000	
Start location		random	
Body length	bl	1	mm
Jump speed		2	bl/ timestep
Sink distance		0.5	bl/ timestep
Stress intensity	I	0 – 1	

(b)

Stressor	Abbreviation	Distribution
Ctenophore predation	p	
hypoxia (moderate)	h_m	$h_m = 0$, if $d \leq 10$, $h_m = 0.1d - 1$, if $d > 10$
hypoxia (severe)	h_s	$h_s = 0$, if $d \leq 10$, $h_s = 0.16d - 1.6$, if $10 < d \leq 15$ $h_s = 0.04d + 0.2$, if $d > 15$

Table 4.2. Copepod's stress avoidance response and impairment under hypoxia toward stress intensity ($0 \leq I \leq 1$) and the sensitive analysis (More/ Less responsive)

Escape responses	Unit	Default behavior	More responsive	Less responsive
Swim speed	cm s ⁻¹	0.15 + 0.3 I	0.15 + (0.3 × 1.5) I	0.15 + (0.3 × 0.5) I
Std of Turning angle	°	90 – 85I	90 – (85 × 1.05) I	90 – (85 × 0.95) I
Jump	% of the population	0.05 + 0.55I	0.05 + (0.55 × 1.5)I	0.05 + (0.55 × 0.5) I
Sink (top layer)	% of the population	0.5 – 0.45I	0.5 – (0.45 × 1.1)I	0.5 – (0.45 × 0.9) I
Sink (bottom layer)	% of the population	0.1 – 0.09I	0.1 – (0.09 × 1.1)I	0.1 – (0.09 × 0.9) I

Table 4.3. The averaged percentage stress response changes (in % slope) and the resulting vertical distribution weighted mean depth (WMD), and total time spent in hypoxia (TIH), predation (TIP), or overall stress (TIS) patch ($I > 0.5$) were calculated after a 6-hr simulation compared with the default setting.

Behavior changes	Speed		Jump		Sink		Turn	
	+50%	-50%	+50%	-50%	+10%	-10%	+5%	-5%
WMD	-6.3%	0.9%	-4.0%	0.0%	-0.1%	-0.9%	-2.2%	-0.2%
0 - 10m	7.3%	2.8%	6.4%	7.7%	0.5%	14.2%	5.8%	8.6%
10 - 15m	-2.6%	-1.0%	-2.3%	-2.8%	-0.2%	-5.2%	-2.1%	-3.1%
TIP	-16.4%	44.2%	-6.3%	19.9%	-1.6%	-7.0%	-8.3%	20.1%
TIH	8.2%	-8.3%	3.9%	2.0%	-5.0%	-1.0%	5.4%	-2.1%
TIS	-8.9%	28.3%	-3.2%	14.5%	-2.6%	-5.2%	-4.2%	13.4%

Figure 4.1. The vertical profile of simulated hypoxia in moderate (blue) and severe hypoxia (red) themes ($x = 50$ cm, $y = 50$ cm, $z = 0 : 200$ cm). The comparative intensity of hypoxia gradually increased from 0 at mid-depth (10 m) to 1 at the bottom in the moderate hypoxia scenario (a), or quickly increased to 0.8 at 15 m and then slowly increased to 1 at the bottom in the severe hypoxia scenario (b).

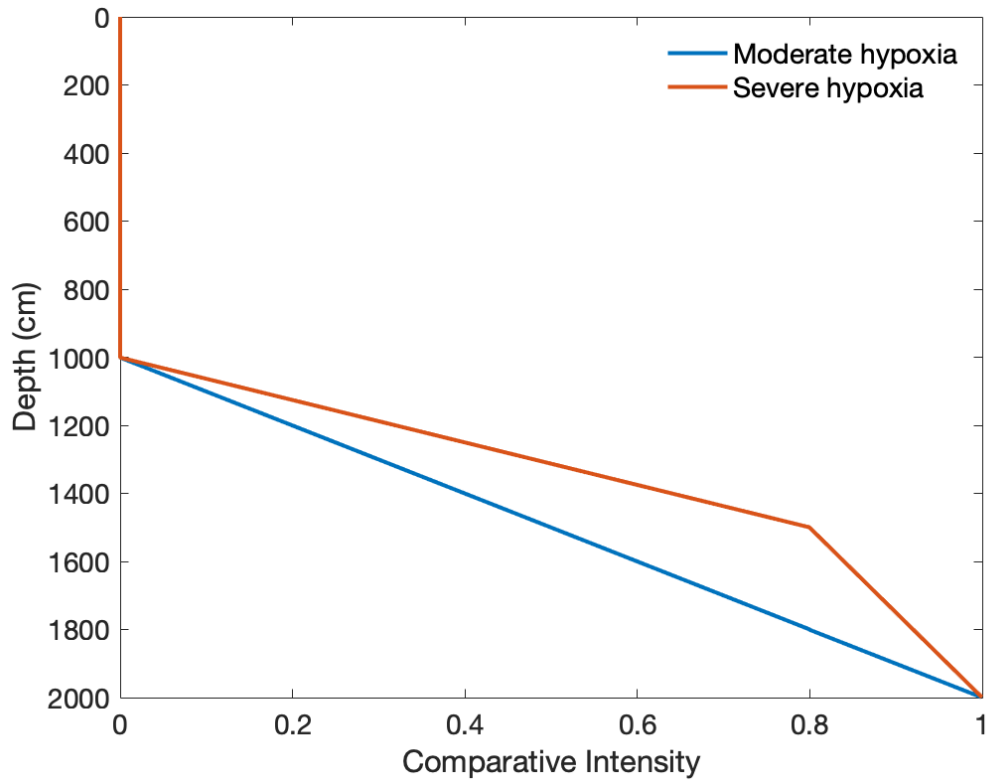
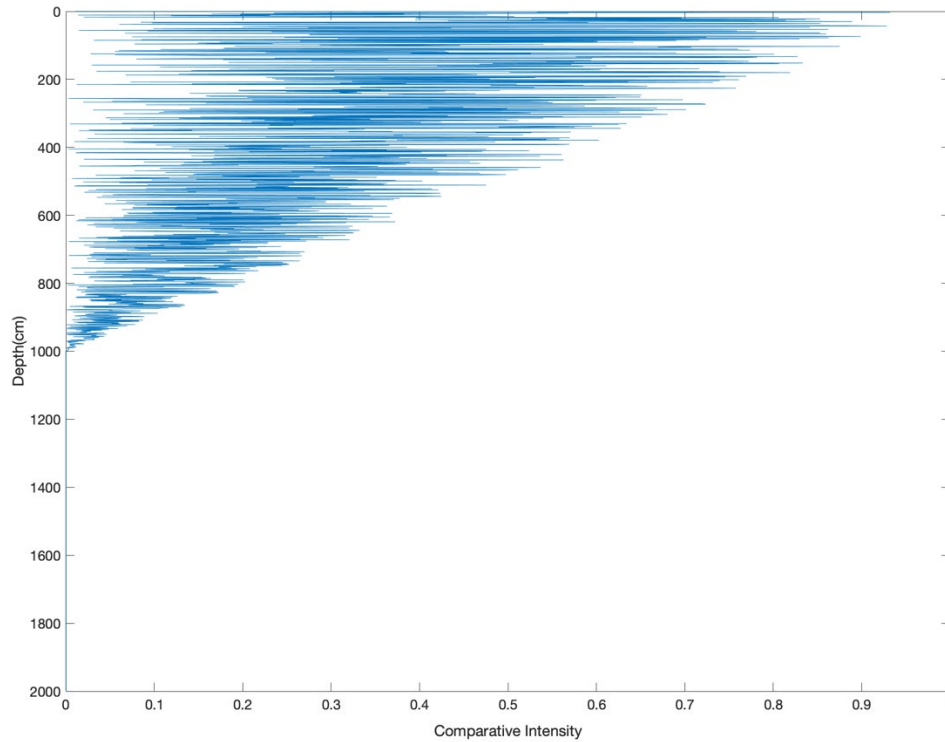


Figure 4.2. An example vertical profile of ctenophore predation stress (e.g., $x = 5$ cm, $y = 50$ cm, $z = 0 - 200$ cm). The comparative maximum intensity of predation stress increased linearly from 0 at mid-depth (100 cm) to 1 at the surface, and the maximum intensity at each vertical grid point was multiplied by a random number to generate stochasticity.



Note: the exact distribution was different in each simulation run due to the random number generator.

Figure 4.3. The combined stress field of the no hypoxia (a), moderate hypoxia (b) and severe hypoxia (c) scenarios. In all cases, predation stress maxima linearly increased from 10 m to surface with stochastic variability within each grid cell, and hypoxia varied according to the scenario. Colors indicate comparative stress intensity (0 – 1).

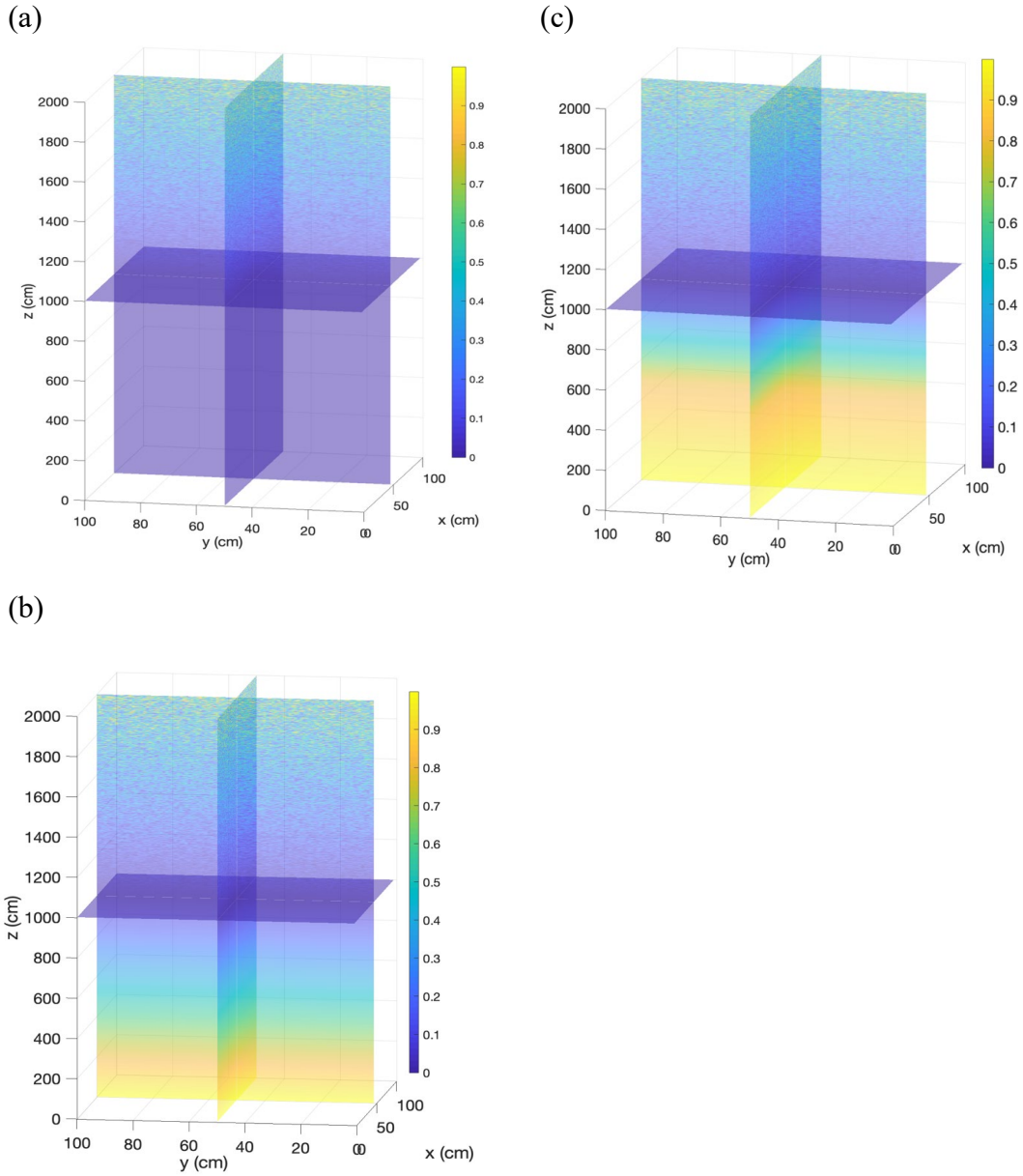


Figure 4.4. Changes in vertical distribution during 6-hr simulations without hypoxia (control). Green indicated well-mixed water above 100 cm, light and dark blue indicated water below 100 cm and below 180 cm.

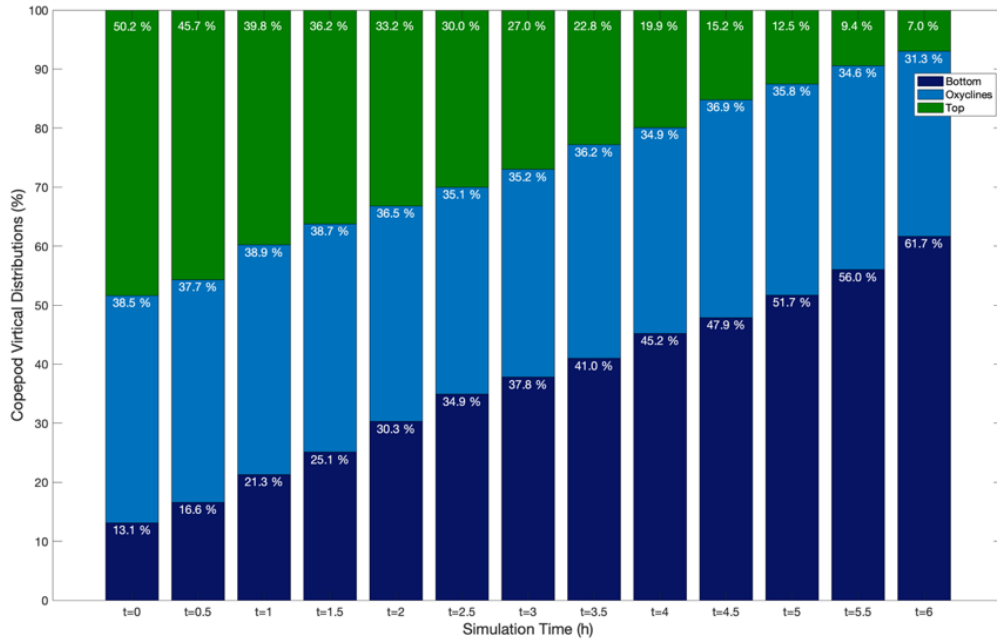


Figure 4.5. The vertical distribution changes during 6-hr simulations under (a) moderate hypoxia and (b) severe hypoxia. Red indicates hypoxia stressor ($I > 0.8$), yellow indicates the oxycline zone ($0 < I < 0.8$), and green ($I = \text{random}$) indicates the well-mixed region with predators with stress intensity linearly increases with random perturbations from mid-depth (10 m) toward the surface.

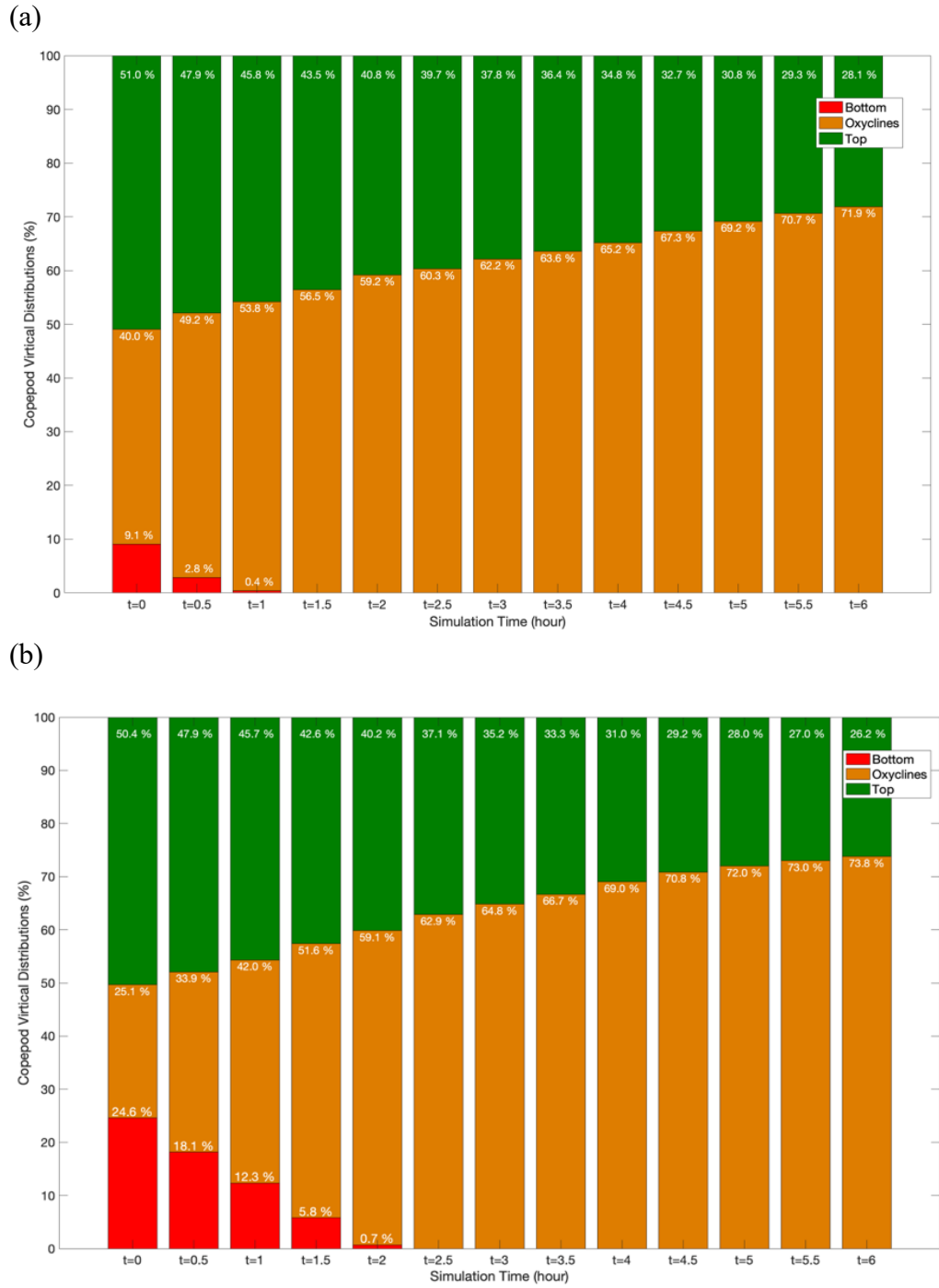


Figure 4.6. The average weighted mean depth (a) and total time spent in hypoxia (b) or predation (c) stress zone ($I > 0.5$) after 6-hr simulation of the no hypoxia, moderate hypoxia, and severe hypoxia scenario.

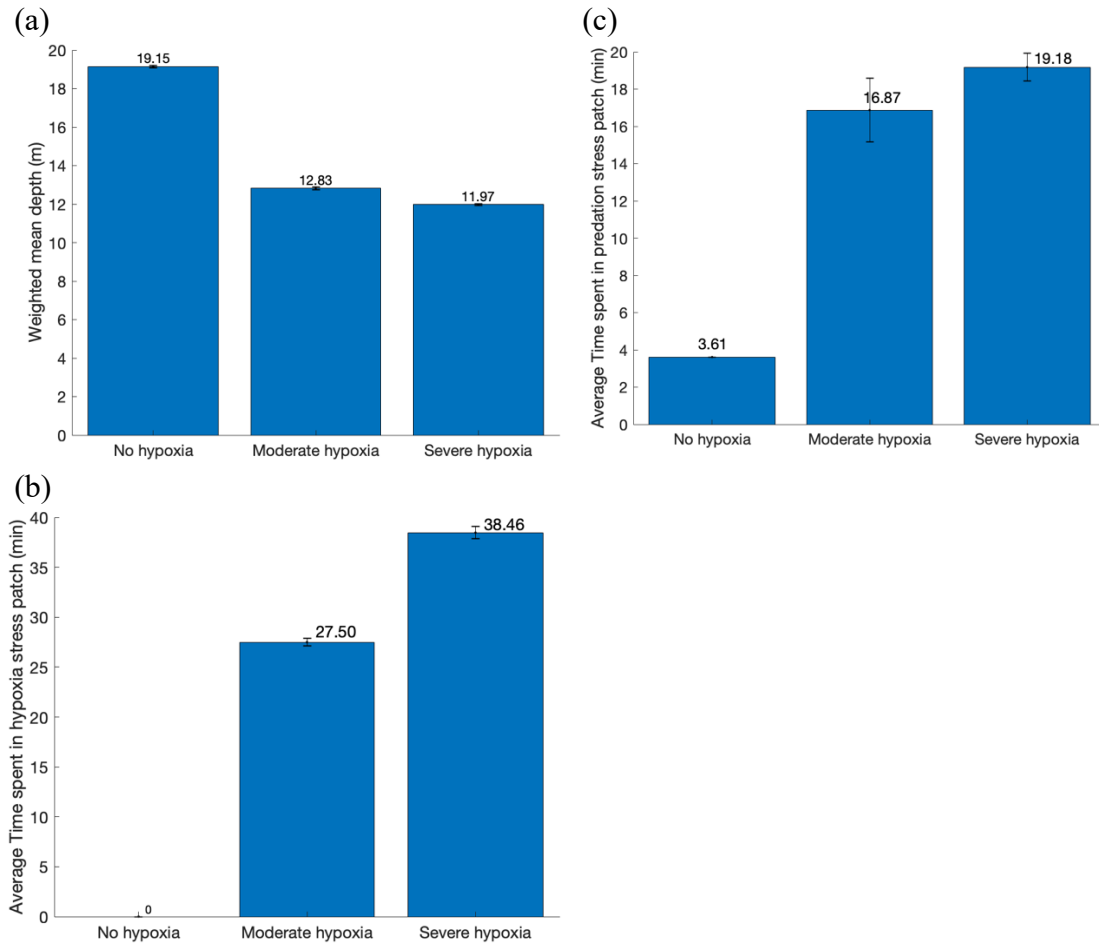


Figure 4.7. The final distributions after 6-hr simulations under three scenarios: (a) no hypoxia, (b) moderate hypoxia, and (c) severe hypoxia

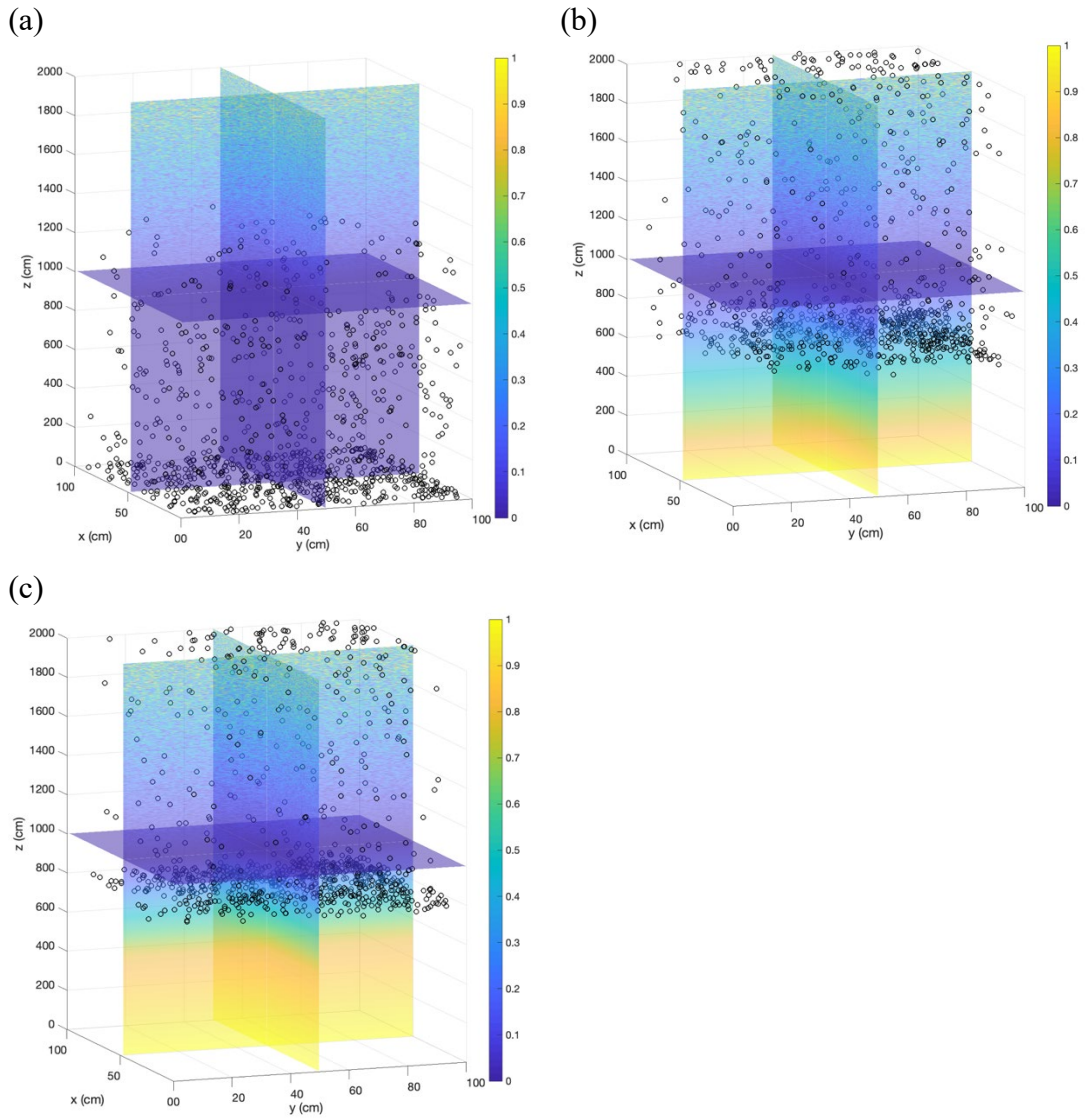


Figure 4.8. The average time spent in hypoxia or predation stress zone ($I > 0.5$) under severe hypoxia scenario with more (blue) or less (green) responsiveness toward stressors compared with the default (red) behavior. Numbers on the labels indicates percent change in slopes compared with the default behavior, and the text indicates which parameter was adjusted.

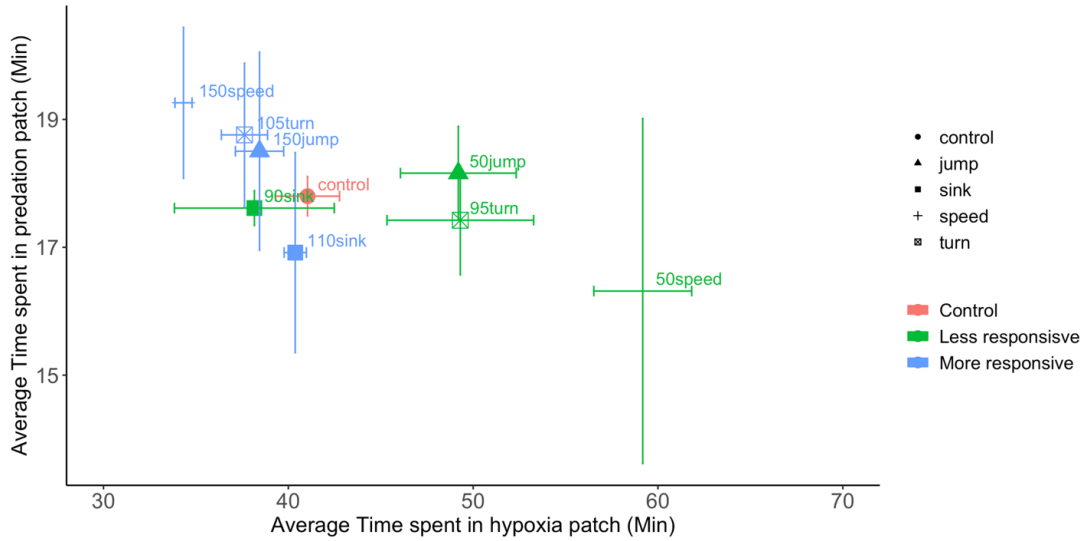


Figure 4.9. (a) Changes in the vertical distribution of simulated copepods and (b) the final distribution in a 6-hr simulation if the sinking rate was 10 – 80%. The swimming speed, turning angle, and jumping rate were the same as the default (shown in Figure 4.5b).

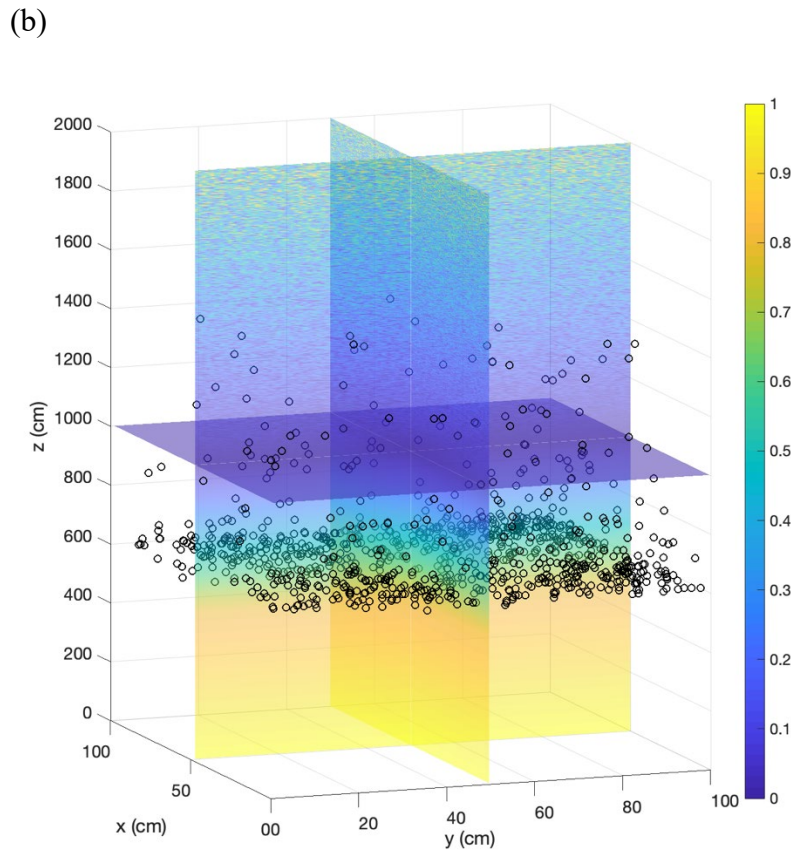
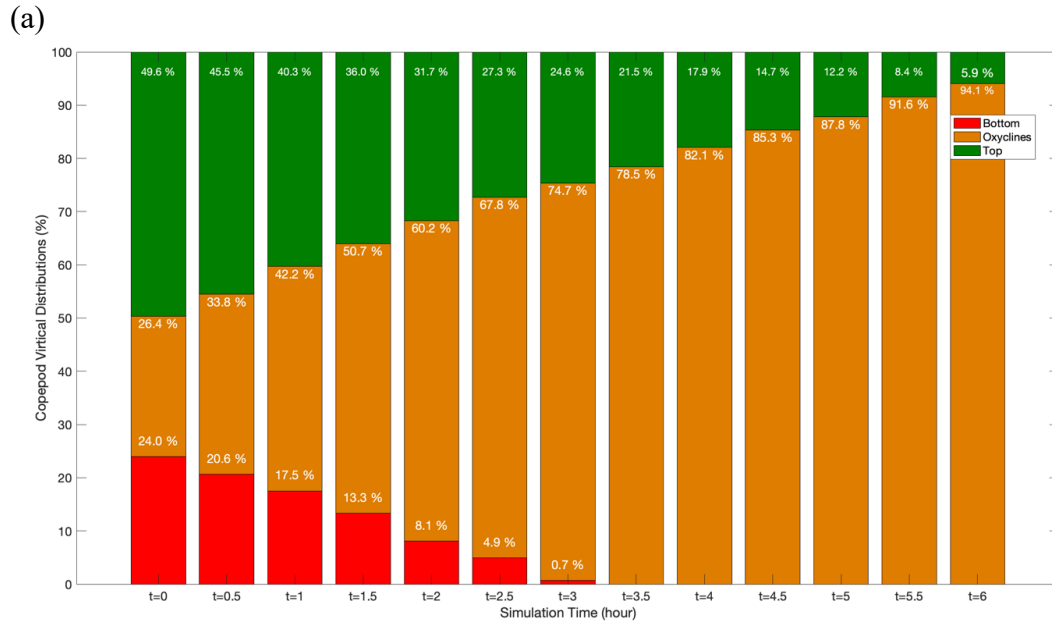


Figure 4.10. (a) Changes of copepod vertical distribution and (b) the final distribution during a 6-hr simulation under the severe hypoxia theme when the sinking rate angle was 1 – 5% (instead of 1 – 50%) and the rest responses were the same as the default.

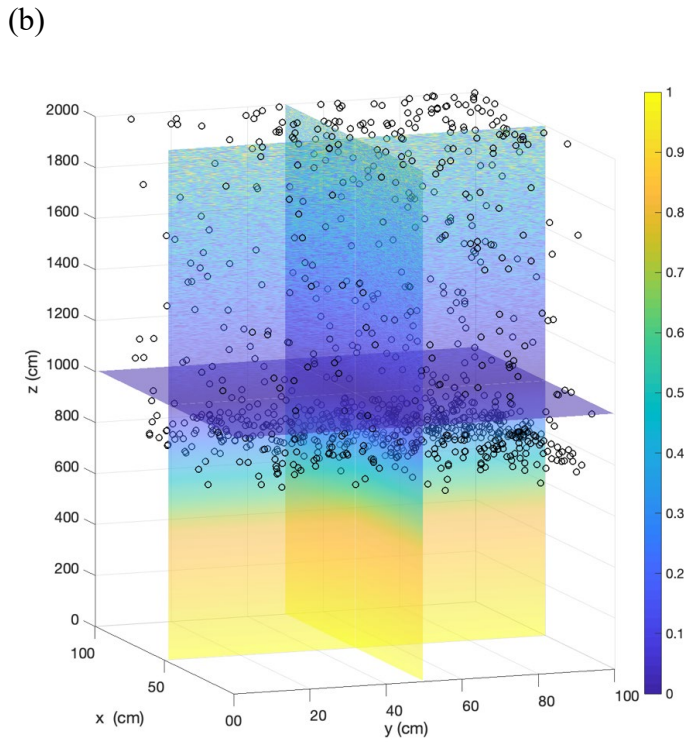
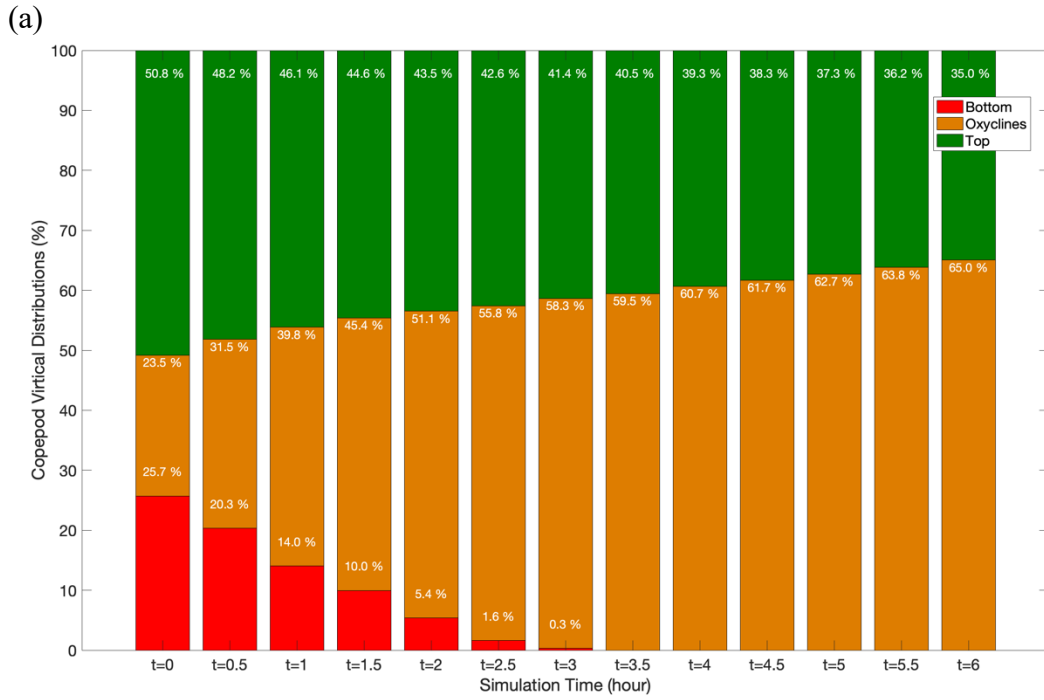
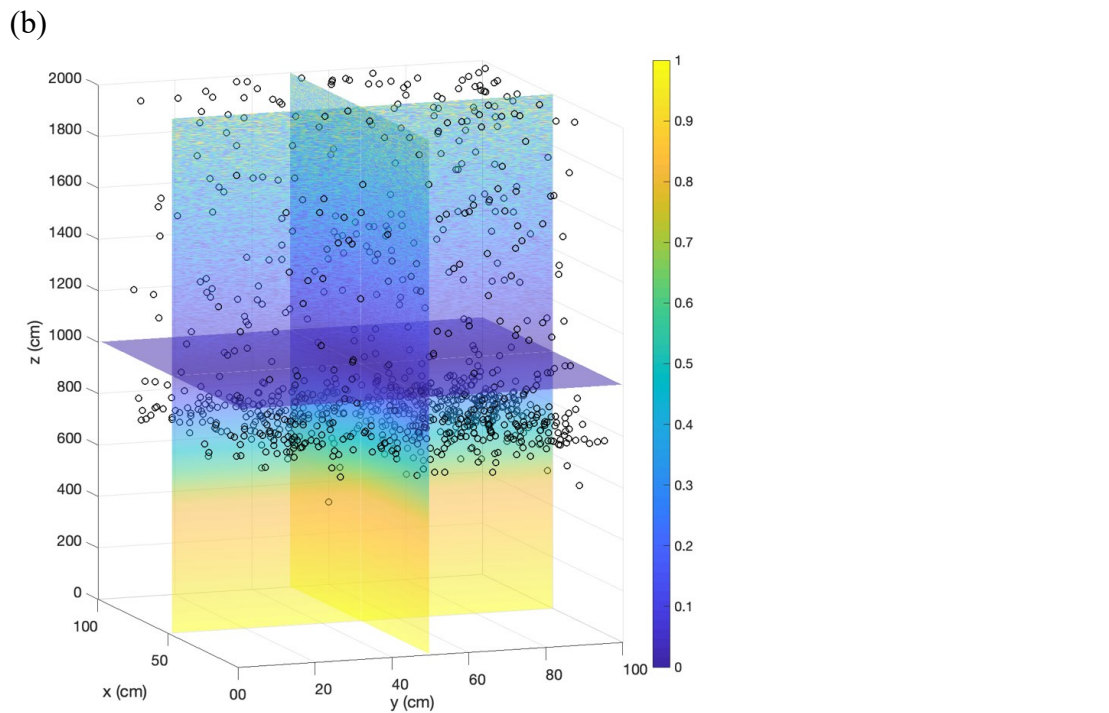
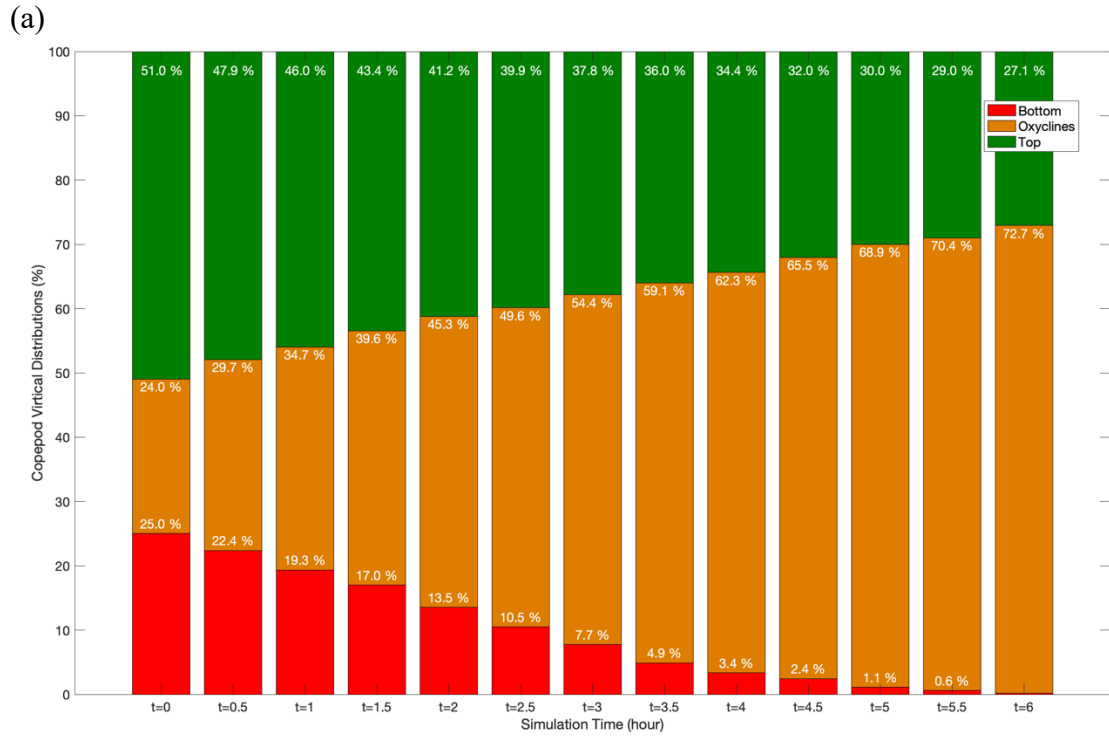


Figure 4.11. (a) The changes of copepod vertical distribution and (b) the final distribution during a 6-hr simulation under the severe hypoxia theme when the minimum turning angle was 30 ° (instead of 5°) and the rest responses were the same as the default.



Chapter Five: Conclusion and Future Research

This dissertation filled a gap in our current knowledge of zooplankton ecology by 1) quantifying the direct and indirect impact of hypoxia on the zooplankton foodweb; 2) untangling the interactions between seasonality and hypoxia on the zooplankton community; 3) elucidating the dynamics of bottom-up and top-down effects of hypoxia on zooplankton and specifying the timing, magnitude, and succession different components of the foodweb; and 4) improving our understanding of the role of zooplankton behavior on vertical distributions and overall survival by illustrating that behavior changes under hypoxia can increase predation risk. Overall this study improved the understanding of how ecosystems change under hypoxia and employed novel methods to investigate the connection between individual responses on population ecology.

Conclusion

My study addressed why zooplankton are less abundant when the bottom waters of the Chesapeake Bay are hypoxic. This question was addressed from different perspectives, including bottom-up effects (direct increases in mortality due to hypoxia), top-down effects (enhanced predation under hypoxia), and behavior changes (different responses to predatory and hypoxic stressors). Environmental and animal abundance data from six week-long research cruises in the main stem of

Chesapeake Bay were conducted from summer to autumn in 2010 and 2011, and results from those cruises indicated that species- and temperature-specific oxygen requirements should be considered when evaluating oxygen deficiency because the impact of oxygen varies with both temperature and salinity, as these factors affect both organism metabolism and dissolved oxygen solubility.

Both hypoxia and jellyfish blooms are most prevalent in summer when copepod populations are often at an annual minimum decline. Because warmer temperature has important effects on the abundance and natural mortality of prey and predators, it was necessary to isolate the effects of hypoxia from seasonal effects to understand the impact of hypoxia on zooplankton populations and interactions. To do this, data were grouped according to the results of a PCA analysis on hydrographic data, and comparisons were made between high and low dissolved oxygen conditions within specific temperature groups. The statistical analyses indicated that both copepod and bay anchovy concentrations were lower under more hypoxic conditions, but comb jellyfish and bay nettle concentrations were higher. This evidence indicated that the jellyfish blooms which are often concurrent with summer hypoxia are not purely coincident, and that gelatinous zooplankton may have an advantage under a hypoxic environment. My analysis also showed that both copepod nonpredatory mortality were higher under hypoxic conditions, suggesting direct hypoxic effects on copepod populations. Both jellyfish predation and fish predation were higher in hypoxic conditions, even when predator concentrations were similar, supporting the assertion that the increased predation under hypoxia was not solely due to predator

phenology or abundance. Thus, both seasonality and hypoxia play role in zooplankton populations and interactions.

This study indicated that both bottom-up and top-down effects contributed to observed decreases in copepod abundance in the presence of hypoxia, and that the bottom-up and top-down effects of hypoxia were not always equally weighted. In spring, when the major predators of copepods were not yet abundant, nonpredatory factors were the major factor affecting population decreases. In summer and autumn, predatory factors became more important and increased with the severity of hypoxia. Predator succession was observed as well: juvenile anchovy predation caused copepod decreases under moderate hypoxia, and ctenophore predation caused copepod decreases under warm and severe hypoxia.

An individual-based model was then built to test whether behavior changes under hypoxia could lead to increased predation. My simulations indicated that by avoiding bottom hypoxia, copepods increased their predation risk by aggregating at a shallower depth, supporting my field observations that predation can increase under hypoxic conditions. The model also elucidated the mechanisms for this finding, by demonstrating that increased swimming speed is critical for quickly escaping bottom hypoxia, and that sinking rate was important for aggregation. Tradeoffs between avoiding hypoxia and predation were revealed by analyzing the time spent by individuals in hypoxia and predation stress patches. Because there is not a universal escape strategy, model results also suggest that different avoidance strategies work best for different stressors. For example, swimming faster and straighter was best for escaping bottom hypoxia, but larger turning angles worked better for escaping

ambush predators. Although copepod behavior, predator behavior, and environmental conditions were simplified in this model, the model provided a novel way to explore ideas that are difficult to address with field research or lab experiments.

Future research

This study concluded that the copepod population was decreasing under hypoxia due to both increasing direct mortality and increasing predation, and that avoiding hypoxia played an important role in increasing predation risks. However, advection loss under hypoxia was not examined. Because the Chesapeake Bay is an estuary with two-layer circulation, copepods that avoid bottom hypoxia by remaining near the surface would be subject to seaward currents and could be relocated to southern regions of the Bay. Considering the effects of advection will help us understand the biophysical interaction of hypoxia for these animals. In addition, the potential differences between sexes and cryptic species were not examined in this study and would be a fruitful area of research. Previous research has shown that female *A. tonsa* avoid hypoxia more than male *A. tonsa* (Pierson et al. 2017). Hence, the importance of nonpredatory and predatory factors are likely different between the sexes. In addition, two reproductively-isolated cryptic *A. tonsa* species have been found in the Bay, and one prefers fresher water and another prefers more saline water (Plough et al. 2018). In addition, *A. tonsa* from different locations, Tampa Bay and the Chesapeake Bay, were shown to react to hypoxia differently (Stalder & Marcus 1997, Decker et al. 2003), so the two cryptic *A. tonsa* species in Chesapeake Bay may also respond to hypoxia differently. There is still more to

understand about this key copepod in the Bay and everywhere it is found, and its interactions with the environment and other species.

The individual-based model simulation in this study indicated different levels of tradeoffs among various stressor avoidance strategies, for example swimming faster was riskier than sinking less from the perspective of increasing ambush predation. Although the model developed here is much simplified compared with the actual ecosystem, this approach could help fill the gap between field research and lab experiments, because zooplankton responses are difficult to manipulate and repeat. In future modeling efforts, improvement could come from incorporating zooplankton behaviors like feeding, diel vertical migration, and reproduction, as well as parameterizing factors such as life stage, natural mortality, and more realistic predator behaviors (like chasing after prey aggregation). These enhancements also can be applied to different zooplankton species to help understand the mechanisms of animals reacting to multiple cues such as food, predators, mates, light, tides, and habitat, and how their behaviors affect their population dynamics, distribution, and interaction with other species and environment.

References

- Decker MB, Breitburg DL, Marcus NH (2003) Geographical differences in behavioral responses to hypoxia: local adaptation to an anthropogenic stressor? *Ecol Appl* 13:1104–1109.
- Pierson J, Slater W, Elliott D, Roman M (2017) Synergistic effects of seasonal deoxygenation and temperature truncate copepod vertical migration and distribution. *Mar Ecol Prog Ser* 575:57–68.

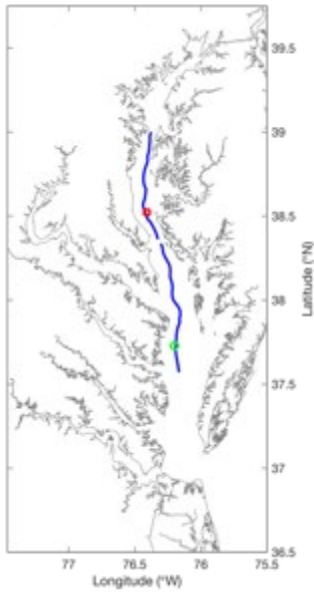
- Plough L, Fitzgerald C, Plummer A, Pierson J (2018) Reproductive isolation and morphological divergence between cryptic lineages of the copepod *Acartia tonsa* in Chesapeake Bay. *Mar Ecol Prog Ser* 597:99–113.
- Stalder LC, Marcus NH (1997) Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. *Mar Biol* 127:599–607.

Appendices

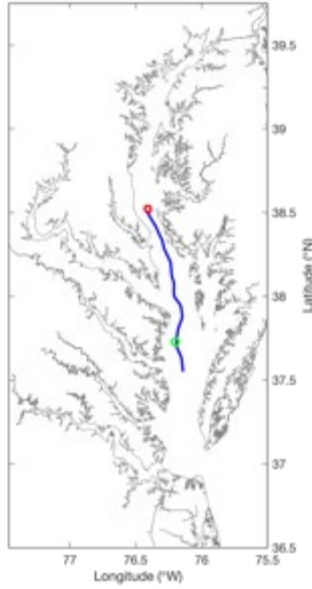
Environmental data collected by Scanfish and the SMS system of the *R/V Hugh R. Sharp* and fluorescence collected by CTD are presented here.

Appendix A. The sampling maps of the Dead Zone Zooplankton research project. Red squares indicated the North Station (38.528° N, 76.418° W), green circles indicated the South Station (37.738° N, 76.208° W), and the blue lines indicated the path of the Scanfish survey.

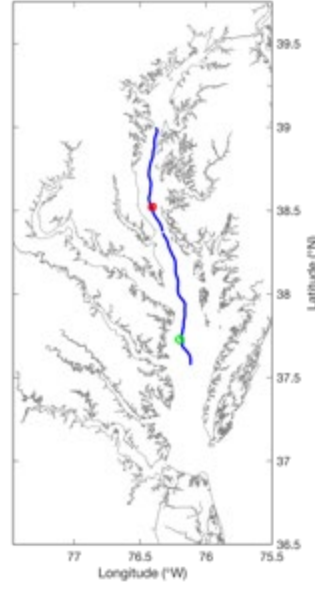
(a) 2010 May



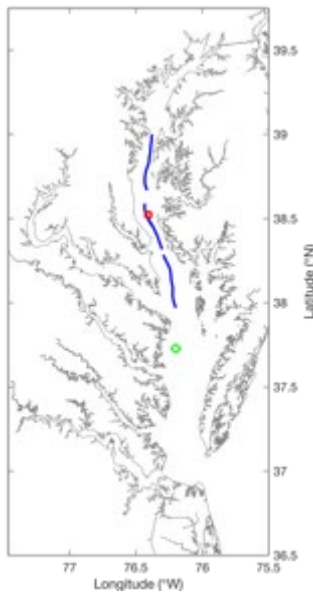
(b) 2010 Aug



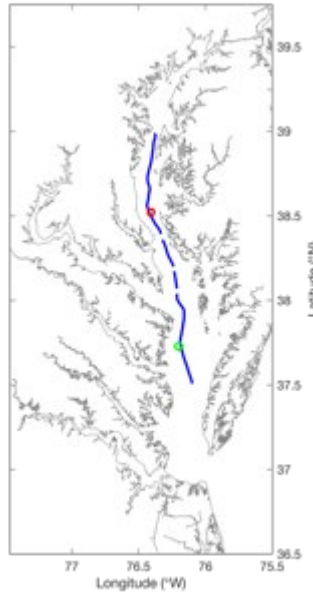
(c) 2010 Sep



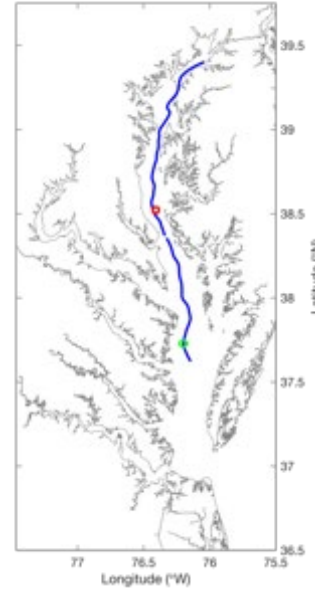
(d) 2011 May



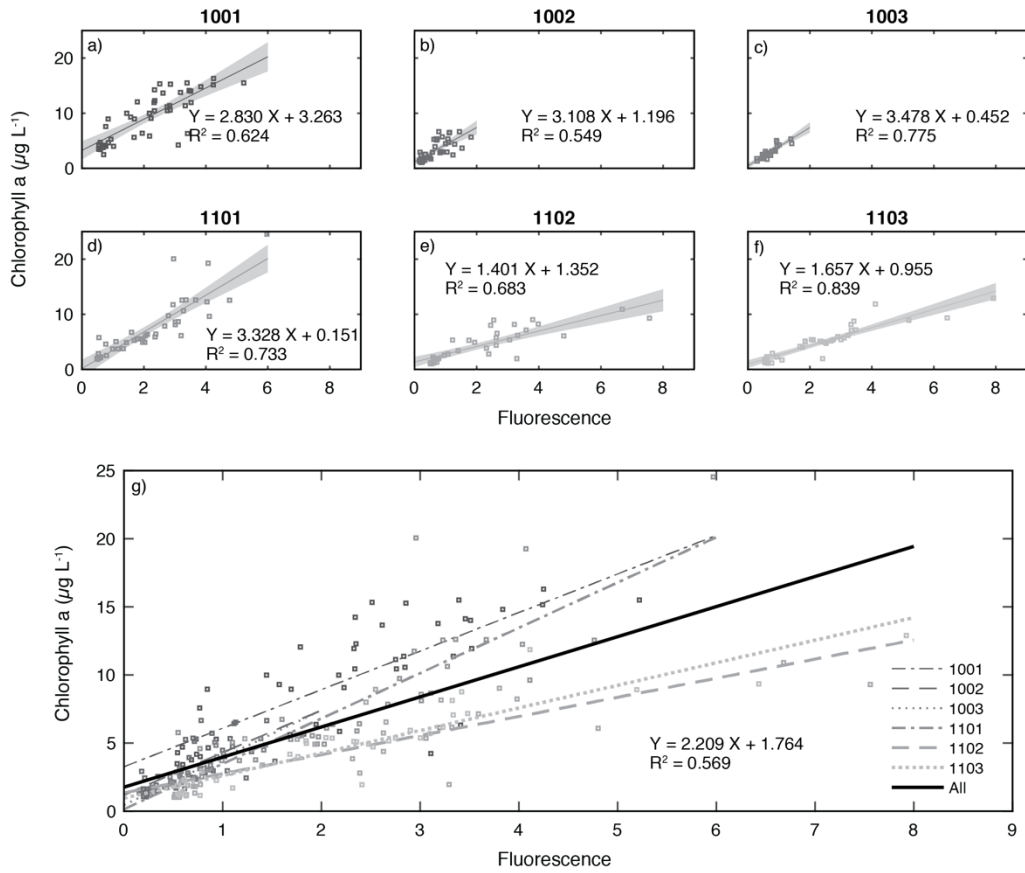
(e) 2011 Jul



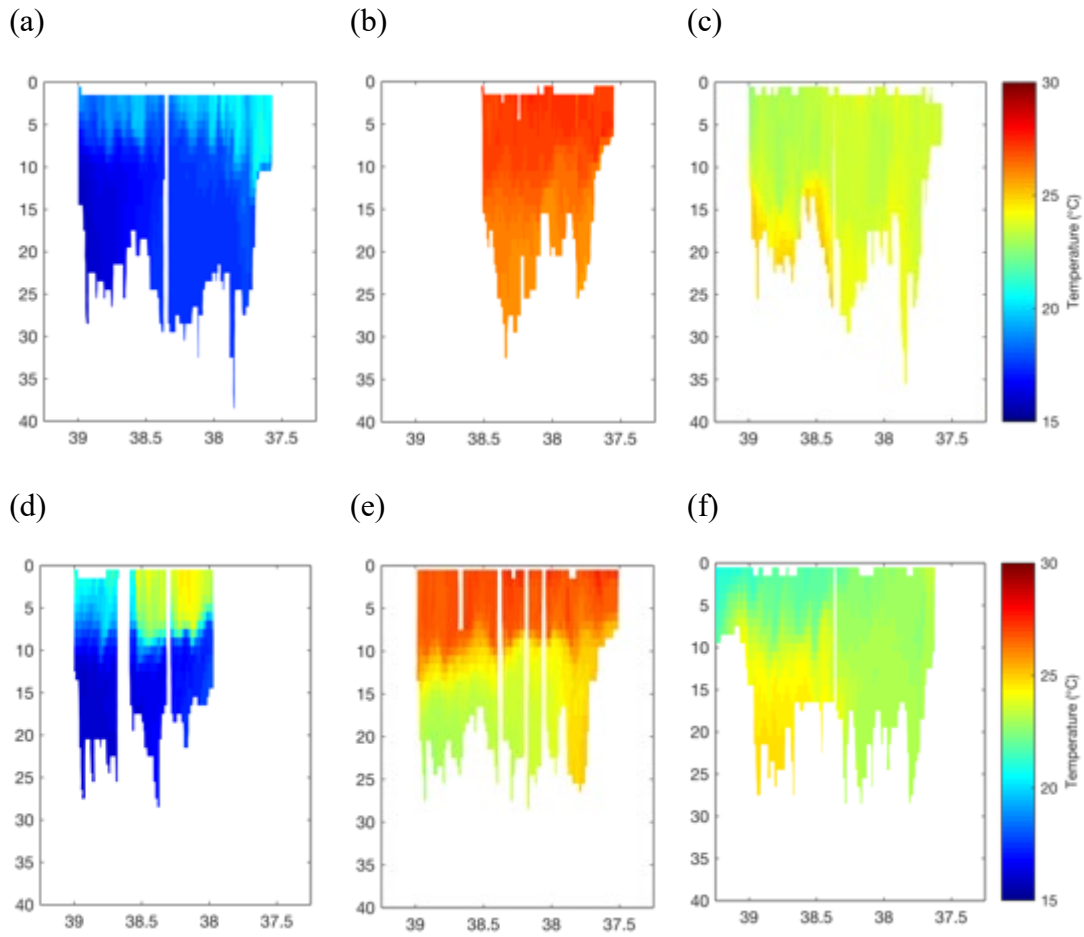
(f) 2011 Sep



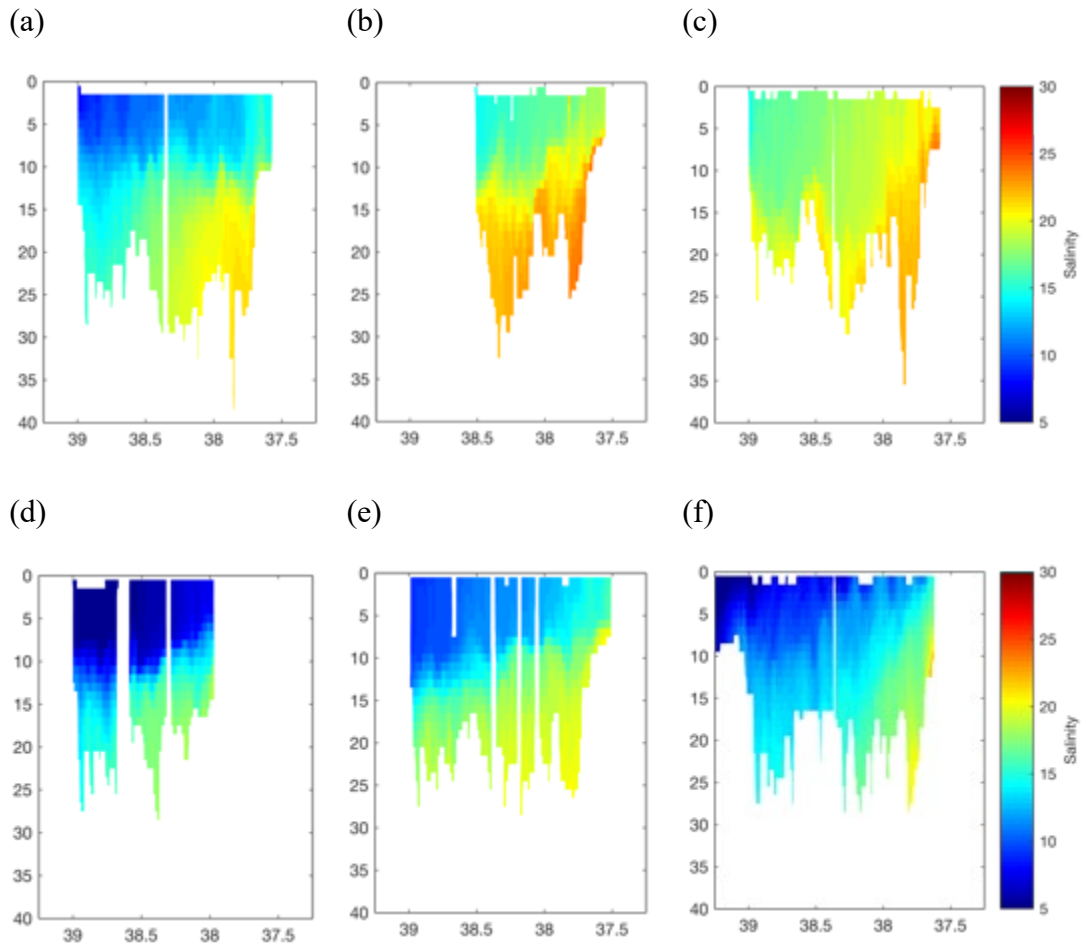
Appendix B. The relationship between relative fluorescence and Chlorophyll-a collected from the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise, and all cruises (g). Regression lines are shown with 95% confidence intervals (grey shading around lines), and linear equations with R^2 values are shown on each panel. The bottom panel includes regression lines for each cruise in addition to the pooled data, with the regression equation and R^2 on bottom panel corresponding to the pooled data.



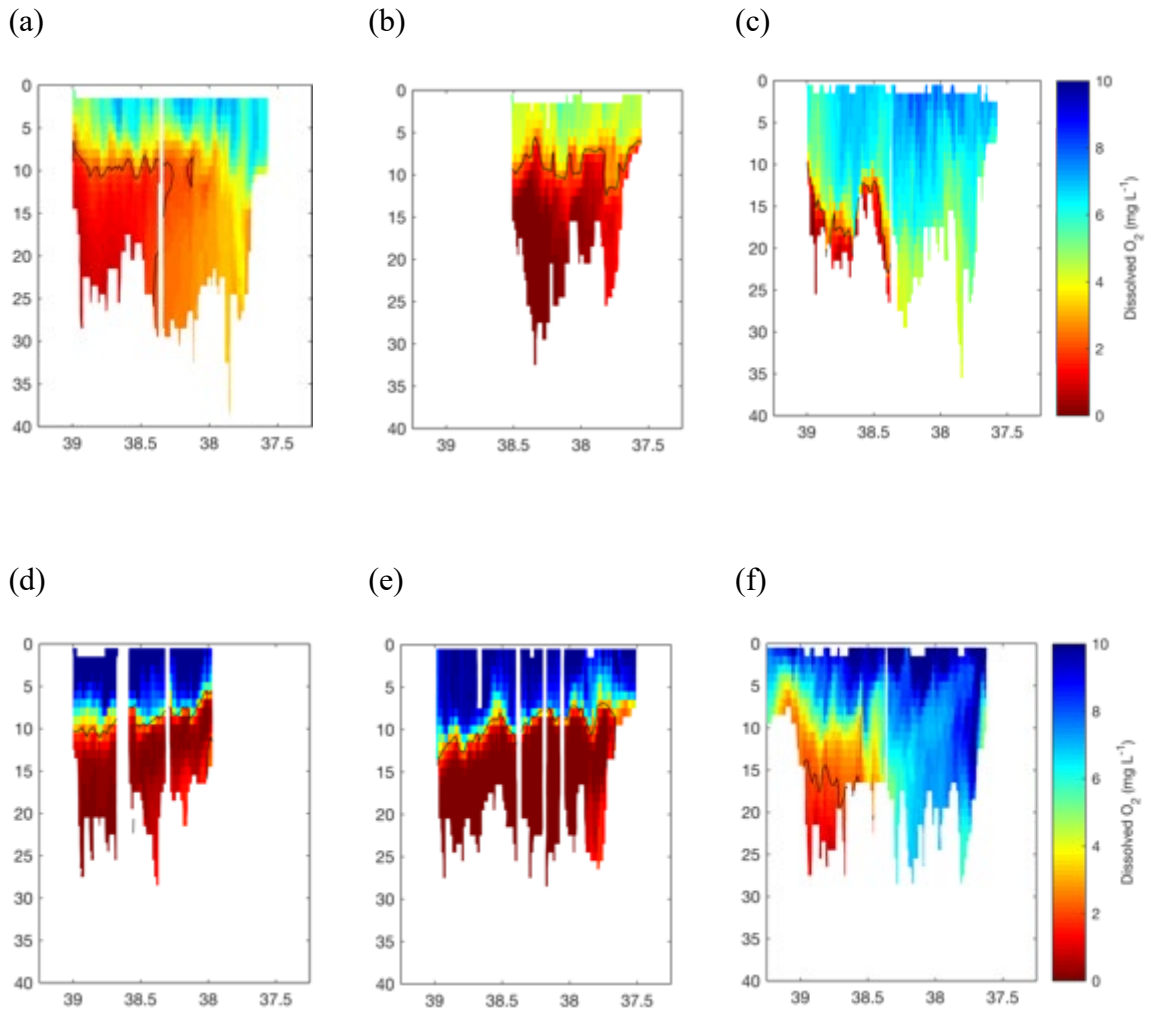
Appendix C. The temperature (color bar, C°) along the main channel of the Chesapeake Bay, collected by the Scanfish during the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise.



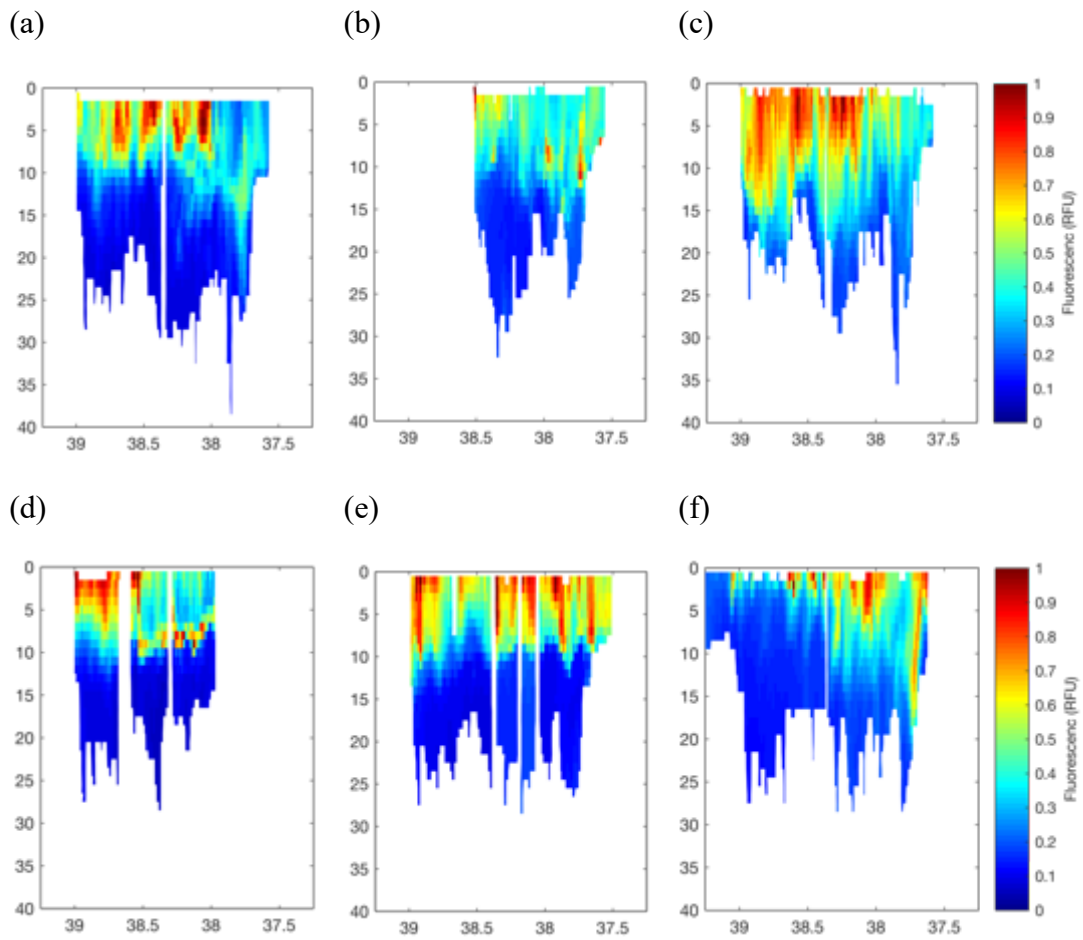
Appendix D. The salinity (color bar, PSU) along the main channel of the Chesapeake Bay, collected by the Scanfish during the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise.



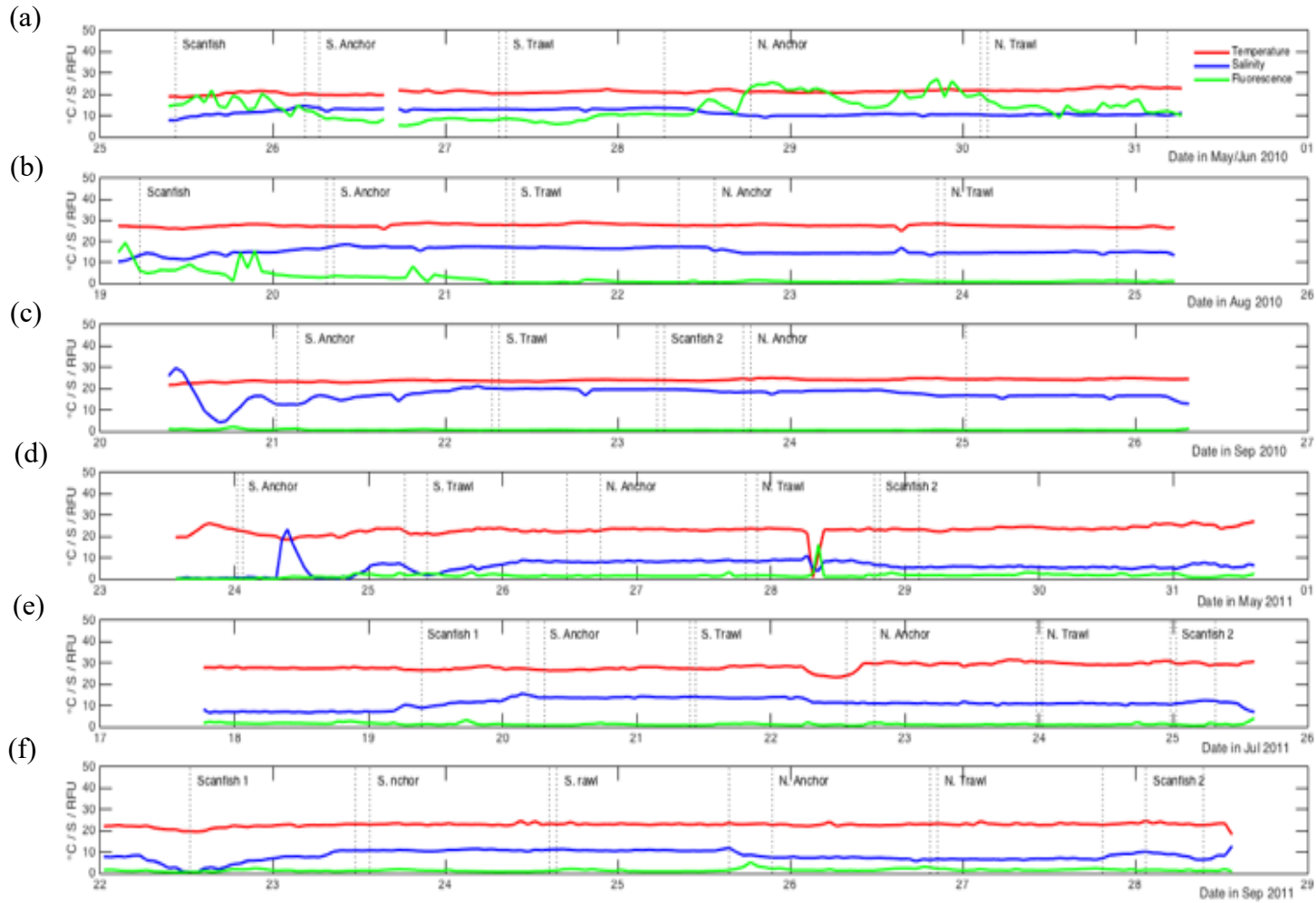
Appendix E. The dissolved oxygen (color bar, mg L^{-1}) along the main channel of the Chesapeake Bay, collected by the Scanfish during the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise. Black lines indicate $\text{DO} = 2 \text{ mg L}^{-1}$.



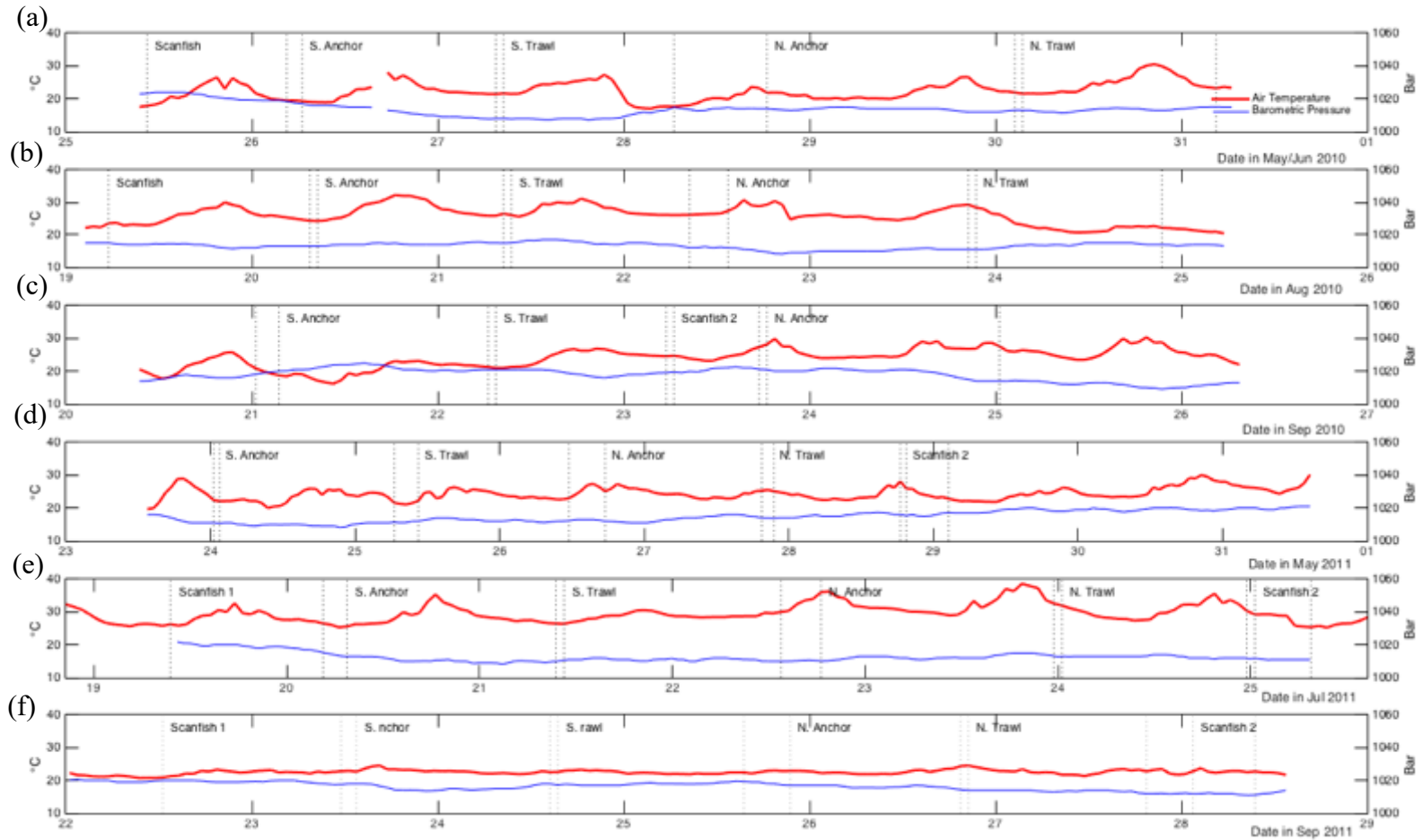
Appendix F. The relative fluorescence (color bar, RFU) along the main channel of the Chesapeake Bay, collected by the Scanfish during the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise.



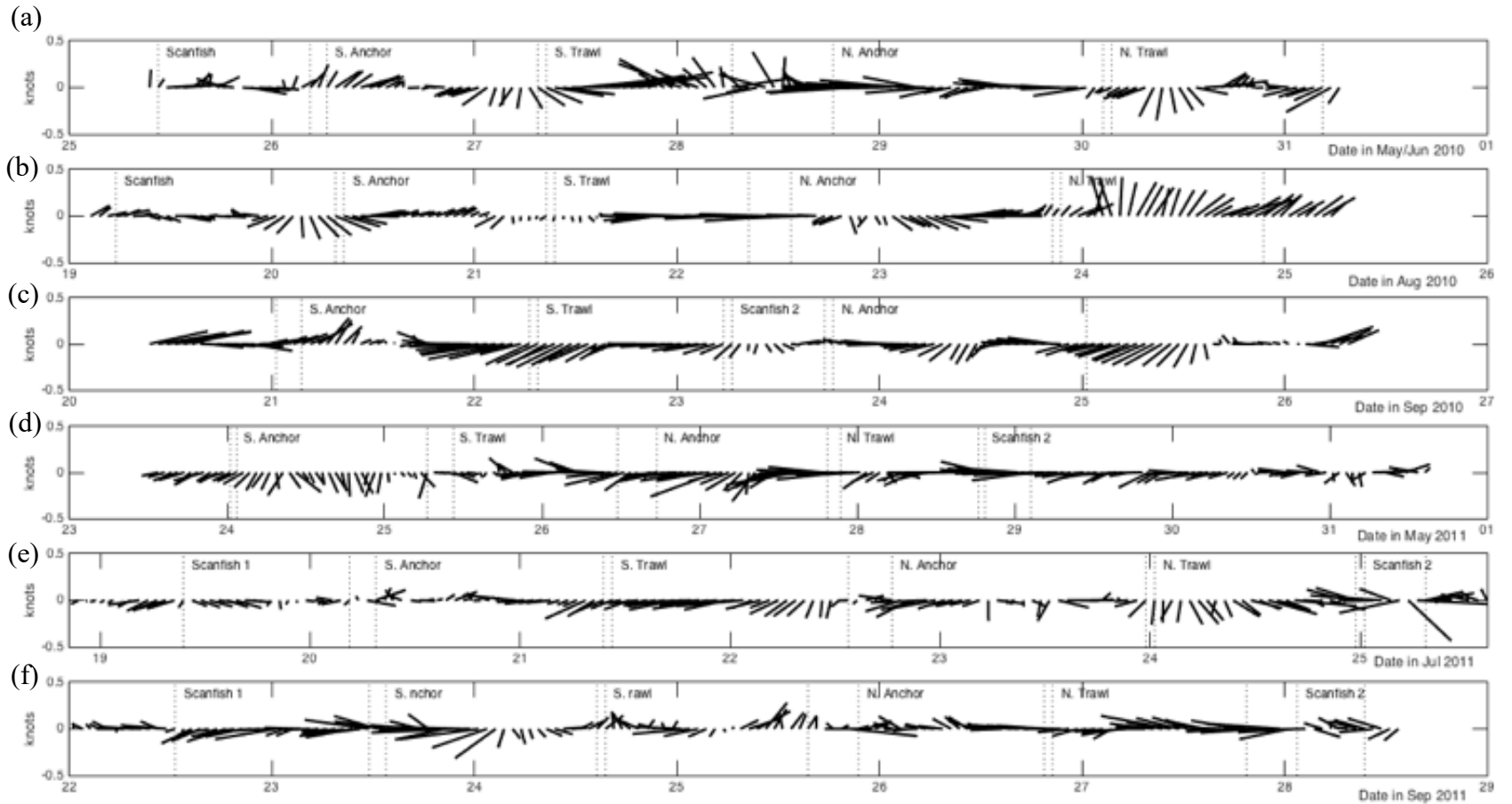
Appendix G. The water surface temperature (red), salinity (blue), and fluorescence (green) along the main channel of the Chesapeake Bay collected SMS system of the *R/V Hugh R. Sharp* when conducting Scanfish, southern anchor, south trawl, north anchor, and north trawl during the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise.



Appendix H. The air temperature (red, °C) and pressure (blue, bar) along the main channel of the Chesapeake Bay collected from the SMS system of the *R/V Hugh R. Sharp* when conducting Scanfish, southern anchor, south trawl, north anchor, and north trawl during the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise.



Appendix I. True wind directions and speed (knots) along the main channel of the Chesapeake Bay collected from the SMS system when conducting Scanfish, southern anchor, south trawl, north anchor, and north trawl during the 2010 May (a), August (b), September (c) and the 2011 May (d), July (e), September (f) cruise.



Bibliography

- Adamack A, Rose K, Breitburg D, Nice A, Lung W (2012) Simulating the effect of hypoxia on bay anchovy egg and larval mortality using coupled watershed, water quality, and individual-based predation models. *Mar Ecol Prog Ser* 445:141–160.
- Alekseev VR, Souissi A (2011) A new species within the *Eurytemora affinis* complex (Copepoda: Calanoida) from the Atlantic Coast of USA, with observations on eight morphologically different European populations. *Zootaxa* 2767:41–56.
- Auth TD (2003) Interannual and Regional Patterns of Abundance, Growth, and Feeding Ecology of Larval Bay Anchovy (*Anchoa Mitchilli*) in Chesapeake Bay. University of Maryland, College Park
- Baird D, Christian RR, Peterson CH, Johnson GA (2004) Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecol Appl* 14:805–822.
- Baird D, Ulanowicz RE (1989) The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol Monogr* 59:329–364.
- Barba AP (2015) Responses of the copepod *Acartia tonsa* to hypoxia in Chesapeake Bay. University of Maryland, College Park
- Bayha KM, Collins AG, Gaffney PM (2017) Multigene phylogeny of the scyphozoan jellyfish family Pelagiidae reveals that the common U.S. Atlantic sea nettle comprises two distinct species (*Chrysaora quinquecirrha* and *C. chesapeakei*). *PeerJ* 5:e3863.
- Bishop JW (1972) Ctenophores of the Chesapeake Bay. *Chesap Sci* 13:S98.
- Borum J (1996) Shallow waters and land/sea boundaries. *Eutrophication Coast Mar Ecosyst* 52:179–203.
- Breitburg D (2002) Effects of Hypoxia, and the Balance between Hypoxia and Enrichment, on Coastal Fishes and Fisheries. *Estuaries* 25:767–781.
- Breitburg D, Burrell R (2014) Predator-mediated landscape structure: seasonal patterns of spatial expansion and prey control by *Chrysaora quinquecirrha* and *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 510:183–200.
- Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240.

- Breitburg DL (1994) Behavioral response of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Mar Biol* 120:615–625.
- Breitburg DL (1992) Episodic Hypoxia in Chesapeake Bay: Interacting Effects of Recruitment, Behavior, and Physical Disturbance. *Ecol Monogr* 62:525–546.
- Breitburg DL, Adamack A, Rose KA, Kolesar SE, Decker B, Purcell JE, Keister JE, Cowan JH (2003) The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. *Estuaries* 26:280–297.
- Breitburg DL, Fulford RS (2006) Oyster-sea nettle interdependence and altered control within the Chesapeake Bay ecosystem. *Estuaries Coasts* 29:776–784.
- Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecol Monogr* 67:489–507.
- Breitburg DL, Pihl L, Kolesar SE (2001) Effects of low dissolved oxygen on the behavior, ecology and harvest of fishes: a comparison of the Chesapeake Bay and Baltic Kattegat systems. *Coast Hypoxia Consequences Living Resour Ecosyst*:241–267.
- Breitburg DL, Steinberg N, DuBean S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar Ecol Prog Ser* 104:235–246.
- Brodeur RD, Link JS, Smith BE, Ford MD, Kobayashi DR, Jones TT (2016) Ecological and economic consequences of ignoring jellyfish: a plea for increased monitoring of ecosystems. *Fisheries* 41:630–637.
- Brodeur RD, Suchman CL, Reese DC, Miller TW, Daly EA (2008) Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. *Mar Biol* 154:649–659.
- Buchheister A, Bonzek CF, Gartland J, Latour RJ (2013) Patterns and drivers of the demersal fish community of Chesapeake Bay. *Mar Ecol Prog Ser* 481:161–180.
- Burdick DS, Hartline DK, Lenz PH (2007) Escape strategies in co-occurring calanoid copepods. *Limnol Oceanogr* 52:2373–2385.
- Burrell VG, Van Engel WA (1976) Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River estuary. *Estuar Coast Mar Sci* 4:235–242.
- Buskey E, Lenz P, Hartline D (2002) Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. *Mar Ecol Prog Ser* 235:135–146.
- Buskey EJ (1994) Factors affecting feeding selectivity of visual predators on the copepod *Acartia tonsa*: locomotion, visibility and escape responses. *Hydrobiologia* 292:447–453.
- Calder DR (1971) Hydroids and hydromedusae of southern Chesapeake Bay.
- Capriulo GM, Smith G, Troy R, Wikfors GH, Pellet J, Yarish C (2002) The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. In:

- Nutrients and Eutrophication in Estuaries and Coastal Waters*. Orive E, Elliott M, de Jonge VN (eds) Springer Netherlands, Dordrecht, p 263–333
- Cargo DG, Schultz LP (1967) Further observations on the biology of the sea nettle and jellyfishes in Chesapeake Bay. *Chesap Sci* 8:209–220.
- Cervetto G, Gaudy R, Pagano M (1999) Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). *J Exp Mar Biol Ecol* 239:33–45.
- Chen G, Hare MP (2008) Cryptic ecological diversification of a planktonic estuarine copepod, *Acartia tonsa*. *Mol Ecol* 17:1451–1468.
- Chesney EJ (2008) Foraging behavior of bay anchovy larvae, *Anchoa mitchilli*. *J Exp Mar Biol Ecol* 362:117–124.
- Chesney EJ, Houde ED (1989) Laboratory studies on the effects of hypoxic waters on the survival of eggs and yolk-sac larvae of the bay anchovy, *Anchoa mitchilli*. Center for Environmental Science, Chesapeake Biological Laboratory.
- Childress JJ, Seibel BA (1998) Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *J Exp Biol* 201:1223–1232.
- Cohen JH, Forward RB (2009) Zooplankton diel vertical migration - a review of proximate control. *Oceanogr Mar Biol* 47:77–110.
- Condon RH, Decker MB, Purcell JE (2001) Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (*Chrysaora quinquecirrha*). *Jellyfish Blooms Ecol Soc Importance*:89–95.
- Condon RH, Steinberg DK, del Giorgio PA, Bouvier TC, Bronk DA, Graham WM, Ducklow HW (2011) Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proc Natl Acad Sci* 108:10225–10230.
- Cooper SR, Brush GS (1993) A 2,500-year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries Coasts* 16:617–626.
- Costello J, Loftus R, Waggett R (1999) Influence of prey detection on capture success for the ctenophore *Mnemiopsis leidyi* feeding upon adult *Acartia tonsa* and *Oithona colcarva* copepods. *Mar Ecol Prog Ser* 191:207–216.
- Coutant CC (1985) Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. *Trans Am Fish Soc* 114:31–61.
- Coutant CC, Benson DL (1990) Summer habitat suitability for striped bass in Chesapeake Bay: reflections on a population decline. *Trans Am Fish Soc* 119:757–778.
- Cowan JH, Houde ED (1993) Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. *Mar Ecol-Prog Ser* 95:55–55.
- Cowan JH, Houde ED (1992) Size-dependent predation on marine fish larvae by Ctenophores, Scyphomedusae, and Planktivorous fish. *Fish Oceanogr* 1:113–126.

- Cowan JL, Boynton WR (1996) Sediment-water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: seasonal patterns, controlling factors and ecological significance. *Estuaries Coasts* 19:562–580.
- Cuker B, Watson M (2002) Diel vertical migration of zooplankton in contrasting habitats of the Chesapeake Bay. *Estuaries Coasts* 25:296–307.
- Decker MB, Breitburg D, Purcell JE (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar Ecol Prog Ser* 280:163–72.
- Decker MB, Breitburg DL, Marcus NH (2003) Geographical differences in behavioral responses to hypoxia: Local adaptation to an anthropogenic stressor? *Ecol Appl* 13:1104–1109.
- Detwyler R, Houde ED (1970) Food selection by laboratory-reared larvae of the scaled sardine *Harengula pensacolatae* (Pisces, Clupeidae) and the bay anchovy *Anchoa mitchilli* (Pisces, Engraulidae). *Mar Biol* 7:214–222.
- Deutsch C, Brix H, Ito T, Frenzel H, Thompson L (2011) Climate-forced variability of ocean hypoxia. *Science* 333:336–339.
- Deutsch C, Ferrel A, Seibel B, Portner H-O, Huey RB (2015) Climate change tightens a metabolic constraint on marine habitats. *Science* 348:1132–1135.
- Diaz RJ (2001) Overview of hypoxia around the world. *J Environ Qual* 30:275–281.
- Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr Mar Biol Annu Rev* 33:245–03.
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *science* 321:926–929.
- Din B, Gunter G (1986) The food and feeding habits of the common bay anchovy, *Anchoa mitchilli* (Valenciennes). *PERTANIKA* 9:99–108.
- Dong Z, Liu D, Keesing JK (2010) Jellyfish blooms in China: dominant species, causes and consequences. *Mar Pollut Bull* 60:954–963.
- Eby LA, Crowder LB, McClellan CM, Peterson CH, Powers MJ (2005) Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Mar Ecol Prog Ser* 291:249–262.
- Ekau W, Auel H, Poertner H, Gilbert D (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7:1669–1699.
- Elliott DT (2010) Copepod carcasses, mortality and population dynamics in the tributaries of the Lower Chesapeake Bay. The College of William and Mary
- Elliott DT, Pierson JJ, Roman MR (2013a) Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. *J Plankton Res* 35:1027–1034.
- Elliott DT, Pierson JJ, Roman MR (2013b) Predicting the Effects of Coastal Hypoxia on Vital Rates of the Planktonic Copepod *Acartia tonsa* Dana. *PLoS ONE* 8:e63987.

- Elliott DT, Tang KW (2009) Simple staining method for differentiating live and dead marine zooplankton in field samples. *Limnol Oceanogr Methods* 7:585–594.
- Evans GT (1989) The encounter speed of moving predator and prey. *J Plankton Res* 11:415–417.
- Farmer L, Reeve MR (1978) Role of the free amino acid pool of the copepod *Acartia tonsa* in adjustment to salinity change. *Mar Biol* 48:311–316.
- Gerritsen J, Strickler JR (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *J Fish Board Can* 34:73–82.
- Gilbert OM, Buskey EJ (2005) Turbulence decreases the hydrodynamic predator sensing ability of the calanoid copepod *Acartia tonsa*. *J Plankton Res* 27:1067–1071.
- Gilly WF, Beman JM, Litvin SY, Robison BH (2013) Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone. *Annu Rev Mar Sci* 5:393–420.
- Glaspie CN, Clouse MA, Adamack AT, Cha Y, Ludsin SA, Mason DM, Roman MR, Stow CA, Brandt SB (2018) Effect of Hypoxia on Diet of Atlantic Bumpers in the Northern Gulf of Mexico. *Trans Am Fish Soc*.
- Glibert PM (2010) Long-term changes in nutrient loading and stoichiometry and their relationships with changes in the food web and dominant pelagic fish species in the San Francisco estuary, California. *Rev Fish Sci* 18:211–232.
- Glibert PM, Burkholder JM (2006) The complex relationships between increases in fertilization of the earth, coastal eutrophication and proliferation of harmful algal blooms. *Ecol Harmful Algae*:341–354.
- Gracey AY, Troll JV, Somero GN (2001) Hypoxia-induced gene expression profiling in the euryoxic fish *Gillichthys mirabilis*. *Proc Natl Acad Sci* 98:1993–1998.
- Granhag L, Moller LF, Hansson LJ (2011) Size-specific clearance rates of the ctenophore *Mnemiopsis leidyi* based on in situ gut content analyses. *J Plankton Res* 33:1043–1052.
- Gray JS, Wu RS, Or YY (2002) Effects of hypoxia and organic enrichment on the coastal marine environment. *Mar Ecol Prog Ser* 238:249–279.
- Grove M, Breitburg DL (2005) Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. *Mar Ecol Prog Ser* 301:185–198.
- Hagy JD, Boynton WR, Keefe CW, Wood KV (2004) Hypoxia in Chesapeake Bay, 1950–2001: Long-term change in relation to nutrient loading and river flow. *Estuaries* 27:634–658.
- Harding LW, Mallonee ME, Perry ES, Miller WD, Adolf JE, Gallegos CL, Paerl HW (2019) Long-term trends, current status, and transitions of water quality in Chesapeake Bay. *Sci Rep* 9.
- Haury L, Weihs D (1976) Energetically efficient swimming behavior of negatively buoyant zooplankton I: Zooplankton swimming behavior. *Limnol Oceanogr* 21:797–803.

- Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW (2011) High activity and Levy searches: jellyfish can search the water column like fish. *Proc R Soc B Biol Sci* 279:465–473.
- Heinle DR (1966) Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River estuary. *Chesap Sci* 7:59–74.
- Hirsch RM (2012) Flux of nitrogen, phosphorus, and suspended sediment from the Susquehanna River Basin to the Chesapeake Bay during Tropical Storm Lee, September 2011, as an indicator of the effects of reservoir sedimentation on water quality. US Geological Survey.
- Houde ED, Schekter RC (1981) Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. *Rapp Proces-Ver- Baux Reun Cons Int Pour Explora- Tion Mer*:441–453.
- Houde ED, Zastrow CE (1991) Bay anchovy, *Anchoa mitchilli*. In: *Habitat Requirements for Chesapeake Bay Living Resources. Chesapeake Bay Program, Annapolis, MD.*, 2nd ed. p 8.1-8.14
- Huse G, Fiksen Ø (2010) Modelling encounter rates and distribution of mobile predators and prey. *Prog Oceanogr* 84:93–104.
- Johnson W, Allen D, Ogburn M, Stancyk S (1990) Short-term predation responses of adult bay anchovies *Anchoa mitchilli* to estuarine zooplankton availability. *Mar Ecol Prog Ser* 64:55–68.
- Jonsson P, Tiselius P (1990) Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Mar Ecol Prog Ser* 60:35–44.
- Jung S, Houde ED (2004) Recruitment and spawning-stock biomass distribution of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay. *Fish Bull* 102:63–77.
- Jung S, Houde ED (2003) Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. *Estuar Coast Shelf Sci* 58:335–351.
- Justić D, Rabalais NN, Turner RE, Dortch Q (1995) Changes in nutrient structure of river-dominated coastal waters: stoichiometric nutrient balance and its consequences. *Estuar Coast Shelf Sci* 40:339–356.
- Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. *Mar Ecol Prog Ser* 205:43–59.
- Kemp WM, Boynton WR, Adolf JE, Boesch DF, Boicourt WC, Brush G, Cornwell JC, Fisher TR, Glibert PM, Hagy JD, others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Mar Ecol Prog Ser* 303:1–29.

- Kimmel DG, Boynton WR, Roman MR (2012) Long-term decline in the calanoid copepod *Acartia tonsa* in central Chesapeake Bay, USA: An indirect effect of eutrophication? *Estuar Coast Shelf Sci* 101:76–85.
- Kimmel DG, Roman MR (2004) Long-term trends in mesozooplankton abundance in Chesapeake Bay, USA: influence of freshwater input. *Mar Ecol Prog Ser* 267:71–83.
- Kjørboe T (2013) Attack or Attacked: the sensory and fluid mechanical constraints of copepods' predator-prey interactions. *Integr Comp Biol* 53:821–831.
- Kjørboe T (2011) How zooplankton feed: mechanisms, traits and trade-offs. *Biol Rev* 86:311–339.
- Kjørboe T, Jiang H (2012) To eat and not be eaten: optimal foraging behaviour in suspension feeding copepods. *J R Soc Interface* 10:20120693–20120693.
- Klebasko MJ (1991) Feeding ecology and daily ration of bay anchovy (*Anchoa mitchilli*) in the mid-Chesapeake Bay. University of Maryland at College Park
- Kolesar S, Breitbart D, Purcell J, Decker M (2010) Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: clearance rates and vertical habitat overlap. *Mar Ecol Prog Ser* 411:173–188.
- Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. *J Am Stat Assoc* 47:583–621.
- Lampert W (1989) The adaptive significance of diel vertical migration of zooplankton. *Funct Ecol* 3:21.
- Lance J (1965) Respiration and osmotic behaviour of the copepod *Acartia tonsa* in diluted sea water. *Comp Biochem Physiol* 14:155–165.
- Lange R, Staaland H, Mostad A (1972) The effect of salinity and temperature on solubility of oxygen and respiratory rate in oxygen-dependent marine invertebrates. *J Exp Mar Biol Ecol* 9:217–229.
- Leising A (2001) Copepod foraging in patchy habitats and thin layers using a 2-D individual-based model. *Mar Ecol Prog Ser* 216:167–179.
- Leising AW, Franks PJ (2000) Copepod vertical distribution within a spatially variable food source: A simple foraging-strategy model. *J Plankton Res* 22:999–1024.
- Leising AW, Pierson JJ, Cary S, Frost BW (2005) Copepod foraging and predation risk within the surface layer during night-time feeding forays. *J Plankton Res* 27:987–1001.
- Libes S (2011) Introduction to marine biogeochemistry. Academic Press.
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Lippson AJ, Lippson RL (2006) Life in the Chesapeake Bay. JHU Press.

- Lipton D, Hicks R (2003) The cost of stress: Low dissolved oxygen and economic benefits of recreational striped bass (*Morone saxatilis*) fishing in the Patuxent River. *Estuaries* 26:310–315.
- Ludsin SA, Zhang X, Brandt SB, Roman MR, Boicourt WC, Mason DM, Costantini M (2009) Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implications for food web interactions and fish recruitment. *J Exp Mar Biol Ecol* 381:S121–S131.
- Lutz RV, Marcus NH, Chanton JP (1992) Effects of low oxygen concentrations on the hatching and viability of eggs of marine calanoid copepods. *Mar Biol* 114:241–247.
- Lynam CP, Gibbons MJ, Axelsen BE, Sparks CA, Coetzee J, Heywood BG, Brierley AS (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Curr Biol* 16:R492.
- Lynam CP, Heath MR, Hay SJ, Brierley AS (2005) Evidence for impacts by jellyfish on North Sea herring recruitment. *Mar Ecol Prog Ser* 298:157–167.
- MacGregor JM, Houde ED (1996) Onshore-offshore pattern and variability in distribution and abundance of bay anchovy *Anchoa mitchilli* eggs and larvae in Chesapeake Bay. *Mar Ecol Prog Ser* Oldendorf 138:15–25.
- Mallin MA, Posey MH, Shank GC, McIver MR, Ensign SH, Alphin TD (1999) Hurricane effects on water quality and benthos in the cape fear watershed: natural and anthropogenic impacts. *Ecol Appl* 9:350–362.
- Mandic M, Todgham AE, Richards JG (2009) Mechanisms and evolution of hypoxia tolerance in fish. *Proc R Soc B Biol Sci* 276:735–744.
- Marcus NH, Richmond C, Sedlacek C, Miller GA, Oppert C (2004) Impact of hypoxia on the survival, egg production and population dynamics of *Acartia tonsa* Dana. *J Exp Mar Biol Ecol* 301:111–128.
- Matanoski J, Hood R, Purcell J (2001) Characterizing the effect of prey on swimming and feeding efficiency of the scyphomedusa *Chrysaora quinquecirrha*. *Mar Biol* 139:191–200.
- Matsumoto GI, Harbison GR (1993) In situ observations of foraging, feeding, and escape behavior in three orders of oceanic ctenophores: Lobata, Cestida, and Beroida. *Mar Biol* 117:279–287.
- Mayer AG (1910) *Medusae of the World: The Scyphomedusae*. Carnegie Institution of Washington.
- Mayor AG (1912) *Ctenophores of the Atlantic coast of North America*. Carnegie Institution of Washington.
- McClelland JW, Valiela I (1998) Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. *Mar Ecol Prog Ser*:259–271.

- McDougall TJ, Barker PM (2011) Getting started with TEOS-10 and the Gibbs Seawater (GSW) oceanographic toolbox. SCORIAPSO WG 127:1–28.
- McNamara M, Lonsdale D, Cerrato R (2014) Role of eutrophication in structuring planktonic communities in the presence of the ctenophore *Mnemiopsis leidyi*. Mar Ecol Prog Ser 510:151–165.
- McNamara ME, Lonsdale DJ, Aller RC (2013a) Elemental composition of *Mnemiopsis leidyi* A. Agassiz 1865 and its implications for nutrient recycling in a Long Island estuary. Estuaries Coasts 36:1253–1264.
- McNamara ME, Lonsdale DJ, Cerrato RM (2013b) Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores. Estuar Coast Shelf Sci 133:2–10.
- McNamara P (1955) Sea nettles observed to feed on sea walnuts in laboratory. Md Tidewater News 12:3–3.
- Miller RJ (1974) Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). Chesap Sci 15:1–8.
- Monteleone DM, Duguay LE (1988) Laboratory studies of predation by the ctenophore *Mnemiopsis leidyi* on the early stages in the life history of the bay anchovy, *Anchoa mitchilli*. J Plankton Res 10:359–372.
- Morales-Alamo R, Haven DS (1974) Atypical mouth shape of polyps of the jellyfish, *Aurelia aurita*, from Chesapeake Bay, Delaware Bay, and Gulf of Mexico. Chesap Sci 15:22–29.
- Murdy EO, Birdsong RS, Musick JA (1997) Fishes of Chesapeake Bay. Smithsonian Institution Press.
- Murphy RR, Kemp WM, Ball WP (2011) Long-term trends in Chesapeake Bay seasonal hypoxia, stratification, and nutrient loading. Estuaries Coasts 34:1293–1309.
- Najjar RG, Pyke CR, Adams MB, Breitburg D, Hershner C, Kemp M, Howarth R, Mulholland MR, Paolisso M, Secor D, Sellner K, Wardrop D, Wood R (2010) Potential climate-change impacts on the Chesapeake Bay. Estuar Coast Shelf Sci 86:1–20.
- Newberger TA, Houde ED (1995) Population biology of bay anchovy *Anchoa mitchilli* in the mid Chesapeake Bay. Mar Ecol Prog Ser 116:25–37.
- Newell RI (1988) Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*. Underst Estuary Adv Chesap Bay Res 129:536–546.
- Noone KJ, Diaz RJ, Sumaila UR (2013) Managing ocean environments in a changing climate: sustainability and economic perspectives, First edition. Elsevier, Burlington, MA.
- North EW, Houde ED (2004) Distribution and transport of bay anchovy (*Anchoa mitchilli*) eggs and larvae in Chesapeake Bay. Estuar Coast Shelf Sci 60:409–429.

- Ohman MD (1988) Behavioral responses of zooplankton to predation. *Bull Mar Sci* 43:530–550.
- Olesen NJ (1995) Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. *Mar Ecol Prog Ser Oldendorf* 124:63–72.
- Olney JE (1983) Eggs and early larvae of the bay anchovy, *Anchoa mitchilli*, and the weakfish, *Cynoscion regalis*, in lower Chesapeake Bay with notes on associated ichthyoplankton. *Estuaries Coasts* 6:20–35.
- Olson MM (1987) *Ecological studies in the middle reach of Chesapeake Bay*. pringer-Verlag.
- Oviatt CA (2004) The changing ecology of temperate coastal waters during a warming trend. *Estuaries* 27:895–904.
- Palinkas CM, Halka JP, Li M, Sanford LP, Cheng P (2014) Sediment deposition from tropical storms in the upper Chesapeake Bay: Field observations and model simulations. *Cont Shelf Res* 86:6–16.
- Parsons TR, Lalli CM (2002) Jellyfish population explosions: revisiting a hypothesis of possible causes. *La mer* 40:111–121.
- Peierls BL, Christian RR, Paerl HW (2003) Water quality and phytoplankton as indicators of hurricane impacts on a large estuarine ecosystem. *Estuaries* 26:1329–1343.
- Pierson J (2017) Zooplankton from hypoxic waters of Chesapeake Bay. 10.1575/1912/bco-dmo.687996
- Pierson J, Decker MB (2017) DeZoZoo Cruise Data. 10.1575/1912/bco-dmo.687984
- Pierson J, Houde ED (2015) Anchovy data of Chesapeake Bay. 10.1575/1912/bco-dmo.687979
- Pierson J, Slater W, Elliott D, Roman M (2017) Synergistic effects of seasonal deoxygenation and temperature truncate copepod vertical migration and distribution. *Mar Ecol Prog Ser* 575:57–68.
- Pierson JJ, Roman MR, Kimmel DG, Boicourt WC, Zhang X (2009) Quantifying changes in the vertical distribution of mesozooplankton in response to hypoxic bottom waters. *J Exp Mar Biol Ecol* 381:S74–S79.
- Plough LV, Fitzgerald C, Plummer A, Pierson JJ (2018) Reproductive isolation and morphological divergence between cryptic lineages of the copepod *Acartia tonsa* in Chesapeake Bay. *Mar Ecol Prog Ser* in press.
- Pollock MS, Clarke LMJ, Dubé MG (2007) The effects of hypoxia on fishes: from ecological relevance to physiological effects. *Environ Rev* 15:1–14.
- Powers DA (1980) Molecular ecology of teleost fish hemoglobins: strategies for adapting to changing environments. *Am Zool*:139–162.
- Purcell J, Decker M, Breitburg D, Broughton K (2014) Fine-scale vertical distributions of *Mnemiopsis leidyi* ctenophores: predation on copepods relative to stratification and hypoxia. *Mar Ecol Prog Ser* 500:103–120.

- Purcell JE (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. *Mar Ecol-Prog Ser* 87:65–76.
- Purcell JE (2009) Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* 616:23–50.
- Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu Rev Mar Sci* 4:209–235.
- Purcell JE (1988) Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. *Mar Ecol Prog Ser Oldendorf* 45:197–200.
- Purcell JE, Breitbart DL, Decker MB, Graham WM, Youngbluth MJ, Raskoff KA (2001a) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: *Coastal and Estuarine Studies*. p 77–100
- Purcell JE, Cowan Jr JH (1995) Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores. *Mar Ecol Prog Ser*:63–70.
- Purcell JE, Decker MB (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987-2000. *Limnol Oceanogr* 50:376–387.
- Purcell JE, Nemazie DA (1992) Quantitative feeding ecology of the hydromedusan *Nemopsis bachei* in Chesapeake Bay. *Mar Biol* 113:305–311.
- Purcell JE, Shiganova TA, Decker MB, Houde ED (2001b) The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. In: *Jellyfish Blooms: Ecological and Societal Importance*. Springer, p 145–176
- Purcell JE, White JR, Nemazie DA, Wright DA (1999) Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Mar Ecol Prog Ser* 180:187–196.
- Purcell JE, White JR, Roman MR (1994) Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. *Limnol Oceanogr* 39:263–278.
- Rabalais NN, Diaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J (2010) Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7:585–619.
- Reeve MR (1981) Large cod-end reservoirs as an aid to the live collection of delicate zooplankton. *Limnol Oceanogr* 26:577–580.
- Rhein M al, Rintoul SR, Aoki S, Campos E, Chambers D, Feely RA, Gulev S, Johnson GC, Josey SA, Kostianoy A, others (2013) Observations: ocean. *Clim Change*:255–315.
- Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol Evol* 24:312–322.

- Richmond C, Marcus NH, Sedlacek C, Miller GA, Oppert C (2006) Hypoxia and seasonal temperature: Short-term effects and long-term implications for *Acartia tonsa* dana. *J Exp Mar Biol Ecol* 328:177–196.
- Robinette HR (1983) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico): Bay anchovy and Striped anchovy.
- Robinson K, Ruzicka J, Decker MB, Brodeur R, Hernandez F, Quiñones J, Acha M, Uye S, Mianzan H, Graham W (2014) Jellyfish, Forage Fish, and the World’s Major Fisheries. *Oceanography* 27:104–115.
- Roman M, Zhang X, McGilliard C, Boicourt W (2005a) Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. *Limnol Oceanogr*:480–492.
- Roman MR, Boicourt WC, Kimmel DG, Miller WD, Adolf JE, Bichy J, Harding LW, Houde ED, Jung S, Zhang X (2005b) Chesapeake Bay plankton and fish abundance enhanced by Hurricane Isabel. *Eos Trans Am Geophys Union* 86:261.
- Roman MR, Brandt SB, Houde ED, Pierson JJ (2019) Interactive Effects of Hypoxia and Temperature on Coastal Pelagic Zooplankton and Fish. *Front Mar Sci* 6.
- Roman MR, Gauzens AL, Rhinehart WK, White JR (1993) Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnol Oceanogr* 38:1603–1614.
- Roman MR, Pierson JJ, Kimmel DG, Boicourt WC, Zhang X (2012) Impacts of hypoxia on zooplankton spatial distributions in the northern Gulf of Mexico. *Estuaries Coasts* 35:1261–1269.
- Rowshantabari M, Finenko GA, Kideys AE, Kiabi B (2012) Effect of temperature on clearance rate, daily ration and digestion time of *Mnemiopsis leidyi* from the southern Caspian Sea. *Casp J Env Sci* 10:157–167.
- Saiz E, Alcaraz M (1992) Free-swimming behaviour of *Acartia clausi* (Copepoda: Calanoida) under turbulent water movement. *Mar Ecol Prog Ser* 80:229–236.
- Schmitt FG, Seuront L (2001) Multifractal random walk in copepod behavior. *Phys Stat Mech Its Appl* 301:375–396.
- Schmitt FG, Seuront L, Hwang J-S, Souissi S, Tseng L-C (2006) Scaling of swimming sequences in copepod behavior: Data analysis and simulation. *Phys Stat Mech Its Appl* 364:287–296.
- Sedlacek C (2003) Effect Hypoxia has on Feeding and Egg Production Rates of *Acartia tonsa* Dana 1849 (Copepoda: Calanoida).
- Sellner KG, Sellner SG (2016) Copepod, Ctenophore, and Schyphomedusae Control in Structuring the Chesapeake Bay Summer Mesohaline Planktonic Food Web. In: *Aquatic Microbial Ecology and Biogeochemistry: A Dual Perspective*. Glibert PM, Kana TM (eds) Springer International Publishing, Cham, p 273–283

- Shahrestani S, Bi H (2018) Settlement and survival of *Chrysaora chesapeakei* polyps: implications for adult abundance. *Mar Ecol Prog Ser* 601:139–151.
- Shoji J, Kudoh T, Takatsuji H, Kawaguchi O, Kasai A (2010) Distribution of moon jellyfish *Aurelia aurita* in relation to summer hypoxia in Hiroshima Bay, Seto Inland Sea. *Estuar Coast Shelf Sci* 86:485–490.
- Shoji J, Masuda R, Yamashita Y, Tanaka M (2005a) Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*. *Mar Biol* 147:863–868.
- Shoji J, Masuda R, Yamashita Y, Tanaka M (2005b) Predation on fish larvae by moon jellyfish *Aurelia aurita* under low dissolved oxygen concentrations. *Fish Sci* 71:748–753.
- Singarajah KV (1969) Escape reactions of zooplankton: the avoidance of a pursuing siphon tube. *J Exp Mar Biol Ecol* 3:171–178.
- Slater WL, Pierson JJ, Decker MB, Houde ED, Lozano C, Seuberling J (2020) Fewer copepods, fewer anchovies, and more jellyfish: how does hypoxia impact the Chesapeake Bay zooplankton community? *Diversity* 12(1):35.
- Stalder LC, Marcus NH (1997) Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. *Mar Biol* 127:599–607.
- Steinberg DK, Condon RH (2009) Zooplankton of the York River. *J Coast Res*:66–79.
- Stevens PW, Blewett DA, Casey JP (2006) Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of hurricane Charley. *Estuaries Coasts* 29:997–1003.
- Stoecker DK, Hansen PJ, Caron DA, Mitra A (2017) Mixotrophy in the marine plankton. *Annu Rev Mar Sci* 9:311–335.
- Stone SL (1994) Distribution and abundance of fishes and invertebrates in Mid-Atlantic estuaries. US Department of Commerce, National Oceanic and Atmospheric Administration
- Sullivan BK, Keuren DV, Clancy M (2001) Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. *Hydrobiologia* 451:113–120.
- Svetlichny LS, Hubareva ES, Erkan F, Gucu AC (2000) Physiological and behavioral aspects of *Calanus euxinus* females (Copepoda: Calanoida) during vertical migration across temperature and oxygen gradients. *Mar Biol* 137:963–971.
- Taylor J (2003) Spatial overlap and distribution of anchovies (*Anchoa* spp.) and copepods in a shallow stratified estuary. *Aquat Living Resour* 16:191–196.

- Taylor JC, Rand PS, Jenkins J (2007) Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. *Mar Biol* 152:939–957.
- Team RC (2013) R: A language and environment for statistical computing.
- Thuesen EV (2005) Intragel oxygen promotes hypoxia tolerance of scyphomedusae. *J Exp Biol* 208:2475–2482.
- Thuesen EV, Rutherford LD, Brommer PL (2005) The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. *J Mar Biol Assoc U K* 85:627–633.
- Tinbergen N, Franck D, Impeken M (1967) An experiment on spacing-out as a defence against predation. *Behaviour* 28:307–320.
- Tinson S, Laybourn-Parry J (1985) The behavioural responses and tolerance of freshwater benthic cyclopoid copepods to hypoxia and anoxia. *Hydrobiologia* 127:257–263.
- Tiselius P (1992) Behavior of *Acartia tonsa* in patchy food environments. *Limnol Oceanogr* 37:1640–1651.
- Tiselius P, Jonsson P (1990) Foraging behaviour of six calanoid copepods: observations and hydrodynamic analysis. *Mar Ecol Prog Ser* 66:23–33.
- Uye S (2008) Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas. *Plankton Benthos Res* 3:125–131.
- Uye S (2011) Human forcing of the copepod–fish–jellyfish triangular trophic relationship. *Hydrobiologia* 666:71–83.
- Vargo SL, Sastry AN (1977) Acute temperature and low dissolved oxygen tolerances of brachyuran crab (*Cancer irroratus*) larvae. *Mar Biol* 40:165–171.
- Vazquez AV (1989) Energetics, trophic relationships and chemical composition of bay anchovy, *Anchoa mitchilli*, in the Chesapeake Bay. University of Maryland, College Park
- Waggett R, Buskey E (2007) Copepod escape behavior in non-turbulent and turbulent hydrodynamic regimes. *Mar Ecol Prog Ser* 334:193–198.
- Waggett R, Buskey E (2006a) Copepod sensitivity to flow fields: detection by copepods of predatory ctenophores. *Mar Ecol Prog Ser* 323:205–211.
- Waggett R, Costello JH (1999) Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*. *J Plankton Res* 21:2037–2052.
- Waggett RJ, Buskey EJ (2006b) Calanoid copepod escape behavior in response to a visual predator. *Mar Biol* 150:599–607.
- Wang SB, Houde ED (1994) Energy storage and dynamics in bay anchovy *Anchoa mitchilli*. *Mar Biol* 121:219–227.

- Weiss RF (1970) The solubility of nitrogen, oxygen and argon in water and seawater. In: *Deep Sea Research and Oceanographic Abstracts*. Elsevier, p 721–735
- White JR, Roman MR (1992) Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. *Mar Ecol-Prog Ser* 86:251–251.
- Wiebe PH (1976) A multiple opening/closing net and environment sensing system for sampling zooplankton. *J Mar Res* 34:313–326.
- Wilson CB, Museum USN (1932) The copepod crustaceans of Chesapeake Bay. Smithsonian Institution Press.
- Wishner KF, Outram DM, Seibel BA, Daly KL, Williams RL (2013) Zooplankton in the eastern tropical north Pacific: Boundary effects of oxygen minimum zone expansion. *Deep Sea Res Part Oceanogr Res Pap* 79:122–140.
- Wolf NG, Kramer DL (1987) Use of cover and the need to breathe: the effects of hypoxia on vulnerability of dwarf gouramis to predatory snakeheads. *Oecologia* 73:127–132.
- Wong CK, Ramcharan CW, Sprules WG (1986) Behavioral responses of a herbivorous calanoid copepod to the presence of other zooplankton. *Can J Zool* 64:1422–1425.
- Wood SC, Johansen K (1972) Adaptation to hypoxia by increased HbO₂ affinity and decreased red cell ATP concentration. *Nature* 237:278–279.
- Woodson CB, Webster DR, Weissburg MJ, Yen J (2007) Cue hierarchy and foraging in calanoid copepods: ecological implications of oceanographic structure.
- Wu RS (2002) Hypoxia: from molecular responses to ecosystem responses. *Mar Pollut Bull* 45:35–45.
- Zastrow CE, Houde ED, Morin LG (1991) Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy *Anchoa mitchilli* in mid-Chesapeake Bay. *Mar Ecol Prog Ser*:161–171.