

ABSTRACT

Title of Document: THE EFFECTS OF LOW DISSOLVED OXYGEN ON PREDATION INTERACTIONS BETWEEN *MNEMIOPSIS LEIDYI* CTENOPHORES AND LARVAL FISH IN THE CHESAPEAKE BAY ECOSYSTEM

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Differences in predator and prey tolerances to low dissolved oxygen (DO) concentrations are important to planktonic food webs in seasonally hypoxic environments like Chesapeake Bay. Hypoxia alters field distributions, encounter rates, and predator-prey interactions between hypoxia-tolerant ctenophores, *Mnemiopsis leidyi*, and less tolerant ichthyoplankton and zooplankton prey. To examine the effect of hypoxia on estuarine food web species' interactions, I conducted medium and small-scale experiments, field sampling, and collaborated on individual-based model development, focusing on ctenophore-larval fish dynamics. Laboratory estimates of clearance rates for ctenophores on bay anchovy (*Anchoa mitchilli*) eggs and yolk sac larvae, and naked goby (*Gobiosoma bosc*) feeding larvae were the same at low and high DO. Field sampling for *M. leidyi*, ichthyoplankton, mesozooplankton, and scyphomedusae (*Chrysaora quinquecirrha*) during day and night at two sites in the Patuxent River indicated increased abundance of most species in the bottom layer with increasing bottom DO. Vertical overlap between predator and prey pairs also increased with higher bottom DO, increasing potential encounters and predation. Larval fish swimming speeds did not

differ significantly with DO, but ctenophores swam significantly faster at intermediate DO (2.5 mg L^{-1}) than at either low or high DO. DO did not significantly affect ingestion. Greater ingestion of fish larvae by ctenophores followed multiple encounters (56%) than initial encounters (10%) at all DO concentrations, highlighting the potential importance of repeated predator-prey interactions. DO did not significantly affect encounter model estimates of ingestion rates. Ingestions averaged $0.4 \text{ fish larvae d}^{-1} \text{ m}^{-3}$ for first encounters and $2 \text{ fish larvae d}^{-1} \text{ m}^{-3}$ for multiple encounters. Results from laboratory and field studies parameterized a spatially-explicit individual based model of a ctenophore-ichthyoplankton-copepod intraguild predation food web. Ctenophore predation had a bigger effect on survival of modeled ichthyoplankton than did competition between ctenophores and fish larvae for shared zooplankton prey, but competition more strongly affected larval fish growth rates. DO did not alter the relative importance of ctenophore predation and competition, but low DO did decrease larval fish survival and increase growth rates. Results suggest that effects of DO on vertical distribution and species overlap are more important to predation than direct DO effects.

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INTERACTIONS BETWEEN *MNEMIOPSIS LEIDYI* CTENOPHORES AND
LARVAL FISH IN THE CHESAPEAKE BAY ECOSYSTEM

By

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Foreword

In accordance with the University of Maryland Graduate Catalogue, it is recognized that a graduate student may co-author work with colleagues that should be included in a Dissertation. A portion of the Dissertation, Chapter 4, was co-authored by the committee member Dr. Kenneth Rose from Louisiana State University. Dr. Rose was responsible for composing the Fortran model code and contributed to the intellectual content and substance of the text. His contributions fall within the normal bounds of graduate supervision. The candidate worked closely with Dr. Rose to construct the relevant model simulations, provide model input parameters, conduct replicate model runs, ground-truth model results, and compose the chapter text. The candidate solely authored all other chapters, although the committee provided comments of substance. This foreword to the Dissertation, as approved by the Dissertation Committee, serves to state that the candidate made substantial contributions to the relevant aspects of the jointly authored work included in the Dissertation.

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Table of Contents

Foreword.....	ii
Acknowledgements.....	iii
Table of Contents.....	iv
List of Tables.....	vi
List of Figures.....	vii
List of Figures.....	vii
Chapter 1: Introduction.....	1
Chapter 2: Effects of hypoxia on spatial distribution and predation on ichthyoplankton and zooplankton by the ctenophore <i>Mnemiopsis leidyi</i> in the Chesapeake Bay system	6
INTRODUCTION.....	6
MATERIALS AND METHODS.....	9
<i>Organism Collection & Rearing</i>	9
<i>Predation Experiments</i>	10
<i>Field Sampling</i>	12
STATISTICAL ANALYSIS.....	14
<i>Predation Experiments</i>	14
<i>Field Data Analysis</i>	15
RESULTS.....	17
<i>Laboratory Predation Experiments</i>	17
<i>Field Sampling</i>	18
DISCUSSION.....	23
<i>Effects of DO on Clearance Rates</i>	23
<i>Effects of DO on Vertical Distribution & Overlap</i>	25
<i>Effects of Predators & Competitors on Vertical Distribution & Overlap</i>	27
Chapter 3: The effect of low dissolved oxygen on behavioral interactions and swimming speeds of ctenophore predators and larval fish prey.....	44
INTRODUCTION.....	44
MATERIALS AND METHODS.....	48
<i>Encounter Sequence Interactions</i>	49
<i>Swimming Speeds of Predator & Prey</i>	52
<i>Encounter Model</i>	54
RESULTS.....	56
<i>Small-Scale Predation Interactions</i>	56
<i>Swimming Speeds of Predator & Prey</i>	57
<i>Encounter Model</i>	58
DISCUSSION.....	59
<i>Effects of Swimming Speeds on Encounter & Ingestion</i>	59
<i>Encounter Model</i>	62
<i>Other Factors Affecting Encounter & Ingestion</i>	63
Chapter 4: Individual-based model of an intraguild predation food web: ctenophores, larval fish, and copepods in the Patuxent River estuary.....	77
INTRODUCTION.....	77
<i>Food Web Theory & Intraguild Predation</i>	77

MODEL DESCRIPTION AND METHODS	81
<i>Overview</i>	81
<i>Water Column Structure</i>	82
FISH LARVAE	83
<i>Larval Fish Spawning</i>	83
<i>Larval Fish Growth</i>	84
<i>Larval Fish Consumption</i>	85
<i>Larval Fish Assimilation and Metabolism</i>	86
<i>Larval Fish Mortality</i>	86
<i>Fish Movement</i>	87
CTENOPHORES	87
<i>Ctenophore Growth</i>	87
<i>Ctenophore Consumption</i>	88
<i>Ctenophore Assimilation</i>	91
<i>Ctenophore Respiration</i>	91
<i>Ctenophore Reproduction</i>	92
<i>Ctenophore Mortality</i>	93
<i>Ctenophore Movement</i>	93
ZOOPLANKTON	94
DISSOLVED OXYGEN EFFECT	95
NUMERICAL CONSIDERATIONS	96
DESIGN OF MODEL SIMULATIONS	98
RESULTS	101
<i>Baseline Model Behavior & Corroboration</i>	101
<i>Model Corroboration</i>	106
<i>Importance of Predation & Competition to Larval Fish Survival & Growth</i>	108
<i>Effect of DO on the Relative Importance of Predation & Competition</i>	111
DISCUSSION	115
Chapter 5: Conclusions and Implications	140
LITERATURE CITED	145

List of Tables

Table 2.1. Conditions for predation experiments in 100 L tanks.....	32
Table 2.2. Bottom layer DO in the Patuxent River.....	33
Table 2.3. <i>Mnemiopsis leidyi</i> , effects of DO on predation and clearance rates.....	34
Table 2.4. Mean field densities.....	35
Table 2.5. Schoener’s Index of habitat overlap.....	36
Table 2.6. Effects of bottom layer DO on vertical overlap.....	37
Table 2.7. Significant stepwise regression analysis results for predator and prey overlap with bottom DO.....	40
Table 3.1. A summary of physical properties measured in laboratory predation interactions between ctenophores and larval fish.....	68
Table 3.2. A summary of physical properties measured in laboratory swimming speed experiments for ctenophores and larval fish.....	69
Table 3.3. Results from modeled ctenophore interactions with larval fish.....	70
Table 4.1. Variable names used in the individual-based model.....	122
Table 4.2. Results from five replicate runs of model simulations in the baseline IGP, relaxed predation, and relaxed competition food webs at both high and low DO..	123
Table 4.3. Values for the mean proportion of biomass (mgdw) of each copepod life stage in modeled larval fish diets for three size classes of larval fish.....	124
Table 4.4. Copepods comprise the majority of ctenophore diets during the 100-day model simulation.....	125

List of Figures

Figure 2.1. <i>Mnemiopsis leidyi</i> , laboratory clearance rates.....	41
Figure 2.2. Field proportions of ichthyoplankton.....	42
Figure 2.3. Field proportions of zooplankton.....	43
Figure 3.1. The sequence of events leading to ingestion of a larval fish prey by a ctenophore predator.....	71
Figure 3.2. A schematic of the set-up used for filming ctenophore and larval fish swimming speeds.....	72
Figure 3.3. Typical measurements of cumulative mean three-dimensional swimming speed (mm s^{-1}) over time (s) for a) a ctenophore and b) a larval fish.....	73
Figure 3.4. Results from small-scale predation interactions in the laboratory between a ctenophore and a larval fish.....	74
Figure 4.1. The modeled mesohaline summertime Chesapeake Bay system food web.	128
Figure 4.2. Equation for ctenophore assimilation used in the model determined from published data on ctenophore assimilation as well as information on ctenophore bioenergetics.....	129
Figure 4.3. Modeled simulations included three food webs with five total simulations	130
Figure 4.4. Larval fish length (mm) plotted against Ordinal Day for 6 different simulations.....	131
Figure 4.5. Copepod number m-3 by layer plotted against ordinal day for the adult life stage during both day (●) and night (x) for a representative simulation for each of 6 different food webs.....	132
Figure 4.6. Ctenophore number m-3 by layer plotted against ordinal day during both day (●) and night (x) for a representative simulation for each of 6 different food webs	133
Figure 4.7. Ctenophore weight (mgdw) plotted against Ordinal Day for 6 different simulations.....	134
Figure 4.8. Fish larvae number m-3 by layer plotted against ordinal day during both day (●) and night (x) for a representative simulation for each of 6 different food webs	135
Figure 4.9. Mean daily larval fish average water column densities.....	136
Figure 4.10. Mean daily ctenophore average water column densities.....	137
Figure 4.11. Mean daily adult copepod average water column densities.....	138
Figure 4.12. Vertical habitat overlap for three predator – prey pairs in the 6 different simulations.....	139

Chapter 1: Introduction

Differences in predator and prey tolerances to low dissolved oxygen (DO) concentrations are important to planktonic food webs in seasonally hypoxic environments like Chesapeake Bay. Hypoxia alters spatial distributions, encounter rates, and predator-prey interactions between hypoxia-tolerant ctenophores, *Mnemiopsis leidyi*, and their less tolerant ichthyoplankton and zooplankton prey. To examine the effect of hypoxia on interactions within an estuarine food web, I conducted laboratory experiments, field sampling, and collaborated with one of my committee members to develop an individual-based model with a focus on ctenophore-larval fish dynamics. Below I provide brief background information on low DO and the specific trophic interactions I studied, and then outline the three research chapters of my dissertation. The goal of my dissertation was to understand the effect of low DO on trophic interactions between ctenophores and their ichthyoplankton prey.

Hypoxia, often defined as oxygen concentrations less than 2 mg L^{-1} (Turner and Rabalais 1994), occurs in many estuaries and coastal regions worldwide (Diaz and Rosenberg 1995, Diaz et al. 2004). Increased anthropogenic nutrient loading has led to frequent and widespread occurrences of low DO in a variety of environments, including the Chesapeake Bay ecosystem. Because Chesapeake Bay is strongly stratified during late spring and summer, the effects of eutrophication are manifested in seasonal bottom water hypoxia and anoxia. Low DO can have both lethal and sublethal effects on organisms (Kramer 1987, Poucher and Coiro 1997, Wannamaker and Rice 2000, Breitburg 2002), including shifts in vertical habitat use (Keister et al. 2000) and trophic

interactions (Rahel and Kolar 1990, Kolar and Rahel 1993, Rahel and Nutzman 1994, Breitburg et al. 1999).

Key species in the Chesapeake Bay food web affected by changes in DO include the lobate ctenophore predator, *M. leidy*, as well as dominant summertime mesohaline ichthyoplankton and zooplankton species: naked goby (*Gobiosoma bosc*) larvae and bay anchovy (*Anchoa mitchilli*) eggs and larvae, and the calanoid copepod *Acartia tonsa*. Because of its abundance, high feeding rates, and temporal coincidence with fish spawning and peak copepod abundance, *M. leidy* can consume large portions of zooplankton and ichthyoplankton in the Chesapeake Bay system (10 – 65 % d⁻¹) (Monteleone and Duguay 1988, Cowan and Houde 1993, Purcell et al. 1994a & b, Purcell and Decker 2005). Since current ctenophore densities are higher than in the past (Purcell and Decker 2005, Breitburg and Fulford 2006) the potential for predation on and competition with ichthyoplankton is even greater.

Ctenophores and their larval fish and copepod prey differ in their tolerances and responses to low DO (Breitburg et al. 1997, 1999; Purcell et al. 2001b, Breitburg 2002). Both laboratory experiments and field distributions indicate that ctenophores are more tolerant of low DO than their larval fish and copepod prey. Vertical distributions of ctenophores, ichthyoplankton, and zooplankton shift with declining DO concentrations (Keister et al. 2000) as available habitat volume decreases with decreasing bottom layer DO, but DO concentrations avoided and the use of surface versus pycnocline layers vary. Encounter rates between predator and prey with different tolerances to DO may, therefore, change as bottom DO declines.

The effect of low DO on ctenophore predation of ichthyoplankton was the focus of my first research chapter, Chapter 2. My goal was to determine if DO affected predator - prey interactions between co-occurring ctenophores and ichthyoplankton, vertical habitat overlap, and resulting encounters. I conducted laboratory experiments and field sampling to determine whether low DO influences predation by *M. leidyi* on ichthyoplankton by affecting either predation rates or vertical overlap between ctenophores and their prey.

Effects of hypoxia on individual behaviors of both predator and prey also include changes in swimming and escape ability (Breitburg 1994, Breitburg et al. 1997, Weltzien et al. 1999). Low DO can modify behavior in planktonic food webs (Robb and Abrahams 2002), and the effect of low DO on behavior can change predator-prey interactions, so it is likely that low DO will alter predation rates. Although the effects of predation are also realized at the scale of the population, interactions occur at the individual level and therefore both predator and prey behavior have an important influence on the outcome (Letcher and Rice 1997, Fuiman and Cowan 2003, Hampton 2004).

For Chapter 3, I hypothesized that low DO would decrease encounters between predator and prey but increase ctenophore predation on larval fish, based on the expectation that larval fish swimming ability would be adversely affected by low DO but that ctenophore swimming speeds would not be affected due to their higher tolerance of low DO. Also, the influence of low DO on fish larvae is inversely related to age (Breitburg 1994), so I hypothesized that younger larvae would fare worse than older larvae, experiencing a greater decrease in swimming speeds (Bailey 1984) and increase in

ingestion by ctenophores at low DO. I observed videotaped interactions between a single ctenophore and fish larva to determine the sequence of events leading to ingestion following both the first and multiple encounters. Three-dimensional swimming speeds of ctenophores and larval fish were measured using motion analysis of videotapes from orthogonal cameras. Finally, in order to examine the potential for hypoxia to influence predation on a population scale I fit an encounter model incorporating my measured encounters, ingestions, and swimming speeds and compared it to published clearance rate estimates of ctenophores on fish larvae (Cowan and Houde 1993, Purcell et al. 2001b).

M. leidyi is an omnivore that feeds on zooplankton as well as early life stages of the bay anchovy. Intraguild predation (IGP) is a specialized case of omnivory involving the consumption of one competitor by another, simultaneously conferring nutritional gain to the IG predator and elimination of a competitive rival, the IG prey (Polis et al. 1989). It is recognized that both omnivory (Martinez 1993, Wissinger and McCrady 1993, Holt and Polis 1997, Mylius et al. 2001, Rosenheim 2001) and intraguild predation are widespread (Ehler 1996) and particularly ubiquitous in aquatic systems (Polis et al. 1989, Polis 1991, Diehl 1993, Winemiller 1996).

I was interested in determining which effect of ctenophores on larval fish populations in the Chesapeake Bay IGP food web was more important — predation or competition — and how low versus high DO conditions in the water column affect the relative importance of these biotic interactions. While the effect of ctenophore predation on ichthyoplankton is documented both in the literature (Cowan and Houde 1993, Purcell et al. 2001a & b, Breitburg et al. 2003) and in Chapter 2 of my dissertation, measuring the effect of competition is more challenging. Additionally, separating the indirect

effects of competition from the direct effects of predation on an organism may be difficult (Wissinger and McCrady 1993, Diehl 1995, Navarette et al. 2000).

Understanding this particular Chesapeake Bay IGP food web may also provide insight into other systems with similar trophic complexity.

In Chapter 4, I isolated the effects of predation and competition, as well as the environmental influences of low DO, on larval fish survival and growth by using a spatially-explicit individual-based simulation model of the IGP food web. My committee member, Kenneth Rose, wrote the model code, while my role was model parameterization, validation and data interpretation. Simulations were performed that allowed for effects of competition and predation on larval fish by ctenophores to be separated from each other under conditions of high and low DO concentrations.

Model results were used to address three questions: 1) How does high and low DO affect the growth and survival of larval fish in the baseline IGP food web?; 2) Is competition or predation the more important effect of ctenophores on larval fish survival and growth?; and 3) What is the effect of low versus high DO on the relative importance of competition and predation to larval fish survival and growth within the IGP food web?

Chapter 2: Effects of hypoxia on spatial distribution and predation on ichthyoplankton and zooplankton by the ctenophore *Mnemiopsis leidyi* in the Chesapeake Bay system

INTRODUCTION

Hypoxia, often defined as dissolved oxygen (DO) concentrations less than 2 ml L⁻¹ (2.8 mg L⁻¹) (Diaz and Rosenberg 1995) or 2 mg L⁻¹ (1.42 ml L⁻¹) (Turner and Rabalais 1994), is deleterious to aquatic organisms that depend on aerobic respiration for survival, having both lethal and sublethal effects (Kramer 1987, Poucher and Coiro 1997, Wannamaker and Rice 2000, Breitburg 2002). Sublethal consequences of hypoxia include reduced growth rate, altered behavior, decreased foraging ability, and increased susceptibility to predation (Breitburg 1992, Breitburg 1994, Howell and Simpson 1994, Petersen and Pihl 1995, Crocker and Cech 1997). Subtle shifts in trophic interactions caused by hypoxia may have a large effect on interactions among species (Rahel and Kolar 1990, Kolar and Rahel 1993, Rahel and Nutzman 1994). For example, sub-lethal oxygen concentrations may increase predation risk as predators opportunistically feed on prey species made vulnerable by low oxygen stress (Pihl et al. 1992). In addition, low DO in aquatic ecosystems can compress organisms into reduced volumes of higher DO (Coutant 1985, Breitburg et al. 1997), thereby increasing predator and prey encounter rates.

Increased anthropogenic nutrient loading has led to frequent and widespread occurrences of low DO in a variety of environments ranging from enclosed seas and bays to open continental shelf areas (Diaz and Rosenberg 1995, Diaz et al. 2004). In particular, changes in land-use patterns during the last three centuries have modified the Chesapeake Bay ecosystem, the largest semi-enclosed estuary in the United States. Conversion of forests and farms to urban areas, increased population, and increased

fertilizer use have altered runoff patterns and increased nutrient inputs into the bay, which in turn has elevated algal production and biomass, and increased the intensity and extent of summer oxygen depletion (Cooper and Brush 1993, Boynton 1997, Karlsten et al. 2000, Hagy et al. 2005). Because Chesapeake Bay is strongly stratified during late spring and summer, the effects of eutrophication are manifested in seasonal bottom water hypoxia and anoxia.

One of the key species in the Chesapeake Bay food web that may be affected by changes in hypoxia is the lobate ctenophore, *Mnemiopsis leidyi*. This species is an important predator on both zooplankton and the early life-stages of fish (Bishop 1967, Reeve and Walter 1978, Kremer 1979, Monteleone and Duguay 1988, Cowan and Houde 1992, Cowan and Houde 1993, Houde et al. 1994, Purcell et al. 1994 a & b, Purcell et al. 2001b), and can therefore act as both a predator and a competitor of planktivorous fish (Cowan et al. 1992, Purcell and Arai 2001). All stages of ichthyoplankton, including eggs (of species with planktonic eggs), yolk sac larvae, and older feeding larvae, are exploited by ctenophores. *Mnemiopsis* is a year-round inhabitant of Chesapeake Bay, peaking in abundance during late spring - summer (Kremer 1994, Purcell et al. 2001b), and declining during July and August of some years, coincident with the decline of their copepod prey and the peak abundance of predatory scyphomedusae, *Chrysaora quinquecirrha* (Kremer 1994, Purcell and Cowan 1995, Purcell et al. 2001b).

Predation is a major source of mortality for ichthyoplankton (Bailey and Houde 1989). The high abundance of ctenophores in the summertime Chesapeake Bay system makes them important predators of dominant mesohaline ichthyoplankton, such as naked goby (*Gobiosoma bosc*) larvae and bay anchovy (*Anchoa mitchilli*) eggs and larvae.

Calculations indicate that field populations of ctenophores can consume 10 - 65% d⁻¹ of the ichthyoplankton in the Chesapeake Bay and its tributaries (Monteleone and Duguay 1988, Cowan and Houde 1993, Purcell et al. 1994a). Because of its abundance, high feeding rates, and temporal coincidence with fish spawning, *M. leidy* can consume large portions of zooplankton and ichthyoplankton (Monteleone and Duguay 1988, Cowan and Houde 1993, Purcell et al. 1994a & b, Purcell and Decker 2005).

The vertical distributions of ctenophores, ichthyoplankton, and zooplankton shift with declining DO concentrations (Keister et al. 2000) and available habitat volume decreases as DO concentrations below the pycnocline decrease because many organisms avoid low DO (Robb and Abrahams 2002). Ctenophores remain below the pycnocline until dissolved oxygen concentrations decline to about 1 mg L⁻¹ in the bottom layer of the water column (Breitburg et al. 2003); however, sensitive organisms, such as the early life stages of fish, avoid low DO waters at oxygen concentrations > 2 mg L⁻¹ (Breitburg 1994, Keister et al. 2000, Breitburg et al. 2003). Therefore, encounter rates between predator and prey with different tolerances to DO may change as bottom DO declines.

I conducted laboratory experiments and field sampling to determine whether low DO influences predation by *Mnemiopsis leidy* on ichthyoplankton by affecting either predation rates or vertical overlap between ctenophores and their prey. Eutrophication and resulting hypoxia in the Chesapeake Bay system seems to favor gelatinous zooplankton over finfish (Breitburg 1992, Breitburg et al. 1997, Purcell et al. 2001a). My goal was to determine if DO affected predator - prey interactions between co-occurring ctenophores and ichthyoplankton, vertical habitat overlap, and resulting encounters. Other species in the food web, such as the medusa, *Chrysaora quinquecirrha*, that prey

on both ctenophores and ichthyoplankton, and a shared copepod prey species (*Acartia tonsa*), were also sampled to determine which organisms might influence the vertical distributions of ctenophores and ichthyoplankton. I sampled the same sites as Keister et al. (2000), which exhibit chronic low bottom DO. Ctenophore densities were very low during 1992 (ctenophore mean density = $0.07 \pm 0.02 \text{ m}^{-3}$), which corresponded with high medusa densities (Keister et al. 2000). My present study occurred during a period of low medusa density, enabling me to determine the relative importance of medusa predators and the effect of DO on ctenophore vertical distribution and overlap with prey.

MATERIALS AND METHODS

Organism Collection & Rearing

Laboratory experiments examined effects of oxygen concentration on predation by ctenophores on three life stages of two Chesapeake Bay fish species: (1) bay anchovy eggs, (2) bay anchovy yolk sac larvae, and (3) 1- and 4- d posthatch (dph) naked goby feeding larvae. I chose these prey because they are the most abundant ichthyoplankton species in the mesohaline Chesapeake Bay during summer when ctenophores are abundant (Keister et al. 2000), and they have similar oxygen tolerances to one another (Breitburg 1994, Zastrow and Houde unpubl.).

Organisms were collected from the mesohaline Patuxent River, a tributary of Chesapeake Bay. *M. leidyi* were dip-netted from the surface, kept no longer than one week in 80 L aquaria in the laboratory at ambient temperature (22 – 24 °C) and salinity (12 - 15), and were fed brine shrimp nauplii (*Artemia* spp.) or, when available, natural zooplankton. I performed 50 % water changes in ctenophore tanks every other day, and small paddlewheels provided gentle surface water movement within the tanks.

Bay anchovy eggs were collected with a 500 μm plankton net towed at approximately 1 knot for 2 minutes in the surface layer during the midnight to 7 am peak spawning period (MacGregor and Houde 1996). Eggs were placed in aerated buckets and returned to the laboratory as soon as sufficient numbers were collected. Target experimental abundances between 32 and 200 eggs (dependent on availability) were immediately counted into 2 L holding dishes and then either placed directly into experimental tanks (for egg experiments) or maintained in dishes for approximately 20 h until hatching (yolk sac larvae experiments). Eggs and yolk sac larvae that died prior to the start of experiments were replaced.

Naked goby eggs were collected from nesting trays deployed at several sites along the Patuxent River (Breitburg 1992, 1994). Nests with the guarding male were brought into the laboratory for egg hatching and larval rearing. After developing for up to 1 week, eggs were placed under a directed light source, which triggered hatching, and larvae were transferred to 80 L rearing aquaria (25 larvae L^{-1}) filled with 5- μm filtered Patuxent River water at ambient temperature ($22 - 24 \text{ }^\circ\text{C}$) and salinity (12 - 15). I maintained larval rearing tanks with constant gentle bubbling and 50 % water changes every 2 - 3 days. Larvae were fed laboratory-reared rotifers (*Brachionus plicatus*) at densities of approximately 4000 L^{-1} , and used in predation experiments when they were less than 7 dph.

Predation Experiments

Experiments compared ctenophore clearance rates at 3 different DO concentrations (Table 2.1). Experiments were conducted as a randomized complete block design with date as the blocking factor and DO level as the treatment. I selected 2

low oxygen concentrations (1.5 mg L^{-1} and 2.5 mg L^{-1}) that would not cause direct mortality of organisms during these experiments, but which resulted in different vertical distributions of fish larvae in the laboratory (Breitburg 1994) and in the field (Keister et al. 2000, Breitburg et al. 2003). I also estimated ctenophore clearance rates of prey at an air-saturated control DO concentration around 7 mg L^{-1} . I conducted separate experiments for each of the three ichthyoplankton prey in 100 L tanks with 4 – 6 replicates per DO treatment. Experiments for each stage were conducted over 2 days. Treatments were arbitrarily assigned to tanks. In addition, each day of the experiment one predator-free tank at each of the 3 DO treatments was used to provide a baseline recovery rate to assess prey mortality due to handling and DO stress.

After target oxygen concentrations were reached in the tanks by bubbling with nitrogen gas and measured with a YSI model 52 or 85 dissolved oxygen meter, I placed either (1) 100 - 200 bay anchovy eggs, (2) 32 - 47 yolk sac larvae or (3) 200 naked goby larvae into each tank for 30 minute acclimation to experimental conditions, as larval fish generally acclimate in less than 1 h (Stalder and Marcus 1997 and cited references within). Tanks were maintained in low light at ambient water temperatures ($22 - 24 \text{ }^{\circ}\text{C}$) and salinities (11 – 16). I added 8 - 13 ctenophores ($163.29 \pm 8.16 \text{ ml}$ average total volume) (Table 2.1) to small vessels within experimental tanks, and each experiment was initiated upon mixing of predators and prey. Tanks were sealed and a small amount of nitrogen gas, or air for DO control tanks, was leaked into the headspace to maintain DO conditions for the duration of the experiment. Larger ctenophores were more prevalent as the summer progressed; therefore during the second set of experiments, total predator volume was larger (Table 2.1). I used different experimental durations and predator

numbers for the different prey types to avoid prey depletion (Table 2.1). Rotifers were added to all containers as alternative prey (approx. 450 rotifers L⁻¹) to encourage naked goby larvae and ctenophores to engage in normal swimming and feeding behaviors.

At the end of each experimental period, dissolved oxygen was re-measured and ctenophores were removed with a dip net. Water was slowly siphoned through 65 – 100 µm mesh bags to collect remaining ichthyoplankton. Collection bags were immersed in MS-222 to sedate larvae before preservation in 75% ethanol (larvae and eggs) or 5% buffered formalin (yolk sac larvae). The number of eggs or larvae collected was enumerated with a dissecting scope to determine recovery rates (in the predator-free tanks), percent predation (the difference between the number of prey recovered from the predator-free control tank and experimental tank divided by the number of prey recovered from the control tank), and clearance rates (L ml ctenophore⁻¹ h⁻¹) using the equation from Cowan and Houde (1993).

Field Sampling

Ctenophores, medusae, ichthyoplankton and zooplankton were collected in the summer from June - August in the mesohaline Patuxent River sub-estuary of Chesapeake Bay, in 1992 and 1993 by Keister et al. (2000) and in 1999 and 2001 for the present study. Details of samples collected in 1992 and 1993 are in Keister et al. (2000); 1999 and 2001 methods follow the same general protocol (Table 2.2). Two sites in the mid-channel Patuxent River were chosen based on a history of chronic summertime hypoxia - the mouth of St. Leonard Creek (average depth = 20 m) and south of the mouth of Battle Creek just north of Broomes Island (average depth = 16 m) (Breitburg et al. 2003). Maps of the Patuxent River sampling sites can be found in both Keister et al. (2000) and

Breitburg et al. (2003). Sampling was conducted day and night at both stations by Keister et al. (2000) on July 24, 29, and August 4, 1992 and on July 6, 12, and 16, 1993. I sampled day and night on June 22, July 27, and August 24, 1999, and only during the day at St. Leonard Creek on July 5, 2001 (Table 2.2).

Vertical profiles of the water column for temperature, DO, and salinity were taken at each site using a YSI model 85 DO meter. The pycnocline was determined from these measurements as the depth where the greatest change in temperature, DO, and salinity occurred. Tidal stage and trawl time were also recorded.

Zooplankton was sampled every 1 - 2 m throughout the water column by pumping 50 L of water at 20 L min^{-1} for approximately 2 minutes through a hose (cleared for ~45 s prior to sample collection) into a $35 \mu\text{m}$ plankton net (30 L min^{-1} in 1992 and 1993), and then preserved in 5% buffered formalin for later enumeration and identification with a dissecting microscope in the laboratory. Stempel pipette aliquots of zooplankton samples (at least 200 individuals or $\frac{1}{4}$ of the whole preserved sample) were counted, identified to genus, and separated by life stage. Zooplankton were assigned to water column layers based on a comparison of their sampling depth with physical profiles of the water column.

Duplicate 1.5 – 2 min discrete depth samples for ctenophores, medusae and ichthyoplankton were taken in each of 3 layers (surface, pycnocline and bottom) using a Tucker Trawl with a 1 m^2 mouth area and $212 - 224 \mu\text{m}$ mesh nets and a General Oceanics flowmeter attached in the mouth of the net (average tow volume = $87.9 \pm 4.2 \text{ m}^3$, $n = 111$). The surface layer was sampled with the top of the net skimming the water surface; sampling in the pycnocline was ensured by having a YSI model 52 dissolved

oxygen meter attached to the frame of the net; sampling depth within the bottom layer between the pycnocline and the sediment was established geometrically using cable length and wire angle. Individual live ctenophore total length and sea nettle diameter were measured to the nearest 5 mm and volumes were measured to the nearest 1 ml in graduated cylinders. Whole sample biovolumes were measured to the nearest 50 ml in graduated pitchers. Ichthyoplankton were removed and preserved in 75% ethanol, counted, and identified to genus (species level when possible) for whole preserved samples.

STATISTICAL ANALYSIS

Predation Experiments

Analyses were performed on clearance rates ($L \text{ ml ctenophore}^{-1} \text{ h}^{-1}$) to determine the effect of DO on predation on each of the 3 prey types (bay anchovy eggs, bay anchovy yolk sac larvae, and naked goby larvae). Ctenophore clearance rates of naked goby larvae and bay anchovy yolk sac larvae were untransformed, but clearance rates of bay anchovy eggs were Log_{10} transformed to correct normality of residuals. I performed randomized complete block design analysis of variance (ANOVA), including replication within blocks (date), for all prey types (except yolk sac larvae on the second date when only 1 tank per treatment was run). Simple linear regression between average DO within tanks and clearance rate for each prey type was also computed. For all statistics, significance was set at $\alpha < 0.05$, with observations in the range $0.05 \leq \alpha < 0.10$ noted as a non-significant trend. All data are presented as mean \pm 1 SE.

Field Data Analysis

Schoener's Index of habitat overlap (Schoener 1970) was computed to determine the effect of low DO on vertical overlap of species within the water column. Here I present a more detailed analysis of species overlap than the general summaries provided in Breitburg et al. (2003). Overlap values (as proportions) ranged from 0 (no overlap in habitat use) to 1 (complete overlap). Vertical overlap was determined for five predator and prey groups: (1) numbers of adult and juvenile copepods (mostly *Acartia tonsa*) L⁻¹, (2) fish eggs (predominately bay anchovy eggs, but other species were present in small numbers), (3) bay anchovy larvae < 15mm standard length, (4) naked goby larvae and (5) ctenophores (by number and volume m⁻³). Medusa number and volume m⁻³ were included as secondary contributing factors in stepwise regressions, but were not considered to be primary predators in this ctenophore-focused study. I used both number and volume of gelatinous species because numbers reflect behavioral responses while volume more accurately describes consumption potential. Only samples with more than 8 total ctenophores or medusae at the station were used in calculations in order to avoid error in overlap estimates for very small sample sizes. Samples with zero total ctenophores or medusa collected at a station comprised about a third of all eliminated samples, while the rest of the eliminated samples had station totals equal to less than 0.1 ctenophore or medusa m⁻³. About 20% of ctenophore and medusa samples were excluded using this criteria.

Vertical overlap between each predator and prey pair was calculated as follows:
Schoener's Index = $1 - 0.5 * (| P_{pred SURF} - P_{prey SURF} | + | P_{pred PYCN} - P_{prey PYCN} | + | P_{pred BOTT} - P_{prey BOTT} |)$, where $P_{pred LAYER}$ and $P_{prey LAYER}$ represent the proportions of predators or prey in each layer of the water column (surface, pycnocline, or bottom).

The proportions of gelatinous zooplankton and ichthyoplankton were calculated from densities in pooled duplicate samples at each combination of date, station, and time period, and I used mean zooplankton densities for the depth interval corresponding to each layer (n = 43). An adjustment to the species' proportions for the thickness of each layer was calculated based on the average depth of each sampling site and the DO profiles for each date and time period. The coefficient of variation (CV) was presented along with mean vertical overlaps.

In order to test for relationships between species overlap and bottom DO, I performed simple regression analyses on the arcsine-transformed overlap between 10 pairs of predator and prey in the water column with bottom DO. As an exploratory technique, linear, 2nd order, or 3rd order regression models were fit. The model that best described the relationship was chosen based on the Akaike's Information Criterion (AIC). I performed analysis of vertical overlap separately for day and night data, and then for the time periods combined, after analysis of covariance (ANCOVA) indicated that there were no significant difference between the two time periods. The relationship between vertical overlap and tidal stage was also analyzed with ANCOVA.

I used stepwise regressions to determine if components of the food web with the potential to directly influence the predator and prey contributed to the degree of habitat overlap along with bottom DO. A typical model included bottom DO, as well as predator, prey, and competitor species abundances. I performed principle components analysis to determine collinearity among factors in the stepwise regression. There was high collinearity between bay anchovy and naked goby larvae, and as a result, I used combined "fish larvae" instead of individual species in the stepwise models. Likewise,

either number or volume for each gelatinous predator was included in the model, not both. As an example, the stepwise regression model for overlap between ctenophore number (CTN) and naked goby larvae (GOB) was represented as $OVERLAP = BOTDO + CTN + MED + COP + LRV$, with $BOTDO$ = bottom DO, CTN = number of ctenophore predators, MED = number of medusa predators, COP = number of copepod prey, and LRV = number of combined fish larvae. Models significant at $\alpha < 0.05$ for day, night, and the time periods combined included organismal effects along with bottom DO.

RESULTS

Laboratory Predation Experiments

During all experiments, oxygen levels for both low DO concentrations were maintained within 0.3 mg L^{-1} of target concentrations, while the air-saturated controls were within 1.0 mg L^{-1} of each other (Table 2.1). Recovery rates in tanks without ctenophore predators were at least 91 % for bay anchovy eggs and naked goby larvae, and at least 78 % for yolk sac larvae. Predation calculations were adjusted for recovery rates. Overall, percent predation was smallest for bay anchovy eggs, intermediate for naked goby larvae, and largest for bay anchovy yolk sac larvae (Table 2.3).

Dissolved oxygen concentrations tested did not affect clearance rates ($\text{L ml ctenophore}^{-1} \text{ h}^{-1}$) of ctenophores feeding on bay anchovy eggs, bay anchovy yolk sac larvae, and naked goby larvae (Fig. 2.1a – c). Clearance rates were lowest for naked goby larvae, intermediate for bay anchovy eggs, and about an order of magnitude higher for bay anchovy yolk sac larvae (Table 2.3). Clearance rates at all DO treatments had similar ranges for bay anchovy eggs and naked goby larvae and were an order of magnitude larger for yolk sac larvae, but within each life stage, variation in ctenophore clearance rates was small (Table 2.3).

Regressions between DO and clearance rates were not significant for any prey type; extremely small R^2 values suggested the lack of any biologically meaningful trends for bay anchovy eggs ($R^2 = 0.1247$, $P = 0.15$), bay anchovy yolk sac larvae ($R^2 = 0.0139$, $P = 0.72$), or naked goby larvae ($R^2 = 0.0000$, $P = 0.98$) as prey (Fig. 2.1a – c).

Field Sampling

Addition of 1999 and 2001 field data to the 1992 – 1993 data (Keister et al. 2000) allowed us to examine the effect of DO on vertical distributions and overlap under a wide range of DO and organism density conditions (Table 2.4). All species had higher average numerical densities in 1992 – 1993 than in 1999 and 2001, but ctenophore densities were very low in 1992 (0.03 ± 0.01 ind. m^{-3}), resulting in smaller average volumes of ctenophores in 1992 – 1993 samples than in later years. No fish eggs were present in 2001 samples, and fish egg abundance was low in 1999 compared with abundances found during sampling in earlier years. The average bay anchovy larvae density in 1999 and 2001 was smaller than in 1992 and 1993; bay anchovy densities in 1993 and 1999 were almost identical, but 1992 densities were very large. Naked goby larvae exhibited a slightly smaller combined density in 1999 and 2001 than in 1992 and 1993. Copepod densities in 1999 and 2001 were about a third of those sampled in 1992 and 1993. Medusa densities were an order of magnitude lower in the 1999 and 2001 study than in either 1992 or 1993.

Both bottom DO and time of day (day versus night) influenced proportional densities of organisms in each layer within the water column, but not all species examined were affected by both factors (Figs. 2.2 & 2.3). The vertical distribution of fish eggs, which do not have any behavioral response to DO, was independent of bottom DO

(Fig. 2.2a). Bay anchovy spawning occurs in surface waters at night, and the bottom-centered distribution of eggs during the day presumably results from sinking of eggs released the previous night (Fig. 2.2a). Most nighttime sampling was done shortly after dark and before peak spawning hours; the high proportional density of fish eggs in the bottom layer in these samples is likely dominated by eggs spawned the previous night. The nighttime samples with a high proportional density of fish eggs in the surface layer (Fig. 2.2a) were taken near or after midnight and reflect a predominance of newly spawned eggs.

At bottom DO concentrations less than 1 mg L^{-1} , bay anchovy larvae occurred in either the pycnocline or the surface layer during both day and night and appeared to strongly avoid the bottom layer (Fig. 2.2b). When bottom layer DO was greater than 1 mg L^{-1} , bay anchovy larvae displayed a steady increase in proportional density with increasing DO at night, although the patterns was not as clear during the day (Fig. 2.2b).

Naked goby larvae concentrations increased in the bottom layer with increasing DO during both day and night, and the increase was much more abrupt than the steady increase observed for bay anchovy larvae at night (Fig. 2.2b, c). Naked goby larvae were most abundant in the pycnocline at bottom DO less than 2 mg L^{-1} during both day and night, but at bottom DO concentrations $\geq 2 \text{ mg L}^{-1}$, they were most abundant in the bottom layer, especially at night. Abundances in the pycnocline and surface layers decreased both day and night as DO increased in the bottom layer (Fig. 2.2c).

Vertical distributions of copepods also varied with bottom DO concentrations, exhibiting a general increase in the bottom layer with increasing DO both day and night.

When bottom DO was very low, copepods tended to utilize the pycnocline, especially during the day (Fig. 2.3a).

The relationship between vertical distribution of ctenophores and bottom DO concentration was not quite as clear as for most of the other species, but followed the same general pattern. When bottom DO concentrations were less than 1 mg L^{-1} , ctenophore densities were largest in the pycnocline during the day and in the pycnocline and surface layers at night. At higher DO concentrations, densities tended to be greatest in the bottom layer during both day and night, with densities in the pycnocline and surface layers similar to each other (Fig. 2.3b).

Schoener's Index calculated for vertical overlap including data for all DO concentrations ranged from a low of 0.59 for overlap between ctenophore number and fish egg density to a high of 0.82 for naked goby larvae and copepod densities (Table 2.5). Values for Schoener's Index were relatively high (values can range from 1 to 0, with the overlap value for random distribution = 0.33), which implies a high degree of vertical overlap between predator and prey pairs in my study system. In general, Schoener's Index of habitat overlap between predators and their prey increased with increasing bottom DO (Table 2.6). Ctenophore predators were more abundant in the bottom layer at lower DO concentrations than their prey, while densities of both predator and prey increased in the bottom layer with increasing DO. For the overlap between ctenophores and their prey, vertical overlap tended to decrease as ctenophore number or volume increased, with the only exception being one large overlap value between ctenophores and bay anchovy larvae at the greatest ctenophore density.

I performed ANCOVA to determine if the effect of DO on predator and prey vertical overlap differed between day and night (Table 2.6). Although the vertical distributions of many organisms differed between day and night, time of day modified the effect of DO on predator and prey overlap only for the overlaps between ctenophores and fish eggs. The test for coincidence, a simultaneous test of both intercept and slope, indicated a significant effect of DO on overlap between ctenophore volume and fish eggs ($P = 0.03$), and a trend toward a DO effect on ctenophore number overlap with fish eggs ($P = 0.07$). Overlap in vertical distributions of ctenophores and fish eggs was smaller and tended to be more variable during night time than during the day. During the day, overlap increased with increasing bottom DO, while at night there was no clear pattern of vertical overlap with bottom DO concentrations. Vertical overlap between ctenophores and fish eggs averaged 0.72 ± 0.05 ($CV = 29.7$) and 0.70 ± 0.05 ($CV = 30.8$) during daytime and 0.46 ± 0.08 ($CV = 65.4$) and 0.47 ± 0.08 ($CV = 60.5$) at night for ctenophore volume and number, respectively. The small nighttime overlap reflected small numbers of eggs and large numbers of ctenophores in the bottom and pycnocline waters during some nighttime samples (Fig. 2.2a & 2.3b). There were no highly significant regressions between bottom DO and vertical overlap in the daytime, but 2 predator and prey pairs (ctenophore number and naked goby larvae, and naked goby larvae and copepods) displayed a marginally significant trend (Table 2.6). The influence of bottom DO on vertical overlap was significant at night for 1 predator and prey pair (ctenophore number and copepods), and there was a marginally significant trend for 3 other predator and prey pairs: (1) ctenophore volume with naked goby larvae, (2) ctenophore volume with copepods, and (3) naked goby larvae with copepods (Table 2.6).

Because ANCOVA and regression revealed no significant effects of time of day on the effect of bottom DO on overlap in vertical distribution of most predator and prey pairs, I combined daytime and nighttime overlaps (total $n = 43$) (except for the overlap between ctenophore volume and fish eggs) in order to conduct regression analysis with a larger data set. The combined day and night regressions indicated that bottom DO significantly affected overlap in vertical distributions of 4 pairs of predator and prey: (1) ctenophore volume with naked goby larvae, (2) ctenophore volume with copepods, (3) ctenophore number with copepods, and (4) naked goby larvae with copepods (Table 2.6). In addition, there was a marginally significant trend towards increased overlap between anchovy larvae and copepods with increasing bottom DO ($0.05 \leq \alpha < 0.10$). For all pairs of predator and prey, overlap increased with increasing DO, even if the relationship was not statistically significant, i.e. all of the regression analyses yielded positive slopes. However the percent of variation in vertical overlap explained by bottom DO was low even in cases where the relationship was statistically significant. Tidal stage was not a significant indicator of habitat overlap for any pair of predator and prey.

Stepwise regression was used to determine if predator and prey abundances would explain additional sources of variation in vertical overlap beyond that explained by bottom DO. There were no variables tested in stepwise models that significantly improved upon the simple regression fits with bottom DO as the sole independent variable for daytime samples. For nighttime data, two stepwise regressions explained greater proportions of the variation in vertical overlap than did simple regression models (Table 2.7). These models included (1) medusa volume and bottom DO for the regression model of ctenophore volume and fish egg overlap, and (2) medusa volume and

bottom DO for the regression model of ctenophore volume and copepod overlap. There were also two stepwise regression models for combined day and night data that explained a higher percent of the variation in predator and prey vertical overlap than did the simple regressions. These models included (1) medusa volume and bottom DO in the model of overlap between ctenophore volume and copepods, and (2) medusa number and bottom DO for the overlap between ctenophore number and copepods (Table 2.7). Of note, the stepwise model for the overlap between ctenophore number and copepods at night also explained more variation than the model of overlap with bottom DO alone ($P = 0.01$; $DF = 3, 10, 13$; $R^2 = 0.6642$, $F = 6.59$). Bottom DO had the largest contribution to this model (48 %), and ctenophore number (one of the species considered in the overlap) had the second largest contribution (33 %), while sea nettle number explained the smallest percentage (19 %). Significant stepwise regressions that did not include bottom DO were not considered as part of this analysis but were used to help interpret results that were significant with bottom DO (see discussion below).

DISCUSSION

Effects of DO on Clearance Rates

There was no significant DO effect on *Mnemiopsis leidyi* clearance rates of bay anchovy eggs, bay anchovy yolk sac larvae, or naked goby larvae in the laboratory; estimated predation rates were as high at low DO as they were at high DO (Table 2.3, Fig. 2.1a - c). This result was unexpected as I anticipated differences in clearance rates due to DO based on the results of other predation studies. Laboratory experiments showed *Chrysaora* predation on naked goby larvae (Breitburg et al. 1994, 1997) and ctenophore clearance rates of copepods (Decker et al. 2004) were larger at low or intermediate DO concentrations than at high DO. Different tolerances to low DO of

ctenophores and their prey (Purcell et al. 2001a, Breitburg et al. 2003, Decker et al. 2004) were also expected to affect clearance rates at low DO.

Predation is the result of many small-scale processes, including encounter, escape, and capture (Gerritsen and Strickler 1977, Larson 1987, Purcell 1997, Waggett and Costello 1999, Costello et al. 1999), all of which are directly related to swimming speeds of both predator and prey (Gerritsen and Strickler 1977). Despite a high survival tolerance to low DO concentrations (Breitburg et al. 2003), ctenophore swimming speeds were affected by low DO, with increased swimming speeds in laboratory tanks at intermediate DO concentrations (Kolesar Chapter 3). In contrast, swimming speeds of the more hypoxia sensitive fish larvae were not significantly affected by low DO within the range of DO concentrations tested (Kolesar Chapter 3). The lack of difference in clearance rates at high and low DO may be explained by the absence of a DO effect on swimming speeds of both ctenophores and larval fish at low and high DO concentrations. But the unexpected results for the effect of intermediate DO on swimming speeds of ctenophores cannot account for the absence of a DO effect on clearance rates.

Ctenophore clearance rates ($L \text{ ml ctenophore}^{-1} \text{ h}^{-1}$) in my experiments were highest for bay anchovy yolk sac larvae, intermediate for bay anchovy eggs and lowest for naked goby larvae (Fig. 2.1a - c). These results are similar to those of Monteleone and Duguay (1988), who found that *M. leidyi* predation was higher on bay anchovy yolk sac larvae than on bay anchovy eggs and then declined as larvae grew. Clearance rates calculated from my laboratory experiments were comparable to those found in other studies (Monteleone and Duguay 1988, Cowan and Houde 1993, Purcell and Decker 2005), especially at my control DO concentrations.

Differences in ctenophore clearance rates on the three ichthyoplankton prey may reflect ontogenetic changes in prey swimming speeds (which can affect encounter probability) as well as prey escape ability. Fish eggs are passive and do not swim, are smaller than fish larvae, and have no escape ability. Assuming that the ctenophore reactive distance is constant, fish eggs will have smaller encounter rates than larval fish with ctenophores. The combination of these factors could lead to lower clearance rates for fish eggs than for yolk sac larvae. Bay anchovy yolk sac larvae swim, which increases their encounter rates with ctenophores relative to fish eggs, but they have limited escape abilities compared with older larvae (Bailey and Batty 1984, Purcell et al. 1987). Naked goby larvae were the most developed stage tested here; while they are the fastest swimmers, which would increase encounter rate, they also have the greatest escape abilities. The opposing effects of naked goby larvae swimming speed and escape ability on interactions with ctenophore predators have been used to explain smaller clearance rates on naked goby larvae in other laboratory studies (Monteleone and Duguay 1988); a similar mechanism may explain smaller clearance rates on naked goby larvae in this study.

Effects of DO on Vertical Distribution & Overlap

The responses of organisms to low DO influence how they utilize the water column (Kolar and Rahel 1993, Breitburg 1994, Eby and Crowder 2002). Bottom DO affected the vertical distribution of each species I sampled. My results indicated that DO also affected vertical overlap between species, which might be especially important for interactions between predators and their prey. In all cases in which DO affected overlap between predators and their prey in this study, the degree of vertical overlap increased as

bottom DO increased, and was best described by a simple linear model or multivariate model including both DO and the abundance of another predator or competitor species (Tables 2.6 & 2.7). The proportions of both species of fish larvae, copepods, and ctenophores increased in the bottom layer of the water column as bottom DO increased, regardless of the time of day (Fig. 2.2b & c; Fig. 2.3), consequently increasing vertical overlap between predators and some motile prey at high bottom DO concentrations (Tables 2.5 & 2.6). Other studies of hypoxia and habitat report higher species co-occurrence as species are forced to utilize smaller volumes due to declining DO concentrations (Breitburg et al. 1997, Decker et al. 2004), resulting in habitat compression. Predator and prey in my study have very different tolerances to low D, and declining DO concentrations elicit different responses of predator and prey, resulting in vertical habitat separation at low DO.

Greater vertical overlaps between most of the predator and prey pairs in this study with increasing bottom DO (Tables 2.5 & 2.6) indicate the potential for increased encounters in the field when DO concentrations are high in the bottom layer. Some predators and prey also swim faster at high DO (Decker et al. 2004), increasing encounter potential at high DO. These potential increases are offset by the fact that prey escape ability is generally also greater when DO concentrations are high (Breitburg 1994). As a result, at high DO there could be confounding interactions of increasing encounter rates (due to both increased vertical overlap and faster predator and prey swimming speeds) and the increasing escape abilities of prey, such that although encounters may increase at higher bottom DO concentrations, predation rates may not necessarily increase.

One notable exception to the pattern of increasing vertical overlap with increasing bottom DO was daytime vertical overlap between ctenophore number and naked goby larvae which was best represented by a 3rd order regression ($P = 0.051$, Table 2.6). Overlap was large at low bottom DO because both predator and prey avoided low bottom DO waters and were abundant in the pycnocline. Overlap was large again at high bottom DO when both predator and prey were abundant in the bottom layer. Smaller and more variable overlap at intermediate bottom DO concentrations during the day were probably due to naked goby larvae preferentially using the pycnocline at bottom DO concentrations between 1 - 2 mg L⁻¹, while ctenophores were found in greatest proportion in the bottom layer at those same bottom DO concentrations (Fig. 2.2c & 2.3b).

Effects of Predators & Competitors on Vertical Distribution & Overlap

Simple regression models with bottom DO were often improved by including predator and competitor abundances, indicating that both a physical environmental factor (bottom DO) and components of the food web such as medusa predators, influenced habitat utilization and overlap between predators and prey (Table 2.7). In fact, the large percent of overlap explained by medusa predator terms in the significant stepwise regression models may indicate that the effect of predators was comparable in importance to bottom DO in determining vertical overlap between ctenophore predators and their prey. While bottom layer DO may directly affect species distribution, predator density may also affect species distribution, leading to both direct and indirect effects of bottom DO on vertical overlap between predator and prey. Stepwise regressions for some daytime and combined day and night overlaps had significant predator and competitor components even though bottom DO was not significant. The addition of medusae,

ctenophore and fish larvae abundances significantly improved the models for nighttime overlaps between ctenophores and both fish eggs and copepod prey, and ctenophores and larval fish were significant for the combined day and night overlap between copepods and bay anchovy larvae. In general, the proportion of most species was large in the pycnocline at low bottom DO and increased in the bottom layer as bottom DO increased (Fig. 2.2 & 2.3). The positive relationship between predator and prey vertical overlap and their predators and competitors is due to the similar response to bottom DO exhibited by most species examined in the study.

Prey may respond either more strongly or more rapidly (or are removed altogether) to the presence of a biological threat, such as a predator, than to suboptimal but non-lethal physical conditions, such as mild-to-moderate hypoxia, in the water column. In laboratory experiments examining the effect of low DO versus predator presence on fish prey behavior, Robb and Abrahams (2002) found that prey response to the predator was reduced under hypoxia compared with normoxia due to the adverse effect of low DO on predator behavior, rather than due to a direct effect of hypoxia on the prey. Additionally, they concluded that it was important to study the effects of an environmental stressor such as low DO in conjunction with predation in order to obtain an accurate picture of the multiple factors affecting fish prey. Studies in the Neuse River estuary by Eby and Crowder (2002) showed evidence for context-dependent behavioral responses by young fish in areas where both hypoxia and species interactions, including predation and competition, were a factor. They found that habitat selection and species overlap were mitigated by both biotic and abiotic factors, with the importance of each factor depending on the extent and severity of environmental conditions at the time.

Vertical distribution in the water column can affect spatial overlap between a predator and prey pair, potentially altering predation rates. My data suggest that it is the influence of DO on vertical position within the water column, rather than the direct impacts of DO on predation rates that may be important in the interactions between ctenophores and their prey. For example, ctenophore swimming speeds were elevated at intermediate DO concentrations (Kolesar Chapter 3) which could increase predator – prey encounters at low-to-moderate ctenophore densities. In examining the effect of container size on predation rates, De Lafontaine and Leggett (1987) similarly concluded that vertical distributions of predator and prey may be particularly important in relationships between gelatinous predators (the medusa *Aurelia aurita*) and ichthyoplankton prey (larval capelin *Mallotus villosus*).

My laboratory predation experiments resulted in similar predation by ctenophores on the early life stages of fishes regardless of DO concentrations. The unstratified water column used in these experiments eliminated the natural variation in physical habitats found in the field. For example, without an oxygen gradient, there were no areas of different DO concentrations available to organisms as refuges from either DO stress or predation. A lack of refuges may be especially important for motile organisms such as fish larvae (Breitburg 1994), copepods (Decker and Marcus 2003), and ctenophores (Morris et al. unpubl.) that have been shown to actively avoid oxygen concentrations that were non-lethal yet stressful (Miller et al. 2002).

Increasing the number of samples at bottom DO concentrations between 1 – 2 mg L⁻¹, especially at night, may clarify species' responses to declining bottom DO conditions. Based on my data and results from other studies (Breitburg 1994, Keister et

al. 2000, Breitburg et al. 2003), maintaining target Chesapeake Bay bottom DO concentrations $> 2 \text{ mg L}^{-1}$ is a reasonable recommendation for enhancing species' survival.

Vertical stratification (as well as other forms of patchiness) have important implications for all aquatic environments. In the Chesapeake Bay in particular, Govoni and Olney (1991) suggested that the non-uniform distribution of *M. leidy* could potentially affect predation on ichthyoplankton. Biodiversity, conservation and cross-scale processes can all be affected by spatial distribution of organisms in a three-dimensional environment (Resetarits 2005). The spatial structure of consumers in an ecosystem affects food web stability (McCann et al. 2005), and mobile omnivores (McCann and Hastings 1997) in an aquatic environment can be especially important to trophic dynamics. Spatial heterogeneity of species serving as both consumers and prey in aquatic systems (such as zooplankton) can also shape food web interactions (Pinel-Alloul 1995).

Examining physical factors in the water column (such as DO) in conjunction with density, distribution, and abundance of organisms is necessary to determine the importance of physical habitat to predator and prey interactions. While my experiments showed that DO did not directly affect predation between *M. leidy* and ichthyoplankton, effects of DO on swimming speeds, behavior, and vertical distributions of predator and prey are important to food web dynamics in seasonally oxygen-stratified estuarine systems. Further examination of species' responses to DO, both at the level of the individual as well as intraspecific interactions, will provide important answers to basic questions about effects of species' behaviors and spatial distributions on food web

dynamics, taking the next steps towards comprehensive understanding of the role of physical habitat stress and biological dynamics in aquatic systems.

Table 2.1. Conditions for predation experiments in 100 L tanks. The three target dissolved oxygen (DO) concentrations were 1.5 mg L⁻¹, 2.5 mg L⁻¹, and an air-saturated control. Bay anchovy egg and naked goby larvae experiments were performed in 1999 and bay anchovy yolk sac larvae experiments were run in 2001. Naked goby larvae ages were 4 days post hatch (dph) and 1 dph in the June 2 and June 15 experiments, respectively. The number of replicate tanks per DO treatment for each 2 day experimental ‘date’ is indicated by N. Data are presented as mean ± SE.

Prey	Date	Duration (h)	DO Concentrations (mg L ⁻¹)			Prey tank ⁻¹	Ctenophores tank ⁻¹	Ctenophore total vol (ml)	(N)
			Low	Mid	High				
Bay anchovy:									
Eggs	July 8-9	4	1.54 ± 0.02	2.39 ± 0.09	7.65 ± 0.02	200	10	87.56 ± 3.44	3
Eggs	July 15-16	4	1.53 ± 0.08	2.50 ± 0.05	7.65 ± 0.02	100	10 – 11	211.44 ± 9.19	3
Yolk sac larvae	July 12-13	2	1.61 ± 0.02	2.59 ± 0.03	6.87 ± 0.23	35 – 47	8	113.89 ± 3.33	3
Yolk sac larvae	August 8-9	2	1.88 ± 0.07	2.63 ± 0.01	6.86 ± 0.07	32	10	237.67 ± 6.89	1
Naked goby:									
Larvae	June 2-3	6	1.74 ± 0.04	2.66 ± 0.03	7.23 ± 0.17	200	12 – 13	163.67 ± 6.19	3
Larvae	June 1 -16	6	1.68 ± 0.07	2.54 ± 0.06	7.26 ± 0.06	200	11 - 13	215.11 ± 7.74	3

Table 2.2. Bottom layer DO in the Patuxent River. Bottom layer dissolved oxygen (DO) during 1999 and 2001 for St. Leonard's Creek (20 m depth) and Battle Creek (16 m depth). Numbers represent bottom DO measurements (mg L^{-1}) from duplicate samples taken with a YSI model 52 DO meter attached to the frame of the Tucker Trawl net on each date, both day and night. ns = no sample taken, ^a DO from CTD profile used, ^b only one bottom DO sample taken

	Bottom dissolved oxygen (mg L^{-1})			
	22 Jun 99	27 July 99	24 Aug 99	5 Jul 01
<hr/>				
St. Leonard's Creek				
Day	6.1, 6.3	2.3, 2.5	3.8, 4.0	ns, ns
Night	5.8 ^a , 5.8 ^a	3.3, 3.4	4.5, 5.1	2.3, 1.7
Battle Creek				
Day	7.5 ^b , 7.5 ^b	2.9, 2.8	4.5 ^b , 4.5 ^b	
Night	6.0, 6.2	2.7, 2.9	5.4, 5.3	

Table 2.3. *Mnemiopsis leidyi*, effects of DO on predation and clearance rates. Effects of dissolved oxygen (DO) on percent predation and clearance rates of ctenophores on bay anchovy eggs, bay anchovy yolk sac larvae (*Anchoa mitchilli*), and naked goby larvae (*Gobiosoma bosc*). Ctenophore clearance rates on naked goby larvae and bay anchovy yolk sac larvae were untransformed, but clearance rates of bay anchovy eggs were \log_{10} transformed to correct for normality of residuals. The three DO treatments tested were 1.5 mg L^{-1} , 2.5 mg L^{-1} , and an air-saturated control. Ctenophore clearance rate data were analyzed using analysis of variance with date as a blocking factor. Results presented are for the test of the DO main effect. The P-value (P), F-value (F) and degrees of freedom (DF numerator, denominator) are listed. Untransformed predation (%) and clearance rate ($\text{L ml}^{-1} \text{ h}^{-1}$) are presented as mean \pm SE. Statistical significance is set at $\alpha < 0.05$.

Prey	Predation (%)	Clearance ($\text{L ml}^{-1} \text{ h}^{-1}$)	P	F	DF
Bay anchovy eggs	26.9 ± 0.02	0.07 ± 0.008	0.18	1.93	2, 14
Bay anchovy yolk sac larvae	49.3 ± 0.04	0.38 ± 0.05	0.41	1.00	2, 8
Naked goby larvae	39.7 ± 0.03	0.04 ± 0.004	0.81	0.21	2, 14

Table 2.4. Mean field densities. Densities are reported for all organisms examined in this study from 1992, 1993, 1999, and 2001. Numbers are means \pm SE of all years and for the early and later time periods separately, with the number of samples in parentheses. Data from 1992 and 1993 are reanalyzed from Keister et al. (2000).

Organism	All Years (129)	1992 & 1993 (90)	1999 & 2001 (39)
Ctenophore volume (ml) m ⁻³	16.4 \pm 3.0	13.2 \pm 4.0	23.7 \pm 3.7
Ctenophore number m ⁻³	4.4 \pm 1.2	5.1 \pm 1.7	2.9 \pm 0.5
Fish egg number m ⁻³	30.4 \pm 7.2	39.1 \pm 10.0	10.4 \pm 3.5
Bay anchovy larvae number m ⁻³	1.1 \pm 0.2	1.4 \pm 0.3	0.3 \pm 0.1
Naked goby larvae number m ⁻³	5.0 \pm 0.6	6.5 \pm 0.8	1.5 \pm 0.3
Copepod number L ⁻¹	24.6 \pm 2.4	30.8 \pm 3.1	10.5 \pm 1.5
Medusa volume (ml) m ⁻³	4.3 \pm 0.5	6.0 \pm 0.7	0.6 \pm 0.1
Medusa number m ⁻³	0.1 \pm 0.01	0.1 \pm 0.01	0.008 \pm 0.002

Table 2.5. Schoener's Index of habitat overlap. Untransformed values for Schoener's Index of habitat overlap for all predator and prey pairs averaged over DO values and time of day. Numbers are reported as mean \pm SE (N).

Predator and Prey Pair	Vertical Overlap
Ctenophore volume & Fish eggs	0.60 \pm 0.05 (29)
Ctenophore number & Fish eggs	0.59 \pm 0.05 (29)
Ctenophore volume & Copepods	0.71 \pm 0.04 (30)
Ctenophore number & Copepods	0.70 \pm 0.04 (30)
Ctenophore volume & Bay anchovy larvae	0.63 \pm 0.05 (26)
Ctenophore number & Bay anchovy larvae	0.63 \pm 0.04 (26)
Ctenophore volume & Naked goby larvae	0.65 \pm 0.04 (30)
Ctenophore number & Naked goby larvae	0.66 \pm 0.04 (30)
Bay anchovy larvae & Copepods	0.70 \pm 0.03 (39)
Naked goby larvae & Copepods	0.82 \pm 0.02 (43)

Table 2.6. Effects of bottom layer DO on vertical overlap. Effects of bottom layer DO concentration on Schoener's Index of vertical overlap between 10 pairs of predator and prey. Results from simple regressions are presented for combined day and night data (Day / night, n = 43), day separately (Day, n = 24), and night separately (Night, n = 19). Predators are listed in columns and prey are listed in rows. Bold indicates models significant at $\alpha < 0.10$, * model significant at $\alpha < 0.05$, otherwise the model with the smallest Akaike's Information Criteria (AIC) is reported, and is the linear model, unless otherwise indicated (+ 2nd order model, § 3rd order model). NA = not-applicable.

DAY & NIGHT COMBINED

	Ctenophore volume	Ctenophore number	Bay anchovy larvae	Naked goby larvae
Fish eggs	$P_{(DF)} = 0.55_{(27, 28)}$ $R^2 = 0.0134$	0.74 _(27, 28)	NA	NA
Bay anchovy larvae	0.23 _(23, 25) ⁺ 0.1242	0.25 _(23, 25) ⁺ 0.1141	NA	NA
Naked goby larvae	0.01 _(28, 29) [*] 0.2001	0.14 _(27, 29) ⁺ 0.1354	NA	NA
Copepods	0.01 _(28, 29) [*] 0.1960	0.04 _(27, 29) ^{+*} 0.2162	0.08 _(37,38) 0.0814	0.006 _(41,42) [*] 0.1717

DAY

Fish eggs	$P_{(DF)} = 0.41_{(14, 15)}$	$0.29_{(13, 15)}^+$	NA	NA
	$R^2 = 0.0486$	0.1754		
Bay anchovy larvae	$0.92_{(14, 15)}$	$0.73_{(10, 11)}$	NA	NA
	0.0010	0.0127		
Naked goby larvae	$0.12_{(14, 15)}$	$0.051_{(12, 15)}^{\$}$	NA	NA
	0.1643	0.4643		
Copepods	$0.14_{(14, 15)}$	$0.15_{(13, 15)}^+$	$0.32_{(18, 19)}$	0.053 $_{(22, 23)}$
	0.1475	0.2499	0.0546	0.1595

NIGHT

Fish eggs	$P_{(DF)} = 0.56_{(11, 12)}$	$0.96_{(11, 12)}$	NA	NA
	$R^2 = 0.0314$	0.0003		

Bay anchovy larvae	0.35 _(11, 13) ⁺ 0.1748	0.35 _(12, 13) 0.0728	NA	NA
Naked goby larvae	0.054 _(12, 13) 0.2746	0.48 _(12, 13) 0.0425	NA	NA
Copepods	0.052 _(12, 13) 0.2790	0.03 _(12, 13) * 0.3204	0.17 _(17, 18) 0.1080	0.06 _(17, 18) 0.1899

Table 2.7. Significant stepwise regression analysis results for predator and prey overlap with bottom DO. Ten predator and prey pairs are compared, as in Table 2.6. There were no significant stepwise regressions for the daytime data with bottom DO.

	P (DF)	R²	F	Terms, Contribution (%)
DAY & NIGHT COMBINED				
Ctenophore volume & Copepods	0.001 (2, 27, 29)	0.3881	8.56	Medusa volume, 86% Bottom DO, 14%
Ctenophore number & Copepods	0.005 (2, 27, 29)	0.3238	6.46	Medusa number, 76% Bottom DO, 24%
NIGHT				
Ctenophore volume & Fish eggs	0.05 (2, 10, 12)	0.4503	4.10	Medusa volume, 63% Bottom DO, 37%
Ctenophore volume & Copepods	0.01 (2, 11, 13)	0.5366	6.37	Medusa volume, 80% Bottom DO, 20%

Figure 2.1. *Mnemiopsis leidyi*, laboratory clearance rates. Clearance rates of ctenophores in laboratory experiments (L cleared ml ctenophore⁻¹ h⁻¹) adjusted for recovery of three prey types: (a) bay anchovy eggs, (b) bay anchovy yolk sac larvae, and (c) naked goby larvae. Note different y-axis scales for each prey type.

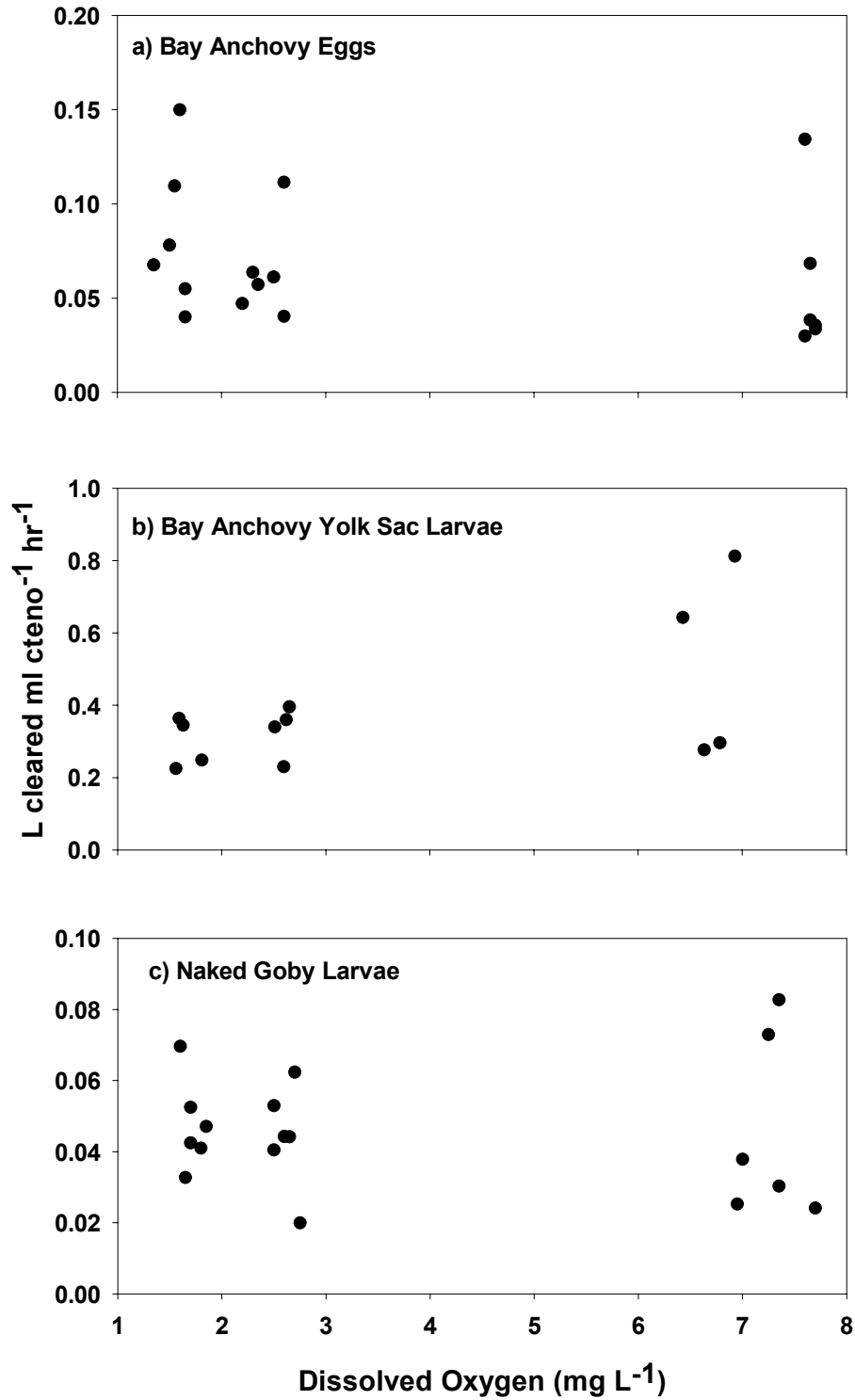


Figure 2.2. Field proportions of ichthyoplankton. Proportion of three ichthyoplankton types [(a) fish eggs, (b) bay anchovy larvae < 15mm, and (c) naked goby larvae] in the three layers of the water column; surface layer ('x's), pycnocline (circles), and bottom layer (triangles) for day and night plotted against bottom DO concentration. For reference, a linear equation is fit to the distribution in the bottom layer.

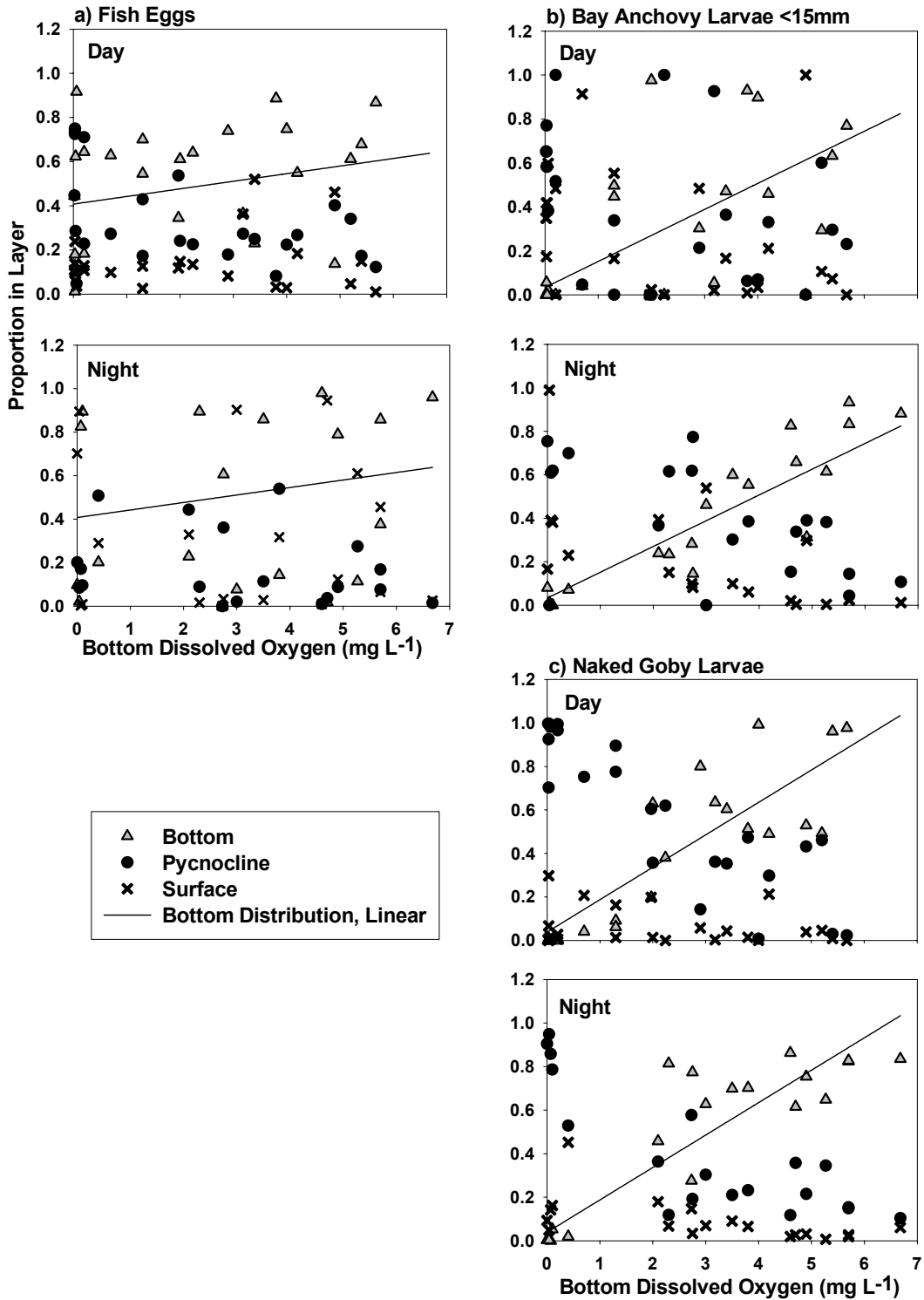
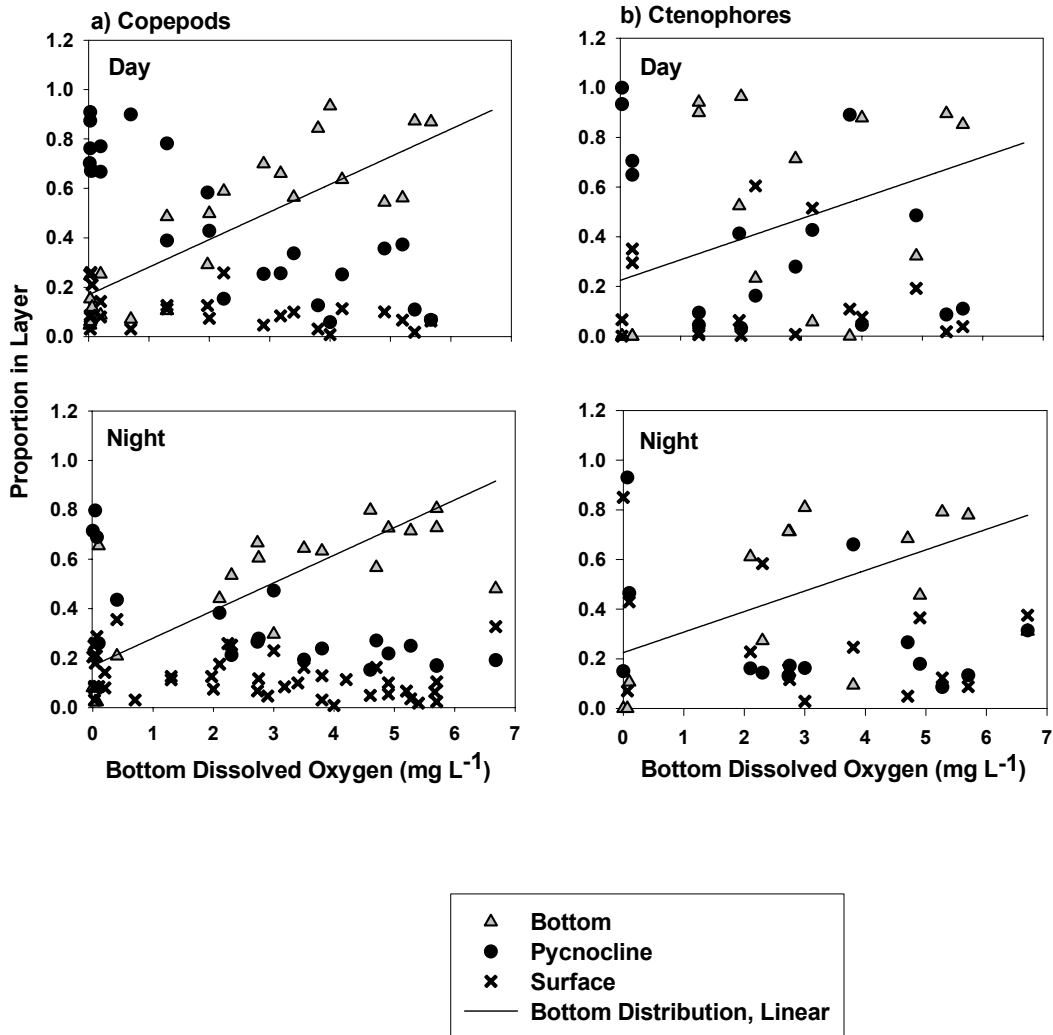


Figure 2.3. Field proportions of zooplankton. Proportion of two zooplankton species [(a) copepods and (b) ctenophores] in the three layers of the water column; surface layer ('x's), pycnocline (circles), and bottom layer (triangles) for day and night plotted against bottom DO concentration. Additionally, in Figure 3a there are 7 hidden observations during the day and 5 hidden observations at night. For reference, a linear equation is fit to the distribution in the bottom layer.



Chapter 3: The effect of low dissolved oxygen on behavioral interactions and swimming speeds of ctenophore predators and larval fish prey

INTRODUCTION

The outcomes of predator-prey interactions can be influenced by both biological and environmental factors, and understanding the interplay of these factors is critical in developing accurate predictions of predator effects. A major challenge in the study of trophic interactions is the coupling of processes occurring among organisms across different scales. Although the effects of predation are often realized at the scale of the population, interactions occur at the individual level and therefore both predator and prey behavior have an important influence on the outcome (Letcher and Rice 1997, Fuiman and Cowan 2003, Hampton 2004). Traditional measurements of clearance rates (Monteleone and Duguay 1988, Cowan and Houde 1993, Kolesar Chapter 2) can obscure the effects of predator and prey behaviors such as encounter rates, escape abilities, or swimming speeds on food web interactions, and scaling up from laboratory experiments to whole systems may not result in accurate estimates of predation rates.

Predator-prey interactions occur as a sequence of interactions between individuals (Fig. 3.1), and factors that alter behavior can potentially affect any of the steps leading to ingestion. Within the sequence from encounter to ingestion, the potential to escape at any point prior to ingestion can be fairly high for large, motile prey, as found by Costello et al. (1999) for ctenophore predation on copepods. However, repeated interactions can occur, and subsequent interactions with the same or different predators can increase the probability of predation (Costello et al. 1999). Population models generally employ cumulative predation (such as measured clearance rate) for populations of predators and prey, but these indices lack the mechanistic information required to predict changes in

predation. Furthermore, since the probability of prey capture depends on specific behaviors of both predator and prey, it is critical to account for environmental factors, such as low dissolved oxygen (DO), that may ultimately affect predation due to the different physiological responses of predators and prey.

Seasonal hypoxia can have a large influence on aquatic food web interactions at a variety of scales. Hypoxia, typically defined as DO less than 2 mg L^{-1} , occurs in many estuaries and coastal regions worldwide (Diaz and Rosenberg 1995, Diaz et al. 2004). Effects of hypoxia on individual behaviors of both predator and prey include changes in swimming and escape ability (Breitburg 1994, Breitburg et al. 1997, Weltzien et al. 1999), as well as shifts in distribution and habitat use (Breitburg 1992, Keister et al. 2000, Eby and Crowder 2002, Breitburg et al. 2003, Bell et al. 2003, North and Houde 2004, Kolesar Chapter 2). Predator and prey may be differentially affected by DO conditions due to different physiological tolerances (Breitburg et al. 1994, 1997, 1999; Rahel and Nutzman 1994, Nestlerode and Diaz 1998, Taylor and Eggleston 2000, Breitburg 2002, Seitz et al. 2003, Mistri 2004), so predicting the influence of hypoxia on food web interactions may not be straightforward. Because low DO can modify behavior in planktonic food webs (Breitburg 1994, Breitburg et al. 1997, Weltzien et al. 1999, Robb and Abrahams 2002), and the effect of low DO on behavior can change predator-prey interactions, it is likely that low DO will alter predation rates (Breitburg et al. 1994, 1997).

Ctenophores (*Mnemiopsis leidyi*) are predatory gelatinous zooplankton native to coastal areas, including Chesapeake Bay (Purcell et al. 2001b). They are voracious predators and can have a large effect on mesozooplankton and ichthyoplankton

communities (Monteleone and Duguay 1988, Govoni and Olney 1991, Cowan and Houde 1992, 1993; Houde et al. 1994, Purcell et al. 1994, 2001a & b). Ctenophore consumption on fish eggs, yolk sac and post-yolk sac fish larvae in the Chesapeake Bay and its tributaries were estimated to range from 10 – 65 % day⁻¹ (Monteleone and Duguay 1988, Cowan and Houde 1993, Purcell et al. 1994a); since current ctenophore densities are higher than in the past (Purcell et al. 2001, Breitburg et al. 2003, Purcell and Decker 2005, Kolesar Chapter 2), the current potential for predation on ichthyoplankton is even greater. Ctenophores are important predators on larvae of fish such as the naked goby (*Gobiosoma bosc*) and bay anchovy (*Anchoa mitchilli*) in the summertime Chesapeake Bay in areas with bottom water hypoxia.

Ctenophores and larval fish differ in their tolerances and responses to low DO (Breitburg et al. 1997, 1999; Purcell et al. 2001b, Breitburg 2002). Both laboratory experiments and field distributions indicate that ctenophores are more tolerant of low DO than their larval naked goby or bay anchovy larval prey. Individual ctenophores held in the laboratory survived for 96 hours at DO concentrations of 0.5 mg L⁻¹ (Breitburg et al. 2003) and large numbers of ctenophores are found inhabiting areas of the Chesapeake Bay system with DO concentrations between 1 and 2 mg L⁻¹ (Keister et al. 2000, Breitburg et al. 2003, Kolesar Chapter 2). In contrast, the 24 to 96 h LC₅₀ for most estuarine fish larvae is 1 - 2 mg L⁻¹ (Miller et al. 2002), and bay anchovy and naked goby larvae actively avoid DO concentrations ≤ 2.0 mg L⁻¹ (Breitburg 1994).

Differences in tolerances and behavioral responses to low DO would be expected to influence many aspects of the interactions between ctenophores and fish larvae. Surprisingly, laboratory experiments indicated that clearance rates of ctenophores feeding

on bay anchovy yolk sac larvae and naked goby larvae at DO concentrations of 1.5 and 2.5 mg L⁻¹ do not differ from clearance rates at DO concentrations near saturation (Kolesar Chapter 2). These results do not preclude the possibility that low DO affects individual components of the predation interaction.

I examined the individual components of predator-prey interactions between a ctenophore predator and its larval naked goby prey to better understand the effects of DO on predation and related behaviors. Two separate approaches were used: 1) small-scale video observations quantifying encounters and ingestion between individual ctenophores and fish larvae and 2) videotaped swimming speed measurements for both ctenophores and larval fish over a range of DO concentrations. In order to examine the potential for hypoxia to influence predation on a population scale, I developed an encounter model incorporating measured encounters, ingestions, and swimming speeds and compared it against published clearance rate estimates of ctenophores on fish larvae (Cowan and Houde 1993, Purcell et al. 2001b, Kolesar Chapter 2).

My primary hypothesis, that low DO would decrease encounters between predator and prey but increase ctenophore predation on larval fish, was based on the expectation that larval fish swimming ability would be adversely affected by low DO but that ctenophore swimming speeds would not be affected due to their higher tolerance of low DO. At low DO, slower swimming fish larvae would encounter fewer ctenophore predators than at high DO, while reduced larval fish escape abilities at low DO would lead to a higher rate of ingestion per encounter at low DO than at high DO. Because the influence of low DO on fish larvae is inversely related to age (Breitburg 1994), I also hypothesized that younger larvae would fare worse than older larvae, experiencing a

greater decrease in swimming speeds (Bailey 1984) and increase in ingestion by ctenophores at low DO. Finally, I hypothesized that multiple encounters between predator and prey, which likely occur under high ctenophore field densities, would lead to higher ingestion rates than from the initial encounter only.

MATERIALS AND METHODS

Encounter rate experiments were conducted in June 2001 and June – July 2002, and swimming speed experiments in June – July 2000 at the Academy of Natural Sciences Estuarine Research Center (ANSERC; now Morgan State University) in St. Leonard, Maryland. All organisms used in experiments were collected in the mesohaline portion of the Patuxent River estuary, MD and maintained in ANSERC laboratory facilities.

Ctenophores were collected in the field either by dip-netting or in short plankton tows, and were maintained in the laboratory for up to a week following the methods of Decker et al. (2004). I selected ctenophores for experiments to represent the average size of individuals in the field. At the end of each trial, I measured displacement volume to the nearest ml and length to the nearest 5 mm of ctenophores used in filming.

Naked gobies are benthic oyster-reef-dwelling fish that lay nests inside oyster shell. Their planktonic larvae inhabit the water column for about 30 days post hatch (dph), or until they reach about 10 mm in length, during which time they are vulnerable to ctenophore predation. Naked goby nests along with the guarding male were field-collected and larval fish were hatched in the laboratory and reared in 80 L tanks at ambient temperature and salinity for up to 1 month. Larval fish were initially stocked at densities of 25 L^{-1} and fed laboratory-reared rotifers (*Brachionus plicatus*). After 2

weeks in the laboratory, larval fish densities were reduced by about half and feeding was supplemented with brine shrimp nauplii (*Artemia spp.*) following the methods outlined in Kolesar Chapter 1. After each day of filming a representative sample of fish larvae (5 – 10 individuals) were anesthetized with MS-222, filmed for subsequent measurements, and preserved in 75% ethanol.

Naked goby larvae used in experiments ranged in age from 1 – 30 dph and were grouped into two categories based on feeding and body morphology: 1) young larvae 1 – 14 dph that feed primarily on microzooplankton, and 2) older larvae 15 – 30 dph that also feed on larger zooplankton. These categories were chosen to reflect not only differences in diet, but also in overall body morphology, swimming capability and physiological tolerances. Naked goby larvae grow from 1 mm to 10 mm in about a month, gaining significant mass during that time. This transition may influence the ability of naked goby larvae to escape ctenophore predators as well as their overall vulnerability to predation.

Encounter Sequence Interactions

To determine the effect of DO on individual-level responses of ctenophores and their larval fish prey, small-scale observations of predation interactions between individual ctenophores (average length = 58.3 ± 0.9 mm, range = 35 – 85 mm, N = 102) and naked goby larvae (age range = 1 – 30 dph) were filmed in the laboratory at low and high DO concentrations. The DO treatments examined were low DO between 1.5 – 2.2 mg L⁻¹ and high DO at air-saturated levels between 5.7 – 8.0 mg L⁻¹ (Table 3.1). Target DO concentrations in the 2 L containers were achieved by bubbling 0.5- μ m filtered Patuxent River water with either nitrogen gas or air prior to introduction of animals. Experimental temperature and salinity reflected ambient summertime conditions in the

mesohaline Chesapeake Bay (Table 3.1). Predator and prey were acclimated in separate chambers to experimental DO concentrations for 30 minutes prior to filming. A non-airtight plexiglass lid was placed over the container during filming to limit gas exchange between the water surface and the atmosphere, and DO measurements were made at the beginning and end of each trial with a YSI model 85 DO meter in order to determine the change in DO during the observation period. The filming container was illuminated from below by a diffuse light source, which did not appear to influence ctenophore or larval fish behavior during videotaping. Filming began immediately following introduction of the organisms. A Sony Handycam Hi-8 video camera with standard resolution and lens (TRV-66 or 95) was used to follow predation interactions for up to 1 hour or until ingestion occurred.

Waggett and Costello (1999) described the sequence of interactions leading to ingestion of zooplankton prey by *Mnemiopsis leidyi* (see also Costello et al. 1999). I modified their classification of a potential predation event assuming that the interaction began upon encounter between a ctenophore predator and a larval fish prey and progressed through interactions including contact and capture as well as a several separate escape probabilities before culminating in ingestion (Fig. 3.1). Interactions were sorted into 4 categories (after Waggett and Costello 1999, Costello et al. 1999): encounter, contact, capture, and ingestion, as well as 3 separate escape stages: post-encounter (EncEscape), post-contact (ConEscape), and post-capture (CapEscape) (Fig. 3.1). Encounter was defined as proximity of predator and prey and depended on the length of both organisms to encompass the area of altered water flow generated by the ctenophore swimming and feeding mechanism, as well as the larval fish prey's body

length. For this study, all encounters occurred when a larval fish was within 10 mm from the lobes of a ctenophore. Contact occurred when a fish larva touched one of the muscular lobes of the ctenophore, which are their primary site of capture for large zooplankton and ichthyoplankton prey (Costello et al. 1999). Capture occurred when the fish larva was actually inside the lobes of the ctenophore, and was usually accompanied by struggling of the prey and movement of the prey by the predator towards the gut cavity. Ingestion occurred when the fish larva was moved into the gut cavity of the ctenophore and struggling ceased.

Encounters were calculated as the positive occurrences of encounter (yes encounter versus no encounter) summed over all trials divided by the total number of trials. The probabilities of all subsequent events (contact, capture, ingestion, EncEscape, ConEscape, and CapEscape) were each computed as the positive occurrence of that event (yes vs. no) summed over all trials divided by the number of positive encounter occurrences for all trials. During the predation sequence the three separate escape probabilities could lead to multiple cycles through the steps leading to ingestion (Fig. 3.1), so the probability of contact, capture, ingestion, and EncEscape, ConEscape, and CapEscape occurring after the first encounter between predator and prey were also each calculated separately.

I analyzed data for the occurrence of encounters (yes versus no) leading to ingestion using exact logistic regression (using SAS version 9.1 statistical software) for all combined encounters between a ctenophore and fish larva for the two DO concentrations and two larval fish age classes. Since both predator and prey can become sensitized to the presence of the other through multiple iterations of the interaction

sequence, the outcome of the first encounter between predator and prey was noted and separately analyzed. Statistical significance was set at $\alpha < 0.05$.

Swimming Speeds of Predator & Prey

In order to determine the effect of DO on swimming ability I measured the three-dimensional swimming speeds of ctenophores and naked goby fish larvae at three DO concentrations. Swimming predator and prey were filmed in a custom-built chamber consisting of a rectangular tank (300 mm wide x 610 mm high) with a 40 L plexiglass cylinder inside (Fig. 3.2). This configuration was designed to eliminate possible effects of tank corners on predator-prey interactions by placing organisms in the interior cylinder while reducing optical distortion from the cylinder on filming by filling the space between the tank and the cylinder with water. Two video cameras (SONY HandyCam models TRV-66 and 95) placed orthogonal to each other provided a three-dimensional measure of swimming speed. Both cameras were situated 15 cm from the outside wall of the tank, and the focus was adjusted so that an 80 mm x 80 mm area in the center of the tank (to minimize the possibility of wall effects on behavior) filled the field of view (Fig. 3.2). Three target DO concentrations were tested: low DO (1.5 mg L^{-1}), intermediate DO (2.5 mg L^{-1}), and high DO which was air-saturated (around 7 mg L^{-1}). Target DO concentrations were adjusted by bubbling 0.5- μm filtered Patuxent River water in the interior of the chamber with nitrogen gas or air prior to addition of organisms. DO, water temperature, and salinity were measured at the start and end of each experiment with a YSI model 85 or 95 DO meter and a hand refractometer (Table 3.2). Four to 10 ctenophores (mean length = $57.1 \pm 2.3 \text{ mm}$, $N = 17$) and a target number of 100 naked goby larvae 3- 20 dph (mean length = $4.5 \pm 0.2 \text{ mm}$, $N = 23$) were included in each trial.

Microzooplankton prey were added to each trial (approximately 200 - 300 ml of the rotifer *Brachionus plicatus* at a density of approximately 300 rotifers ml⁻¹) to encourage normal swimming and feeding behavior of the fish larvae.

Naked goby larvae were acclimated to DO conditions in the inner cylinder approximately 30 minutes prior to the addition of ctenophores, which were acclimated in separate containers. Filming began immediately after introduction of ctenophore predators and lasted for 2 hours. For each trial, both videotapes were stamped with a synchronized time code and simultaneous presence of an individual ctenophore and fish larva was noted. Between 2 – 5 sequences trial⁻¹ for each organism were digitized and three-dimensional swimming speeds were calculated using an Optimus Motion Analysis software macro. Swimming speed measurement duration was 2 seconds for ctenophores and 1.5 seconds for fish larvae; a representative sample of cumulative mean swimming speeds for each species indicated that this was a sufficient duration to capture average swimming speeds (Fig. 3.3a & b).

Swimming speeds of ctenophores and larval fish were separately analyzed using mixed model ANOVA (SAS version 9.1 statistical software) to determine if swimming speeds (mm s⁻¹) differed at the three DO levels. The interaction between swimming speed and length was also examined. Since all interactions were non-significant, interaction terms were dropped from analyses. Means comparisons with Tukey's adjustment were also included to distinguish differences in swimming speeds among the DO concentrations. Statistical significance was set at $\alpha < 0.05$.

Encounter Model

I combined the laboratory measurements of ctenophore and larval fish encounters with swimming speeds in an encounter model to predict the effect of DO concentration on predation potential. The encounter model equation was based on a model described by Gerritsen and Strickler (1977):

$$E = 3.14 * (RLarv + RCteno)^2 * C * Vert * PD$$

where E was the encounter rate (number of fish larvae m^{-3} encountered by an individual ctenophore d^{-1}), and PD was the number of larval fish prey in one cubic meter of water. An adjustment to convert mm to m^{-3} ($Vert = 10^{-9}$) was applied to the encounter equation.

The encounter surface for foraging ctenophore predators consists of both lobes opened, best approximated as an ellipse. Therefore, the encounter radius of each ctenophore predator ($RCteno$) was modeled as an ellipse based on ctenophore length in mm ($CtLn$). The encounter radius of each fish larva ($RLarv$) was modeled as larval fish length in mm ($LvLn$):

$$RCteno = ((0.33 * CtLn) + (0.33 * CtLn / 2.0)) / 2.0$$

$$RLarv = LvLn$$

The distances swum by larval fish and ctenophores ($DLarv$ and $DCteno$, $mm d^{-1}$) were based on measured mean swimming speeds of fish larvae ($LvSsp$) and ctenophores ($CtSsp$), both in $mm s^{-1}$:

$$DLarv = LvSsp * 86400$$

$$DCteno = CtSsp * 86400$$

and used to calculate the foraging rate, C ($mm d^{-1}$). Alternate equations were used depending on which organism swam a greater distance:

$$C = (DLarv^2 + 3.0 * DCteno^2) / (3.0 * DCteno), \text{ if } DCteno > DLarv$$

or

$$C = (DCteno^2 + 3.0 * DLarv^2) / (3.0 * DLarv), \text{ if } DCteno \leq DLarv$$

In order to determine the potential for DO to alter predator-prey encounters and ingestions in the field, I applied the above equation for E, as well as the measured percent ingestions given encounter, to a ctenophore predator and larval fish prey at different DO concentrations. The two DO levels modeled (low DO = 1 - 2 mg L⁻¹ and high DO = 7.0 mg L⁻¹) corresponded to those in my laboratory observations of encounter interactions. Swimming speeds of ctenophores and larval fish were averaged across measurements at low and intermediate DO to correspond to DO levels used for encounter interactions (1 - 2 mg L⁻¹). I also used measured swimming speeds at high DO (7 mg L⁻¹).

The modeled predator and prey were selected to represent typical sizes of ctenophores and larval fish, as well as larval fish densities, present in the summertime mesohaline Chesapeake Bay system. A 50 mm, 14 ml ctenophore was modeled, corresponding to the average size of ctenophores used in all of my laboratory studies as well as the same size used by Purcell et al. (2001b) in their clearance rate estimates. I also modeled two age classes of fish larvae (young larval fish ≤ 14 dph, average length = 3.5 mm and older larval fish > 14 dph, average length = 5.5 mm) which were identical to the classifications used in both laboratory swimming speeds measurements and laboratory predation interactions. Larval fish density was modeled as 2 m⁻³, which is the average density measured in the field (Keister et al. 2000, Purcell et al. 2001a). I used my laboratory measurements of swimming speeds for ctenophores and both larval fish age classes to parameterize the encounter model equation.

RESULTS

Small-Scale Predation Interactions

DO did not significantly affect any of the steps from encounter to ingestion for either the first or subsequent encounters. The percent of trials resulting in encounters between ctenophores and fish larvae for all DO levels and larval fish ages was at least 90% (Fig. 3.4). For the first encounter between predator and prey, there was no significant effect of DO alone on any of the steps in the sequence from encounter to ingestion (Fig. 3.4a, all $P > 0.5$). Ingestion of fish larvae by ctenophores following the first encounter at both high and low DO was almost identical and averaged about 10% for both age classes of larval fish combined (Fig. 3.4a). For cumulative encounters between a ctenophore predator and larval fish prey there was no significant effect of DO alone on any of the steps from encounter to ingestion (Fig. 3.4b, all $P > 0.1$). Ingestion resulting from cumulative encounters averaged about 50% and was slightly higher at high DO (65%) than at low DO (47%) (Fig. 3.4b).

For the first encounter, larval fish age had a significant effect on some of the interactions between a ctenophore predator and a larval fish prey. Contact resulting from the first encounter tended to be higher but not statistically significant for younger fish larvae than for older fish larvae ($P > 0.2$). Capture of younger fish larvae was significantly higher than capture of older fish larvae ($P < 0.04$) (Fig. 3.4a). The percent of both EncEscape and ConEscape tended to be higher, but not statistically significant, for older fish larvae for the first encounter between predator and prey (both $P > 0.2$) while CapEscape was significantly higher for younger fish larvae ($P < 0.03$) (Figure 3.4a). There was no significant difference in ingestion between younger and older fish larvae for the first encounter between predator and prey (both $P > 0.5$), but the percent

ingestion tended to be larger for younger fish larvae at high DO and larger for older fish larvae at low DO (Fig. 3.4a).

For cumulative encounters (mean = 6.4, range = 2 – 18) capture was significantly higher for younger fish larvae than for older fish larvae (Fig. 3.4b, $P < 0.001$). In contrast, both EncEscape and ConEscape were significantly higher for older fish larvae than for younger fish larvae following cumulative encounters (Fig. 3.4b, both $P < 0.001$).

Ingestion resulting from multiple encounters was significantly higher for younger fish larvae (Fig. 3.4b, $P < 0.05$) and reached as high as 88% for young larvae at high DO and as low as 42% for older larvae at high DO (Fig. 3.4b). Larval fish escaping from prolonged contact with ctenophores were covered with strands of mucus from the ctenophore's colloblasts.

Swimming Speeds of Predator & Prey

Ctenophore swimming speeds were fairly constant during 2 s intervals (Fig. 3.3a) and were not affected by ctenophore length ($R^2 = 0.004$, $P = 0.8$). Swimming speeds were therefore estimated from 2 s duration observations and ctenophore length was not included in analyses.

Dissolved oxygen significantly affected ctenophore swimming speeds (mm s^{-1}) (ANOVA: $P_{2,13} = 0.02$; Fig. 3.5). Ctenophores swam significantly faster at intermediate DO (2.5 mg L^{-1} , $22.5 \pm 1.2 \text{ mm s}^{-1}$) than at either low DO (1.5 mg L^{-1} , $18.2 \pm 1.0 \text{ mm s}^{-1}$, Tukey's adjustment $P = 0.05$) or high DO (7.0 mg L^{-1} , $17.6 \pm 1.2 \text{ mm s}^{-1}$, Tukey's adjustment $P = 0.02$). Swimming speeds for the highest and lowest DO levels were not significantly different (Tukey's adjustment $P = 0.85$).

Naked goby larvae swam continuously during 2 s observation intervals, but alternated between faster and slower swimming speeds 2 – 3 times per second (Fig. 3.3b). Mean swimming speeds during 2 s intervals were used for analyses. Larval fish swimming speed unadjusted for body size was not significantly affected by DO ($P_{1,19} > 0.5$), or larval fish age ($P_{1,19} > 0.4$), but tended to be lower at intermediate DO (2.5 mg L^{-1} , $20.4 \pm 0.9 \text{ mm s}^{-1}$) than at either low DO (1.5 mg L^{-1} , $21.2 \pm 1.2 \text{ mm s}^{-1}$) or high DO (7.0 mg L^{-1} , $22.1 \pm 1.1 \text{ mm s}^{-1}$) (Fig. 3.6).

Encounter Model

Application of my encounter model and ingestion calculations yielded predictions of ctenophore predation at all combinations of larval fish age and DO concentration that were larger than expected based on laboratory studies. The number of predicted encounters m^{-3} for all combinations of larval fish age and experimental DO ranged between 3.81 and 4.69 encounters ctenophore $^{-1} \text{ d}^{-1}$ (Table 3.3). More encounters with ctenophores were predicted for older fish larvae than for younger fish larvae regardless of DO concentration (Table 3.3). For first encounters between ctenophores and larval fish the predicted number of ingestions ranged between 0.18 and 0.66 fish larvae m^{-3} ctenophore $^{-1} \text{ d}^{-1}$ (Table 3.3) and was largest for older fish larvae at low DO and younger fish larvae at high DO (Table 3.3). The predicted numbers of ingestions following multiple encounters between ctenophores and larval fish ranged between 1.68 and 3.38 fish larvae m^{-3} ctenophore $^{-1} \text{ d}^{-1}$ and was also largest for older fish larvae at low DO and younger fish larvae at high DO (Table 3.3).

DISCUSSION

Dissolved oxygen did not significantly affect encounters of fish larvae with ctenophores or their ingestion in small-scale laboratory observations of predation interactions. Nevertheless, ctenophore swimming speeds were elevated under moderate hypoxia, which could increase encounter rates between predators and prey in the field, and increase potential larval fish mortality. Although differences in DO did not significantly affect ctenophore ingestion of larval fish, larval fish age affected certain components of the interaction between predator and prey.

Effects of Swimming Speeds on Encounter & Ingestion

The combination of altered swimming speeds that can affect encounter rates between predator and prey, compromised capture abilities of predators and impaired escape responses of prey can confound the overall effect of low DO on predation, making it difficult to predict the overall effect of hypoxia on trophic interactions. Encounter rates between a ctenophore predator and larval fish prey were estimated from swimming speeds of both organisms, but larval fish swimming speeds may be especially important in post-encounter processes such as capture. Direct observations of predation interactions between ctenophores and larval fish revealed that most contacts between predator and prey occurred when a fish larva swam into the oral end of a ctenophore within the encounter radius. Increased swimming speeds of larval fish would be expected to increase the possibility of contact and repeated encounters with ctenophore predators. Potential escape from predation should also increase with increased swimming speeds. Swimming speeds of naked goby larvae were similar under high and low DO, however, perhaps explaining the lack of a DO effect on encounters, contacts, and escapes in these experiments.

Differences in predation strategies may affect the influence of low DO on predation of larval fish. Increased predation at low DO by predators such as medusae may be due to reduction of larval fish burst (escape) swimming speeds at low DO (Breitburg et al. 1997). The effect of DO on larval fish non-burst swimming speeds, as measured in this study, may be a more suitable metric than the effect of DO on burst swimming speeds for predation by a cruising predator such as a ctenophore. The larval fish cruising swimming speeds I measured fall within the normal range for fish of this size; therefore, my laboratory measurements are likely to translate into accurate predictions of field encounters related to larval fish speeds (Hunter 1972, Breitburg 1992, Miller et al. 1988, Fisher et al. 2000, Hunt von Herbing and Gallager 2000, Chamorro 2001).

Larval fish age and developmental stage can also affect escape abilities and swimming speeds, and potentially modify DO effects. For both first encounter and cumulative encounters, percent capture was significantly higher for younger larval fish at high DO than for any other DO condition or larval fish age (Fig. 3.4). Younger fish larvae swam faster than older fish larvae (young larvae mean swimming speed = $22.0 \pm 1.1 \text{ mm s}^{-1}$, N = 11; older fish larvae mean swimming speed = $20.5 \pm 0.6 \text{ mm s}^{-1}$, N = 12) and the fastest larval fish swimming speeds were at high DO (Fig. 3.6). For younger fish larvae, a combination of faster swimming and weaker escape abilities (Bailey and Batty 1984, Purcell et al. 1997) would be expected to result in increased capture by ctenophores. Previous studies documented a decrease in susceptibility to predation for older, larger larval fish (Bailey 1984, Cowan and Houde 1992, Sugisaki et al. 2001), which would suggest that low DO should further impair the ability of a fish larva to

escape ctenophore predation, although I found no evidence of a negative effect of low DO on escape probabilities in my experiment.

My measures of ctenophore swimming speeds were greater than foraging swimming speeds measured by a previous study. Kreps et al. (1997) reported swimming speeds of 2 - 11 mm s⁻¹ for *Mnemiopsis* of lengths 33 – 78 mm foraging on copepods. My measured ctenophore swimming speeds (15.4 – 26.3 mm s⁻¹) were within the range measured for escape (12 – 55 mm s⁻¹) and after contact (7 – 30 mm s⁻¹) with medusae predators (Kreps et al. 1997). Elevated ctenophore swimming speeds in my study may be a response to a faster-moving prey (larval fish) or to the confines of a 40 L container.

The effect of DO on ctenophore swimming speeds may have an important influence on encounter rates, which could ultimately affect overall predation rates. Ctenophore swimming speeds were significantly higher at intermediate DO concentrations than at either high or low DO (Fig. 3.5), which may result from heightened activity as ctenophores attempt to increase water flow across tissues to maintain aerobic metabolism for oxyregulation (Thuesen et al. 2005). The same increased activity may not occur at lower DO levels if ctenophores are conserving energy under more taxing DO conditions, as observed for many bivalves (Sobral and Widdows 1997). In previous, preliminary laboratory experiments, I observed higher ctenophore predation at intermediate DO levels (2.5 mg L⁻¹) on naked goby larvae in 1000 L tanks (Kolesar and Breitburg, unpubl.), which could be due to faster ctenophore swimming at intermediate DO concentrations. However, larval fish recovery rates in those experiments were smaller than desired. I did not find increased predation on naked goby

larvae at intermediate DO levels in the 100 L tanks used in final experiments (Kolesar Chapter 2).

Encounter Model

I compared the results from my ctenophore predator and larval fish prey encounter model and ingestion estimates with clearance rate estimates for a ctenophore predator on larval fish prey using results from a published study of predation in 3.2 m³ field mesocosms (Cowan and Houde 1993) as well as results from predation in the laboratory at three DO levels (Kolesar Chapter 2). Both studies used ctenophores with approximately the same average size as those modeled with my encounter model calculations (ctenophore volume = 15 ml). The ctenophore clearance rate estimates from the two experimental studies fell within the same range. Cowan and Houde (1993) reported an average clearance rate on larval fish of 0.7 L ml ctenophore⁻¹ d⁻¹ (range = 0.0 to 1.3 L ml ctenophore⁻¹ d⁻¹) (also Table 7 Purcell et al. 2001), and ctenophore clearance rates on larval fish in my 100 L tanks averaged 1.1 ± 0.1 L ml ctenophore⁻¹ d⁻¹ across all three DO levels (Kolesar Chapter 2). The clearance rates for ctenophores on larval fish calculated in both predation experiments ranged from 0.01 to 0.02 m³ ctenophore⁻¹ d⁻¹, which corresponds to an ingestion rate of 0.02 to 0.04 fish larvae m⁻³ ctenophore⁻¹ d⁻¹ at average field densities of 2 larval fish m⁻³. The estimates of predation from these laboratory experiments were an order of magnitude lower than those predicted using ingestion rates from my encounter model following first encounters between a ctenophore predator and fish larvae, and two orders of magnitude lower than ingestion rates from my encounter model following cumulative encounters between predator and prey (Table 3.3).

Relatively fast swimming speeds of *M. leidyi* in this study contribute to the high ingestion rates calculated using the encounter model. Ctenophore clearance rates in 100 L tanks on both bay anchovy yolk sac larvae and small naked goby larvae were more variable at high DO than at either low or intermediate DO levels (Kolesar Chapter 2). This high variability may be due to the combination of high encounter rates between predator and prey, as well as uncompromised escape abilities of the fish larvae at high DO concentrations. When using the encounter model, the highest encounter rates for all combinations of DO and larval fish age occurred at low DO for older fish larvae, which was when average swimming speeds of ctenophores ($18.2 \pm 1.0 \text{ mm s}^{-1}$, $N = 6$) and older fish larvae ($20.6 \pm 1.0 \text{ mm s}^{-1}$, $N = 4$) were intermediate with respect to the 3 DO levels tested and were most similar to each other (Figs. 3.5 & 3.6). Similarity in swimming speeds of both ctenophores and larval fish can cause calculations of encounter to be very sensitive to DO effects. Although DO did not directly affect predation in my experiments, increased vertical habitat overlap of predator and prey due to DO may increase encounter rates, leading to elevated larval fish mortality.

Other Factors Affecting Encounter & Ingestion

Fish larvae had a 40% higher probability of being ingested following multiple encounters with a ctenophore predator than after the first encounter (Figure 3.4). This may result from increased susceptibility of larval fish to ingestion caused by prior predator interactions. Following prolonged contact with ctenophores, escaped larval fish were covered with strands of mucus-like material that seemed to impair swimming ability, perhaps rendering them more susceptible to various predators. Impaired larval fish swimming may also inhibit feeding, eventually leading to starvation.

In addition to low DO, various other factors may have a substantial effect on planktonic predation interactions, and laboratory manipulations cannot capture the complete range of possible stressors that exist in the field. Factors such as small-scale turbulence (MacKenzie et al. 1994, Rothschild and Osborn 1988, MacKenzie and Kiorboe 2000), environmental patchiness (Letcher and Rice 1997), eutrophication (Oviatt et al. 1986), food web dynamics (Breitburg et al. 1997), and the larger-scale effects of hypoxia on distribution of organisms in the water column (Breitburg et al. 2003, Hampton 2004, Kolesar Chapter 2) could account for differences between ctenophore and larval fish encounter and ingestion rates calculated using my encounter model and clearance rate estimates from mesocosm and field studies. Larger-scale water column dynamics such as effects on distribution due to low DO (or other sources of environmental patchiness) can have big effects on predator – prey overlap, changing encounter rates and ingestion potential (Kolesar Chapter 2). Additionally, extrapolation of laboratory clearance rate estimates to the field may be influenced by effects of container size on predation (de Lafontaine and Leggett 1987, Cowan and Houde 1993, Toonen and Chia 1993), particularly for gelatinous predators such as ctenophores that may experience behavioral modification due to wall interactions. Estimates of cumulative predation from experiments conducted in finite volume containers increase directly with increasing container size (Gibbons and Painting 1992, Purcell et al. 2001).

Caution is therefore necessary when scaling up results from the laboratory to the field as experiments conducted in different sized containers may yield dissimilar estimates of clearance rates as well as overall predation. Monteleone and Duguay (1998) estimated clearance rates of $1 - 15 \text{ L ml ctenophore}^{-1} \text{ d}^{-1}$ for a single small ctenophore on

fish larvae in a 15 L container, which are an order of magnitude larger than results for ctenophore clearance rates on larval fish in 100 L tanks ($0.1 \text{ L ml ctenophore}^{-1} \text{ d}^{-1}$, Kolesar Chapter 2), 1000 L tanks ($0.1 - 3 \text{ L ml ctenophore}^{-1} \text{ d}^{-1}$, Kolesar and Breitbart, unpublished data), and 3200 L mesocosms ($0.0 - 1.3 \text{ L ml ctenophore}^{-1} \text{ d}^{-1}$, Cowan and Houde 1993), but are at the same order of magnitude as calculations of ingestion resulting from first encounters using my encounter model.

Differences in predation rates between laboratory experiments and encounter model calculations can be due to artifacts resulting from measuring interactions between predator and prey in the laboratory for both methods. Experiments in confined containers may artificially inflate the encounter probabilities between ctenophore predators and larval fish prey or alter swimming behavior. Declining prey densities during laboratory clearance rate experiments may also affect estimates of predation. Direct measurements of predator and prey swimming speeds and probabilities of escape and ingestion following captures can provide more accurate estimates of predation potential between ctenophores and larval fish by minimizing container size effects on cumulative predation measurements and eliminating the problem of prey depletion.

The presence of alternative prey or predators may also affect estimates of ctenophore predation on larval fish. Cowan and Houde (1993) found that alternative prey reduced ctenophore predation on fish larvae by 91%. My laboratory experiments did not specifically address the issue of alternative prey (although alternative prey were included in 100 L laboratory experiments described in Chapter 2), but in mesocosm experiments (Cowan and Houde 1993) and certainly in the field, alternative prey including various types and size classes of zooplankton, as well as other species and life stages of

ichthyoplankton, may be important in reducing ctenophore encounters with and predation on larval fish.

Competition for prey resources and effects on predators may also affect estimates of ctenophore predation on larval fish. Ctenophore predation may be affected by competition with piscivorous fishes (Purcell and Arai 2001) or other gelatinous zooplankton such as scyphomedusae (Purcell 1985). In addition, predation on ctenophores by medusae can change ctenophore abundance (Purcell and Cowan 1995), which in turn could affect encounters with and predation on larval fish.

Hypoxia is prevalent in estuarine environments and can alter trophic dynamics in affected systems (Breitburg et al. 1997, 1999; Eby et al. 2005). The effects of hypoxia on ctenophores, fish larvae, and their trophic interactions can be subtle and effects on individual behaviors can combine in complex ways to influence predation, and the complex array of environmental and biological factors involved in estuarine food web interactions prohibits comprehensive experimental examination. In order to more fully understand trophic dynamics at all scales, a combination of laboratory studies, field sampling, and simulation modeling are necessary to capture all of the mechanisms contributing to predation. Because predator - prey interactions occur on the scale of the individual, carefully examining species interactions and behavior on this scale is critical to development of appropriate models with sufficient mechanistic understanding of the entire predation event. My detailed examination of hypoxic effects on individual predation interactions and behavior provides a unique glimpse into the influence of this environmental factor on a small scale. Further study of predation interactions and behavior under hypoxic conditions, with inclusion of alternative predators and prey, and

physical conditions such as turbulence or stratification to accurately mimic the field, can offer a more complete view of the effect of low DO on food web dynamics.

Table 3.1. A summary of physical properties measured in laboratory predation interactions between ctenophores and larval fish. Two levels of DO were tested, low DO (1 - 2 mg L⁻¹) and high DO (approximately 7.0 mg L⁻¹). Values of temperature, salinity, and DO were recorded at the beginning and end of experiments and averaged to represent the conditions experienced by organisms during interactions in a 2 L container.

Predation Interaction Experiments	Mean ± std error	Range	N =
Low DO			
Temperature (°C)	24.2 ± 0.1	22.1 – 26.7	47
Salinity	13.5 ± 0.2	11.0 – 15.0	47
DO (mg L ⁻¹)	1.8 ± 0.02	1.5 – 2.2	47
High DO			
Temperature (°C)	24.6 ± 0.1	21.0 – 27.0	55
Salinity	13.2 ± 0.2	11.0 – 15.0	55
DO (mg L ⁻¹)	6.7 ± 0.06	5.7 – 8.0	55

Table 3.2. A summary of physical properties measured in laboratory swimming speed experiments for ctenophores and larval fish. Three DO concentrations were tested, low DO (1.5 mg L^{-1}), intermediate DO (2.5 mg L^{-1}), and high DO (7 mg L^{-1}). Values of temperature, salinity, and DO were recorded at the beginning and end of experiments and averaged to represent the conditions experienced by organisms during filming in a 40 L chamber.

Swimming Speed Measurements	Mean \pm std error	Range	N =
Low DO			
Temperature ($^{\circ}\text{C}$)	23.6 ± 0.3	21.8 - 24.3	8
Salinity	10.2 ± 0.2	10.0 – 11.5	8
DO (mg L^{-1})	1.7 ± 0.02	1.7 – 1.9	8
Intermediate DO			
Temperature ($^{\circ}\text{C}$)	23.3 ± 0.6	21.2 – 25.5	8
Salinity	10.5 ± 0.2	10.0 – 11.5	7
DO (mg L^{-1})	2.6 ± 0.1	2.3 - 2.8	8
High DO			
Temperature ($^{\circ}\text{C}$)	23.2 ± 0.6	21.2 – 25.1	7
Salinity	10.0 ± 0.0	10.0	7
DO (mg L^{-1})	7.7 ± 0.2	7.1 - 8.7	7

Table 3.3. Results from modeled ctenophore interactions with larval fish. Two DO levels (low DO, 1 - 2 mg L⁻¹; and high DO, 7 mg L⁻¹) and 2 age classes of larval fish (younger fish larvae ≤ 14 dph, length = 3.5 mm; and older fish larvae > 14 dph, length = 5.5 mm) were modeled using the Gerritsen-Strickler encounter model and percent ingestion following both the initial encounter and cumulative encounters as measured in my laboratory experiments. Interactions occur between a single ctenophore predator of average size (50 mm, 14 ml) and average field densities of larval fish (2 m⁻³, Purcell et al. 2001b).

DO Level	Larval Fish Age	Encounters # d⁻¹ m⁻³	First Encounter Ingestion # d⁻¹ m⁻³	Cumulative Encounters Ingestion # d⁻¹ m⁻³
Low	Younger	3.81	0.23	1.68
Low	Older	4.69	0.66	2.25
High	Younger	3.84	0.61	3.38
High	Older	4.48	0.18	1.88

Figure 3.1. The sequence of events leading to ingestion of a larval fish prey by a ctenophore predator. The sequence includes encounter, contact, capture, and ingestion, with three separate escape probabilities following encounter (EncEscape), contact (ConEscape), and capture (CapEscape). I adapted this figure from Waggett and Costello (1999) and Costello et al. (1999). The dashed arrows represent the potential for multiple encounters between predator and prey following any of the three escape probabilities.

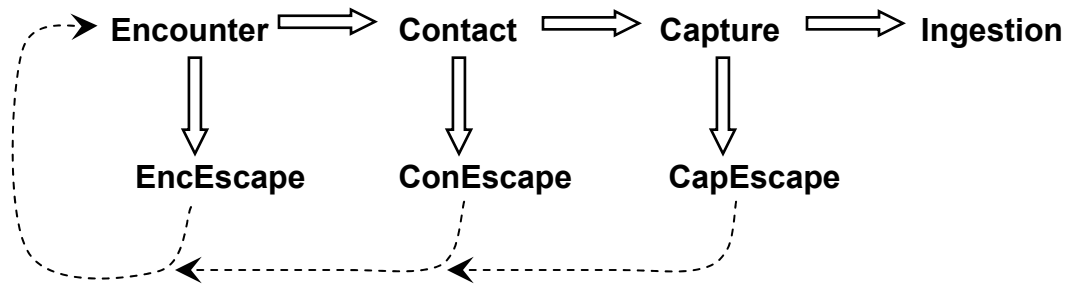


Figure 3.2. A schematic of the set-up used for filming ctenophore and larval fish swimming speeds. The interior 40 L cylindrical chamber (approximately 610 mm height, 300 mm diameter) contained the experimental animals. The space between the cylinder and the outer cube was filled with tap water to reduce optical distortion. Two cameras (X and Y) were positioned orthogonal to each other and focused on an 80 mm x 80 mm area roughly centered in the cylinder. A diffuse light source provided illumination from below, and did not seem to affect organism behavior during the two hour filming trials.

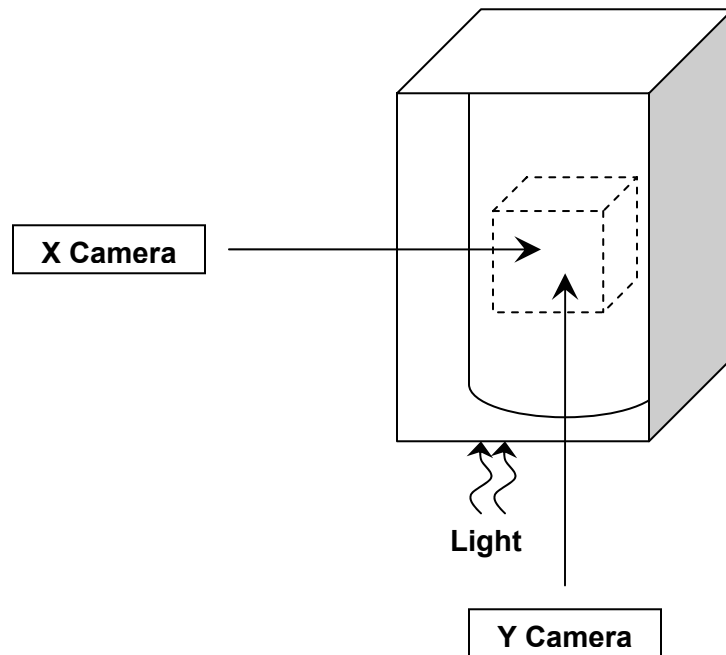
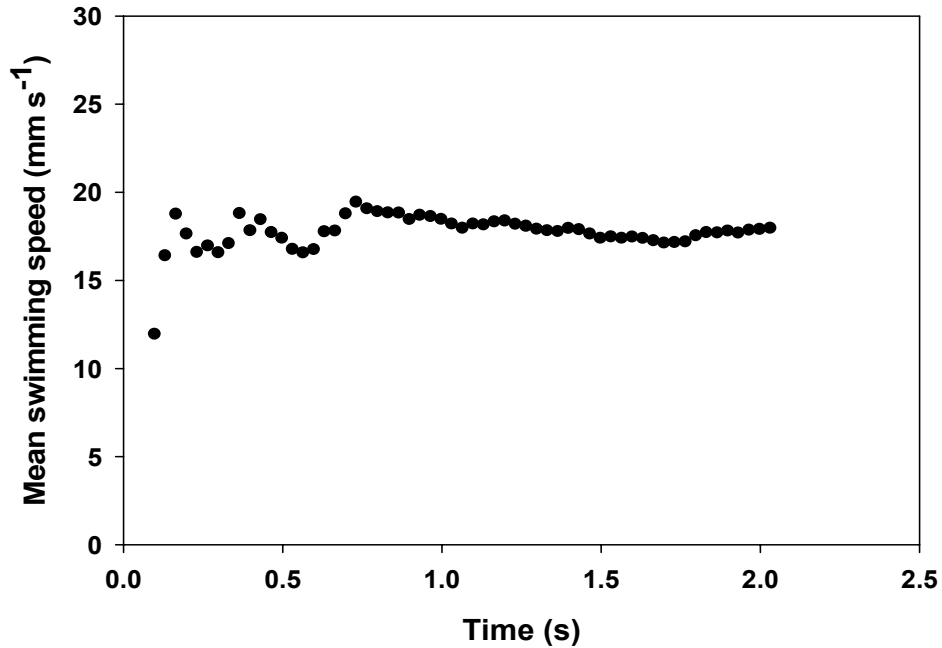


Figure 3.3. Typical measurements of cumulative mean three-dimensional swimming speed (mm s^{-1}) over time (s) for a) a ctenophore and b) a larval fish. The duration selected for swimming speed analyses for each species was on average 2 s for ctenophores and 1.5 s for larval fish. Durations were selected for logistical reasons and seemed sufficient to capture average swimming speeds for each organism.

a)

Typical Ctenophore Swimming Measurement



b)

Typical Larval Fish Swimming Measurement

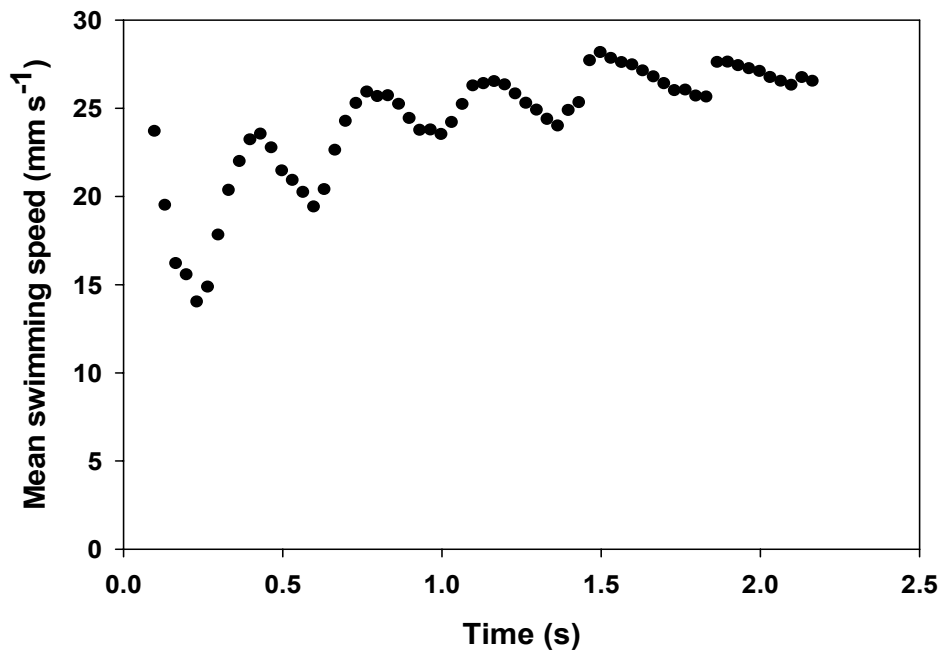


Figure 3.4. Results from small-scale predation interactions in the laboratory between a ctenophore and a larval fish. Three dissolved oxygen (DO) levels (low DO, 1.5 mg L⁻¹; mid DO, 2.5 mg L⁻¹; and high DO, 7.0 mg L⁻¹) and 2 age classes of larval fish (younger fish larvae ≤ 14 days post hatch (dph) and older fish larvae > 14 dph) were tested. I report the overall percentage of positive occurrence (yes vs. no) for each of the seven steps in the interaction sequence (Figure 3.1) after a) the first encounter between predator and prey and b) after cumulative encounters over the one hour experimental duration. N is the number of encounters, asterisks (*) indicate statistical significance at $\alpha = 0.05$ and P-values are reported in the text for exact logistic regression with both age and DO in the model.

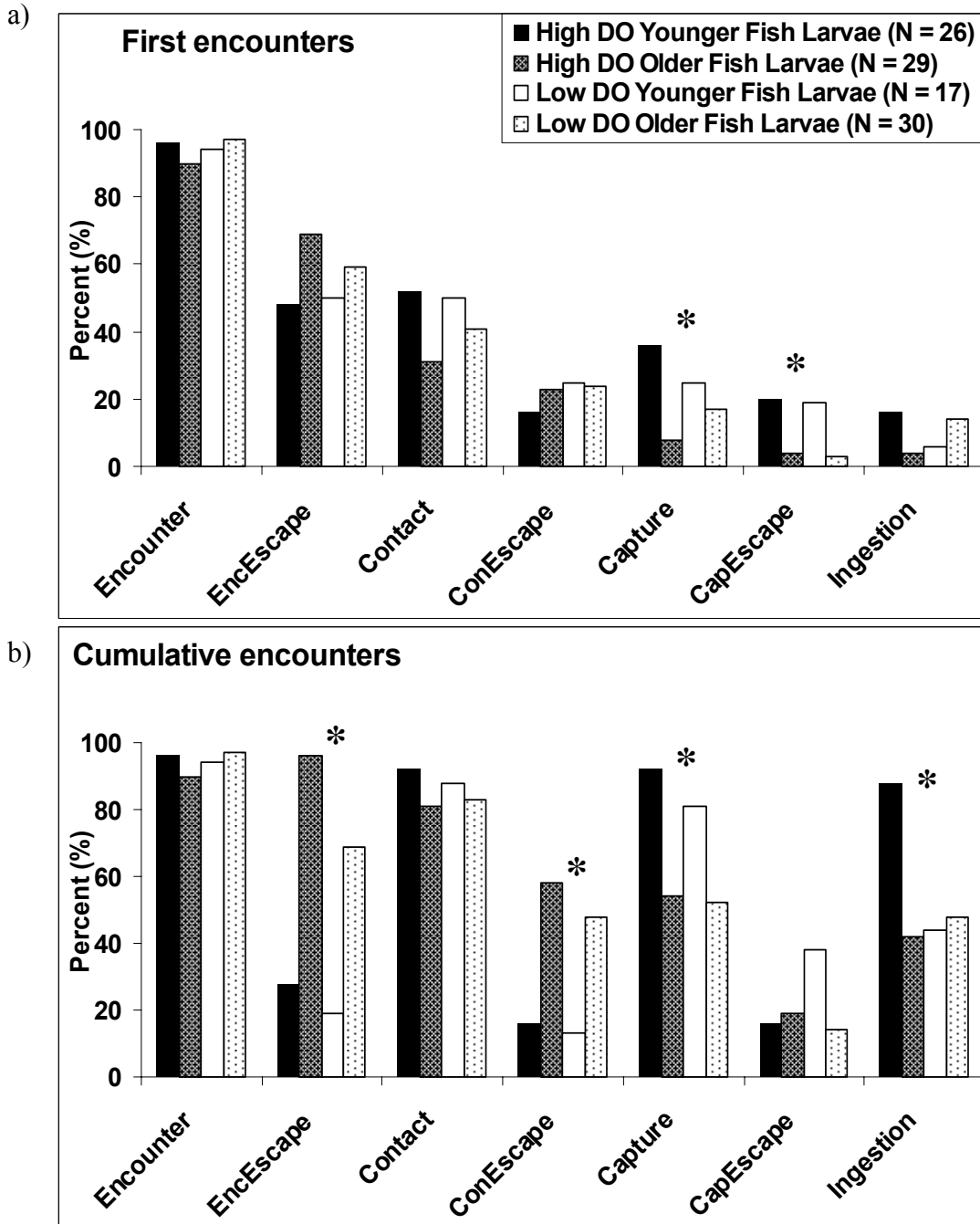


Figure 3.5. The relationship between absolute swimming speed (mm s^{-1}) and length (mm) for ctenophores. Swimming speed trials were filmed for low DO (1.5 mg L^{-1} , open circles), mid DO (2.5 mg L^{-1} , grey circles), and high DO (7.0 mg L^{-1} , dark circles). I fit a regression line to the data: $\text{SSP} = 0.02 * \text{length} + 18.2$, $R^2 = 0.004$ and $P\text{-value} = 0.8$, which is not statistically significant.

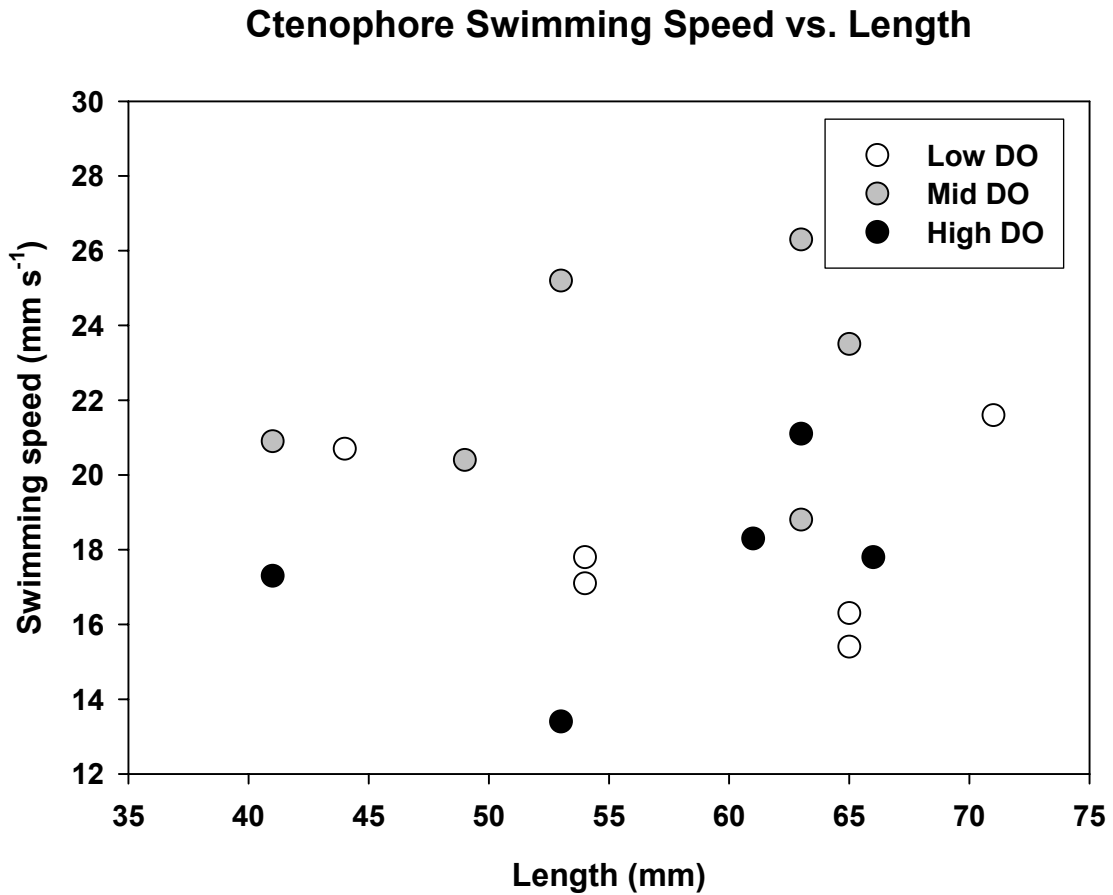
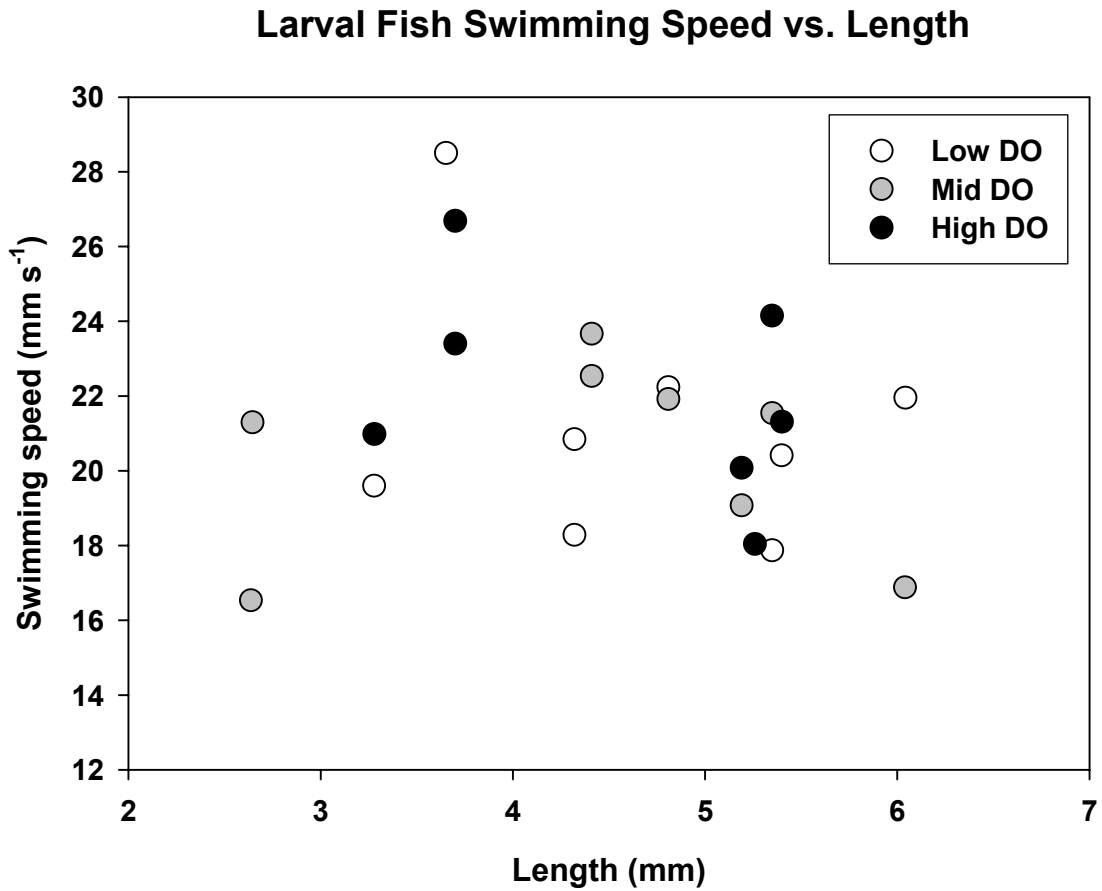


Figure 3.6. The relationship between absolute swimming speed (mm s^{-1}) and length (mm) for larval fish. Swimming speed trials were filmed for low DO (1.5 mg L^{-1} , open circles), mid DO (2.5 mg L^{-1} , grey circles), and high DO (7.0 mg L^{-1} , dark circles). I fit a regression line to the data: $\text{SSP} = -0.5 * \text{length} + 23.6$, $R^2 = 0.03$ and $P\text{-value} = 0.4$, which is not statistically significant.



Chapter 4: Individual-based model of an intraguild predation food web: ctenophores, larval fish, and copepods in the Patuxent River estuary

INTRODUCTION

Food Web Theory & Intraguild Predation

A classic concept of food web function and structure is one of distinct trophic levels and linear energy transfer with strong, top-down (Hairston and Hairston 1993, 1997) or bottom-up (Ginzberg and Akcakaya 1992) control. In natural systems neither bottom-up nor top-down processes act in isolation; rather, they interact (Gurevitch et al. 2000, Navarrette et al. 2000, Rosenheim 2001) such that uncoupling their effect on trophic webs can be difficult. Many systems may be characterized by more complex connections among trophic levels in food webs due to widespread omnivory (Baird and Ulanowicz 1989, Polis and Strong 1996, Williams and Martinez 2000, Rosenheim 2001), defined here as consumers preying at multiple trophic levels. The prevalence of omnivory in natural systems has been widely recognized (Martinez 1993, Wissinger and McCrady 1993, Holt and Polis 1997, Mylius et al. 2001, Rosenheim 2001), most notably in aquatic systems (Polis 1991, Diehl 1993, Winemiller 1996).

Intraguild predation (IGP) is a specialized case of omnivory involving the consumption of one competitor by another, simultaneously conferring nutritional gain to the IG predator and elimination of a competitive rival, the IG prey (Polis et al. 1989). The 'guild' in IGP systems is defined as a group of species with overlapping niche requirements (Root 1967), in this case a group of species feeding on similar prey items. It is recognized that intraguild predation is widespread (Ehler 1996) and particularly ubiquitous in marine systems (Polis et al. 1989).

Increased food web complexity, such as that imposed by omnivory and intraguild predation, can dampen trophic cascades (Polis and Strong 1996, Snyder and Wise 2001). Omnivores weaken trophic cascades caused by strong top-down control in linear food chains by feeding on multiple trophic levels, which disperses predation effects throughout the food web (Polis and Strong 1996) by creating weak trophic links (Polis and Strong 1996, McCann et al. 1998). Weak links occur when a predator is not wholly dependent upon any single resource for survival, such that the predator's actions may be more detrimental to the prey species than beneficial to the predator, as often is the case when early life stages are the prey (Polis and Strong 1996; Holt and Polis 1997, Diehl and Fiebel 2000).

Through the action of feeding on multiple prey resources, omnivores also reduce their ability to deplete any one trophic level in a system. Food limitation may not influence omnivores as strongly as it might influence specialists, and the impact of omnivores on the food web may persist despite controls that would limit specialist consumers. Whether or not omnivores can limit the growth or abundance of competitors by depleting shared food resources is debatable (Polis and Strong 1996).

One of the most common mechanisms promoting species coexistence in IGP systems occurs when the IG prey is more efficient than the IG predator at utilizing the shared resource base (Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997). Typically if the IG predator is superior at resource utilization, either predation on or competition with the IG prey can preclude coexistence. However, when the IG predator is better than the IG prey at exploiting the shared resource (Wissinger 1992), intermediate

levels of disturbance, seasonality or intermediate levels of productivity can increase coexistence (Polis 1984, Diehl and Feiel 2000, Gurevitch et al. 2000, Heithaus 2001).

A spatial or resource subsidy that is unique to one of the members of the IGP food web and unavailable to its competitor can also foster coexistence by reducing niche overlap (Polis 1984, Wissinger 1992, Polis and Strong 1996, Navarette et al. 2000, Heithaus 2001), as can behavioral differences between guild members. Age structure can also be an important factor contributing to trophic persistence in IGP food webs (Polis 1984, 1998), with competition and predation each affecting multiple age classes of the same species. But while the combined interaction of predation and competition can influence the dynamics of a system, it is important to consider that predation usually imposes the greatest impact on overall survival of the prey (Gurevitch et al. 2000). Additionally, separating the indirect effects of competition from the direct effects of predation on an organism may be difficult (Wissinger and McCrady 1993, Diehl 1995, Navarette et al. 2000).

In the Chesapeake Bay IGP food web involving the ctenophore (*Mnemiopsis leidy*), planktivorous fish (the bay anchovy, *Anchoa mitchilli*), and calanoid copepods (*Acartia tonsa*), both larval and adult planktivorous fish share a zooplankton resource base with ctenophores but only the early life stages of fish are ctenophore prey (Fig. 4.1). This trophic relationship corresponds closely to age-structured asymmetrical intraguild predation (Figure 1b in Polis et al. 1989). The ctenophore, *M. leidy*, the IG predator in the food web, is an omnivore that feeds on zooplankton as well as early life stages of the bay anchovy, *Anchoa mitchilli*, an important forage fish species and the most abundant fish in the Chesapeake Bay system (Wang and Houde 1994). Bay anchovy eggs, yolk sac

larvae, and feeding larvae up to approximately 15 mm TL are potential prey for ctenophores (Cowan and Houde 1992). Bay anchovy spawning and maximum ctenophore densities coincide seasonally. The dominant summer mesozooplankton species, the calanoid copepod *A. tonsa*, provides a shared prey resource for adult and larval stages of both ctenophores and bay anchovy. The effect of ctenophore predation on fish larvae has been estimated from laboratory and field mesocosm experiments (Cowan and Houde 1993, Kolesar Chapter 2), field studies (Purcell et al. 2001), and models (Breitburg et al. 2003). Measuring the effect of competition in this food web is more challenging.

In addition to biotic (competition and predation) interactions, physical habitat may also structure food webs in the Chesapeake Bay system. The summertime mesohaline Patuxent River, like the mainstem Chesapeake Bay, experiences varying intensities of hypoxia (Breitburg et al. 2003) and the depletion of dissolved oxygen (DO) in the lower layers of the water column can limit habitat available to organisms and determine their vertical distributions. Field studies indicate that low DO concentrations can cause behavioral responses in habitat use and distribution by motile organisms such as ctenophores, fish larvae, and zooplankton (Breitburg et al. 2003, Kolesar Chapter 2). The potential for DO to structure the water column and determine the degree of spatial overlap among organisms influences the potential for competition and predation among ctenophores, fish larvae, and zooplankton, and therefore the stability and dominant interactions influencing intraguild predation within this IGP food web.

We examined which effect of ctenophores on larval fish populations was more important — predation or competition — and how low versus high DO conditions in the

water column affect the relative importance of these biotic interactions within the ctenophore-fish larvae-copepod IGP food web. Uncovering the mechanism underlying the persistence of the Chesapeake Bay IGP system may also provide insight into other systems with similar food web structure. We isolated the effects of predation and competition, as well as the environmental influences of low DO, on larval fish survival and growth by using a spatially-explicit individual-based simulation model of the IGP food web. The model simulated the predation of ctenophores on fish larvae and zooplankton and the predation of fish larvae on zooplankton in a 3-layer water column for the summer months using information representative of the mesohaline portion of the Patuxent River estuary. Simulations were performed that allowed for effects of competition and predation on larval fish by ctenophores to be separated from each other under conditions of high and low DO concentrations. Model results were used to address three questions: 1) How do high and low DO affect the growth and survival of larval fish in the baseline IGP food web?; 2) Is competition or predation the more important effect of ctenophores on larval fish survival and growth?; and 3) What is the effect of low versus high DO on the relative importance of competition and predation to larval fish survival and growth within the IGP food web?

MODEL DESCRIPTION AND METHODS

Overview

The model followed the growth, mortality, and movement of ctenophores, fish larvae, and copepods every 12 hours to encompass day and night dynamics for the summer months in a 3-layer water column. Ctenophores and fish larvae were followed as individuals; copepods were followed as the numbers in each of three uncoupled life stages (nauplii, copepodites, adults). Reproduction of modeled ctenophores introduced

new ctenophores into the model, while fish larvae were introduced as daily cohorts of eggs that developed into yolk-sac larvae and then into larvae when they were started to be followed as individuals. Temperature was assumed constant throughout the simulation, and dissolved oxygen (DO) concentrations varied over time in each of the three layers. Growth of ctenophores and fish larvae was based on bioenergetics models with consumption dependent on their encounters with their prey. Densities of each copepod life stage were modeled using a version of a discrete logistic population dynamics equation. Ctenophores ate copepods and fish larvae, and fish larvae ate copepods. Mortality of ctenophores was assumed to be constant; mortality of fish larvae and copepods were due to predation by modeled individuals plus an assumed external fixed mortality of fish eggs, yolk sac larvae, and feeding larvae. Dissolved oxygen -dependent movement determined which layer the copepods, ctenophores, and fish eggs, yolk sac larvae, and feeding larvae experienced every 12 hours. Dissolved oxygen concentration affected mortality rates of fish eggs, growth rates of ctenophores and fish larvae, and the vertical movement of ctenophores, fish eggs, yolk sac larvae, feeding larvae, and copepods. Fish eggs and larvae in the model were mostly based upon information about bay anchovy. All variables used in model equations are defined in Table 4.1.

Water Column Structure

The simulated water column was configured to be representative of the summertime conditions typical of the deep, mesohaline region of the Patuxent River that experiences hypoxia. The water column was 1 m x 1 m x 20 m deep and divided into 3 layers with 20% of the volume in the surface layer, 30% in the pycnocline layer, and 50% in the bottom layer. Two DO conditions were simulated: well-mixed with DO

concentrations of 6.0 mg L^{-1} in all three layers and stratified with surface layer DO equal to 6.0 mg L^{-1} , pycnocline layer DO equal to 3.0 mg L^{-1} and bottom layer DO equal to 1.5 mg L^{-1} . The bottom layer low DO concentration of 1.5 mg L^{-1} was selected because previous studies have shown that DO concentrations of 1.5 mg L^{-1} altered the vertical distributions of organisms (Breitburg et al. 2003) and the predator-prey interactions in the Chesapeake Bay food web (Decker et al. 2004). Temperature conditions were held constant at 24°C in all layers for the duration of the simulation; while not necessarily realistic this was a simplifying model assumption. Vertical distributions of zooplankton, fish eggs and yolk sac larvae, as well as each modeled fish larva and ctenophore individual, were determined for each 12 h model time step based on seasonal patterns measured in the Patuxent River and the bottom layer DO concentration (Breitburg et al. 2003).

FISH LARVAE

Larval Fish Spawning

Fish egg cohorts were introduced into the surface layer at night at densities of 100 m^{-3} . Frequency of spawning was dictated seasonally with spawning every 3 days beginning in early June (Ordinal Day 150), increasing to peak spawning occurring daily during July (Ordinal Day 190 – 212), and then tapering off again to spawning every 3 days until spawning ceased in August (Ordinal Day 220).

The abundances of fish eggs and yolk sac larvae in each layer were simulated using a stage-based matrix projection model. Vertical movement shifted the densities of eggs and yolk-sac larvae among layers. Life stage duration was assumed to be 24 h for fish eggs and 2 d for yolk sac larvae. The external mortality rate (EYMort) applied to fish eggs and yolk sac larvae was 0.99 12h^{-1} . Each time step, the mortality due to

ctenophore consumption was computed and added to the external mortality rate to obtain a total mortality rate. From fixed stage duration and total mortality rate for each time step, we derived the diagonal and off-diagonal elements of the matrix model for the egg and yolk sac larval stages (Caswell 2001). The diagonal elements are the probability of surviving a time step and staying in the same stage, and the off-diagonal elements are the probability of surviving a time step and progressing to the next life stage. The numbers of individuals in the egg and yolk sac larval stages were then updated. The diameter of modeled fish eggs was 1 mm and yolk sac larval length was 3 mm. Both eggs and yolk sac larvae weighed 0.00842 milligrams dry weight (mg DW) (Tucker 1989).

At first feeding (exiting the yolk sac larval stage) the surviving fish larvae became individuals in the model. All spawning cohorts that initiated first feeding on the same day were lumped and the total numbers of survivors were followed as individuals. New feeding larvae were assigned a length of 3 mm (Table 4.2) and larval fish weight (LvWt) was computed using the equation (Rose et al. 1999a):

$$LvWt = \text{EXP}^{\text{LOG}(LvLn - \text{LOG}(51.2) / 0.594)}, \text{ if } LvLn < 4.2$$

$$LvWt = \text{EXP}^{(\text{LOG } LvLn - \text{LOG}(12.4) / 0.254)}, \text{ if } LvLn \geq 4.2$$

Larval Fish Growth

Individual larvae grew according to a bioenergetics equation with consumption based on larval encounters and captures of zooplankton. Larval fish weight was incremented each 12 hours based on consumption (LvCon), assimilation (LvAsm), and respiration (LvRsp):

$$LvWt = (LvWt - 1) + (LvCon * LvAsm - LvRsp)$$

Larval length (LvLn) was then determined from weight (LvWt) using a length-weight relationship:

$$LvLn = 51.2 * LvWt^{0.594}; \text{ if } LvWt \leq 0.015$$

$$LvLn = 2.4 * LvWt^{0.254}; \text{ if } LvWt > 0.015$$

Weight was allowed to increase or decrease each time step but length was not allowed to shrink. A new length was computed if the individual was at the weight expected for its length and if the change in weight was positive.

Larval Fish Consumption

Larval fish consumption of copepods (nauplii, copepodites, adults) used a foraging model adapted for bay anchovy by Adamack and Rose (unpublished manuscript) using bay anchovy information in Rose et al. (1999a). Larval bay anchovy maximum consumption was dependent on larval weight and temperature, and was calculated for each time step with the assumption that feeding occurred only during daytime time steps:

$$LvCmax = (47.37 * LvWt^{1.732}) * T; \text{ if } LvWt < 0.022$$

$$LvCmax = (1.1019 * LvWt^{0.727}) * T; \text{ if } LvWt \geq 0.022$$

Realized consumption was determined from a multi-species functional response relationship that depended on maximum consumption rate and copepod densities (Rose et al. 1999b). Larval fish consumption (LvCon) was calculated as the cumulative sum of each copepod life stage eaten in a layer ($ZZ_j \text{ Vol}^{-1}$), based on their vulnerability to larval fish predators (LvCap_j, after Rose et al. 1999a, with corrections for sign), divided by half saturation constants (KK_j), expressed as mgdw of prey weight (ZpWt_j):

$$LvCon_j = (LvCmax * ((ZZ_j / Vol) * LvCap_j / KK_j) / (1 + \sum LvCap_j / KK_j)) * ZpWt$$

Half saturation constants (KK_j) were $50,000 \text{ m}^{-3}$ for copepod nauplii, 2000 m^{-3} for copepodites, and 1500 m^{-3} for adult copepods, based on field densities (Chesapeake Bay Program Website).

Larval Fish Assimilation and Metabolism

Larval bay anchovy assimilation efficiency ($LvAsm$) was set at 0.60 (Rose et al. 1999a). Routine respiration ($LvRRsp$) was dependent upon larval weight ($LvWt$ in mgdw) and water temperature (T in $^{\circ}\text{C}$), and then halved as an adjustment from 24 h to the 12 h time step:

$$LvRRsp = (0.146 * LvWt^{0.997} * \text{EXP}(\text{LOG}(2.2) / 10.0) * (T - 27.0)) * 0.5$$

Active metabolism ($LvARsp$) was assumed to be twice routine respiration:

$$LvARsp = LvRRsp * 2$$

Total metabolism ($LvRsp$) was equal to routine respiration for the nighttime time steps and active metabolism during daytime time steps.

Larval Fish Mortality

Individual fish larvae $<15 \text{ mm}$ in length died from being eaten by ctenophores and from a constant rate from an unspecified external source. Larger larval fish ($\geq 15 \text{ mm}$) were no longer vulnerable to ctenophore predation and were removed from the model as survivors of predation, but still preyed on zooplankton and were subject to the external mortality. The external mortality rate was assumed to be $3\% \text{ 12h}^{-1}$ to reflect predation by *Chrysaora quinquecirrha* medusae and piscivorous fish (Cowan and Houde 1993, Purcell et al. 1994a, Purcell and Arai 2001).

Fish Movement

Proportional densities of eggs and of larval fish in each layer were based on categorized DO concentrations (0.0 – 0.99, 1.0 – 1.99, 2.0 – 2.99, 3.0 – 3.99, and > 4.0 mg L⁻¹) in the bottom layer as in Breitburg et al. (2003). These proportional densities were calculated for a water column with equal volumes of water in all three layers, and then adjusted for model conditions. First, we linearly interpolated the proportional densities for the continuous bottom DO concentrations simulated in the model to obtain proportional densities appropriate for the bottom DO concentration for each time step. Second, WE adjusted the proportional densities for the unequal volumes of the three layers by multiplying by the volume of the layer. Finally, we formed the cumulative distribution of these interpolated, volume-adjusted proportions and generated a random number between zero and one to determine to which layer the individual would move to for the next time step. Separate proportional densities by bottom DO were used for fish eggs and for larvae, and proportional densities of larval fish were also used for yolk sac larvae. Movement of fish egg densities, yolk sac larval densities, and individual model fish larva occurred every time step in the simulation.

CTENOPHORES

Ctenophore Growth

Energy consumed by ctenophore model individuals and remaining after assimilation and respiration was used for growth and reproduction. Immature individuals used all of their excess energy for growth, while mature ctenophores (length \geq 25 mm and weight \geq 178.8 mgdw, Reeve et al. 1989) allocated up to 100% of their excess assimilated energy for reproduction. Ctenophores not meeting caloric demand for routine metabolic processes shrank in both length and weight. Ctenophore weight (CtWt) was

incremented each 12 h based on consumption (CtCon), adjusted for assimilation (CtAsm), respiration (CtRsp), and reproduction (CtRpr):

$$\text{CtWt} = (\text{CtWt} - 1) + (\text{CtCon} * \text{CtAsm} - \text{CtRsp}) * (1 - \text{CtRpr})$$

Ctenophore length (CtLn) was determined from weight (CtWt) using a length-weight relationship (Kremer 1976):

$$\text{CtLn} = 12.383 * (\text{CtWt} * 0.03)^{0.5342}$$

Modeled individual ctenophore predators ranged in length from 25 to about 100 mm.

Ctenophore Consumption

Consumption by individual ctenophores was based on an encounter model similar to the one described by Gerritsen and Strickler (1977), and subsequently modified by Cowan et al. (1999) and Kolesar (Chapter 3). Ctenophores fed during both day and night time steps. Encounters were dependent on swimming speeds of the predator and prey, their respective lengths, and prey densities. Ctenophores were the predators and fish eggs, yolk sac larvae, feeding larvae, and copepods were the prey. The length of the individual ctenophore and individual fish larvae were used; fish eggs and yolk sac larvae and copepods used their assigned fixed lengths. Ctenophore swimming speed was assumed equal to 0.30 body lengths per second (Kolesar Chapter 3). Fish eggs were assumed not to swim; yolk sac larvae, feeding larvae, and copepods swam at 2 body lengths s⁻¹.

Foraging rate (Fpp in mm s⁻¹) was determined by the distance swum by predator and prey in 12 h, and depended on whether the predator or the prey swam farthest (DsPred vs. DsPrey). The distance swum in 12 hours (mm 12h⁻¹) by the predator

(DsPred) and prey (DsPrey) in the model was the product of swimming speed (body length 12h⁻¹) and length of the organism (mm):

$$F_{pp} = F_{pred} \text{ if } DsPred > DsPrey$$

or

$$F_{pp} = F_{prey} \text{ if } DsPred \leq DsPrey;$$

where

$$F_{pred} = (DsPrey^2 + 3.0 * DsPred^2) / (3.0 * DsPred)$$

and

$$F_{prey} = (DsPred^2 + 3.0 * DsPrey^2) / (3.0 * DsPrey)$$

The reactive distance of ctenophore predators was based on their length (mm) and modeled as an ellipse:

$$CtRd = ((0.33 * CtLn) + (0.33 * CtLn / 2.0)) / 2.0$$

Reactive distances for all prey types (PrRd) were assumed to be their length in mm.

The mean number of encounters (E) in 12 hours (number 12h⁻¹ m⁻³) between a ctenophore predator and its prey depended on the reactive distances of both organisms (CtRd and PrRd), the foraging rate (Fpp), and number of prey eligible (PD) for encounter with the ctenophore:

$$E = 3.14 * (PrRd + CtRd)^2 * F_{pp} * 10^{-9} * PD$$

For copepods, fish eggs, and yolk sac larvae, PD was determined by dividing the total number of the particular prey in each layer by the volume of that layer to obtain the number m⁻³. The PD for fish larvae was slightly different because each model larva represented some number of identical population larvae (described below in Numerical Considerations). PD for each modeled fish larva was expressed as the number m⁻³, based

upon the number of population individuals each larva represented divided by the volume of the layer in which they were located. For each ctenophore and prey, the realized number of encounters was generated as a random deviate from a Poisson distribution with mean equal to E.

The actual number of prey encountered and successfully captured was determined as a deviate from a binomial distribution with the number of trials equal to the number of realized encounters and the probability of success set to the probability of capture.

Capture success (CtCap_j) for ctenophores preying on copepods was estimated from Waggett and Costello (1999) as 0.62 for nauplii, 0.54 for copepodites and 0.46 for adults, and as 0.80 for ctenophores preying upon fish eggs and yolk sac larvae (Cowan and Houde 1993). Capture success for ctenophore feeding on individual fish larvae (CtCap_{Lv}) depended on the lengths (mm) of both predator and prey and was not allowed to exceed 0.80 (Cowan and Houde 1993), and were comparable to the ingestion proportions measured in small-scale encounter experiments (Kolesar Chapter 3, which ranged from 0.42 – 0.88:

$$\text{CtCap}_{Lv} = 1.086 - 6.99 * (L_v L_n / \text{Ct} L_n)$$

Ctenophore consumption (CtCon in mgdw 12h⁻¹) was calculated as the sum of ctenophore consumption over each prey type (j):

$$\text{CtCon}_j = ((\text{CtCon}_j - 1) + \text{CtCap}_j * \text{PreyWt}_j)$$

Where CtCap_j (or CtCap_{Lv}) is capture success of each prey type multiplied by the weight of each prey (PreyWt_j or LvWt in mgdw).

To adjust for the difference in energy densities between predator and prey, ctenophore consumption of each prey type was converted into calories (CtConCal).

Ctenophore prey items were converted into calories and divided by the energy density of the ctenophore. Ctenophores contain about half of the calories per mgdw as their prey. Caloric density (calories mgdw⁻¹) was assumed to be 2.967 for ctenophores (Harris et al. 2000), 5.160 for copepods (Laurence 1976), 5.525 for fish eggs, 5.350 for feeding fish larvae, and 5.424 for yolk sac larvae (average of larvae and eggs, Hunter and Leong 1981).

Ctenophore Assimilation

Assimilation (CtAsm) decreased with increasing prey consumption based on data from Kremer (1976), Kremer (1979), Kremer and Reeve (1989), and Reeve et al. (1989). Using their estimates for Narragansett Bay ctenophore assimilation, we fit an equation for ctenophore assimilation expressed as ctenophore consumption per ctenophore weight, both converted to calories for equivalent energy densities (Fig. 4.2):

$$CtAsm = 0.3957 + 0.5176 / (1.0 + EXP^{-(((CtConCal / (CtWt * 2.976)) - 0.0899) / - 0.0158)})$$

Assimilation efficiency was allowed to range from a maximum of 0.9 at low food densities to a minimum of 0.4 at the highest prey densities. Within that range, inflection points for the assimilation efficiency function were determined using metabolic demands of ctenophore respiration plus excretion at low food density (high assimilation efficiency), to metabolic demands of ctenophore respiration, excretion, plus reproduction at high food density (low assimilation efficiency).

Ctenophore Respiration

Respiration (CtRsp in Mgdw 12h⁻¹) was based on formulations from Kremer (1976) for Narragansett Bay ctenophores at 21°C. Adjustments are made to the original Kremer equation to adapt respiration to a 12 h time step (multiplied by 0.5) and to

accommodate a warmer summertime Patuxent River estuary temperature of 24°C
(assume a multiplier of 0.5):

$$CtRsp = ((4.4e^{0.15 * T} * (7.06 * 10^{-4}) * 1.67) * 0.5 * (CtWt)) * 0.5$$

Ctenophore Reproduction

The numbers of ctenophore eggs and larvae in each layer were tracked using a stage-based matrix projection model. Eggs were assumed to have a duration of 1 day, and larvae were assumed to have stage duration of 10 days. Individuals exiting into the lobate stage (typically 10 mm) entered an intermediate holding stage where they waited another 5 - 7 days before entering the model as 25 mm individuals. The elements of the stage-based model were estimated each time step from the number of new eggs produced, and the duration and mortality rates of the egg and larval stages. The numbers of individuals in the egg and larval stages were updated each time step. New lobates were introduced into the same layer as they were spawned, and were assumed to stay there (i.e., no vertical movement) until being introduced into the same layer as new individual model ctenophores about 5 days later.

On each nighttime time step, the proportion of unmetabolized assimilated energy allocated to reproduction (CtRpr) was calculated using the formula in Kremer (1976) based on ctenophore dry weight (CtWt in mgdw):

$$CtRpr = 0.01 e^{0.115 * (CtWt * 0.03)}$$

Egg production was based on mesocosm experiments on Patuxent River ctenophores (Grove and Breitburg 2005). The calories available for ctenophore reproduction (CtRprCal) were a function of calories consumed (CtConCal) adjusted for assimilation

(CtAsm), as well as ctenophore respiration (CtRsp) converted to calories, and the energy allocated to reproduction (CtRpr):

$$\text{CtRprCal} = (\text{CtConCal} * \text{CtAsm} - (\text{CtRsp} * 2.967)) * \text{CtRpr}$$

The number of eggs produced individual ctenophore⁻¹ 12h⁻¹ (CtEgg) was based on calories available for reproduction:

$$\text{CtEgg} = 647.51 * \text{LOG} (\text{CtRprCal}) + 926.75$$

While ctenophore egg release occurred only at night (Grove and Breitburg 2005, Breitburg et al. unpubl.), the calculations for ctenophore reproduction summed day and night egg production. Maximum egg production in the model was approximately 10,000 eggs individual⁻¹ 24 h⁻¹ and ceased after Ordinal Day 228 (August 15). Reproduction was not mass-balanced in that the mass of eggs produced did not necessarily equal the surplus energy devoted to reproduction. No estimates of instantaneous mortality existed for the early life stages of ctenophores. We selected daily values of 0.8 for ctenophore eggs and 0.6 for ctenophore larvae which produced stable model simulations.

Ctenophore Mortality

Individual (adult) ctenophores in the model were subjected to a mortality rate of 5% 12 hr⁻¹, which was increased to 15% 12 hr⁻¹ after August 1 (Ordinal Day 213). The increase in adult ctenophore mortality rates was designed to reflect natural predation by *C. quinquecirrha* and *Beroe ovata* ctenophores in mid-to-late summer (Kreps et al. 1997, Purcell et al. 2001).

Ctenophore Movement

Vertical movement of adult ctenophores (modeled individuals) was done in the same way as for model individual fish larvae. Proportional densities of ctenophores in

each layer based on the DO in the bottom layer provided the fractions of individuals expected in each layer for the next time step. As with fish larvae, we linearly interpolated the proportional densities for the continuous bottom DO concentrations, adjusted the proportional densities for the unequal volumes of the three layers, and randomly determined which layer the individual moved to based on a cumulative distribution of the adjusted proportions.

ZOOPLANKTON

The numbers of individuals in each of three life stages of copepods (nauplii, copepodites, and adults) were simulated separately using a logistic production model with added mortality terms from ctenophore and larval fish predation. Each of the three copepod life stages was characterized by their production rate, equilibrium density, length, weight, and swimming speed. Copepod lengths were set to 0.15 mm for nauplii, 0.6 mm for copepodites, and 1.2 mm for adult. Corresponding weights were 0.00152 mg DW for nauplii, 0.0033 for copepodites, and 0.011 for adult copepods (Tester and Turner 1988). Swimming speeds were assumed to be 2 body lengths (BL) s⁻¹ for all three stages (Buskey 1994). Lengths and swimming speeds were used to determine their encounters with ctenophores and fish larvae; weights were used to determine the biomass consumed by these predators.

The number in each of the three copepod life stages at each time step in each layer were updated. A separate equation was used for each life stage:

$$ZZ_{j,t,i} = ((ZZ_{j,t,i} - 1) + ZProd_{j,t} * (1 - Ztot_{j,t} / TotZ_{j,t})) - \sum LvCon_{j,t,i} m^{-3} - \sum CtCon_{j,t,i} m^{-3}$$

where $ZZ_{t,i,j}$ is the number of each copepod life stage (j) in the model at time t in layer i.

Production rates ($ZProd_{j,t}$, number⁻¹ number⁻¹ 12h⁻¹) were set to 0.6 for nauplii, 0.5 for

copepodites, and 0.4 for adults. $Z_{tot,j,t}$ is the sum of numbers of each copepod life stage over the three layers. Equilibrium densities in the model ($TotZ_{j,t}$) were set to 15,000 m^{-3} for nauplii, 300,000 m^{-3} for copepodites, and 10,000 m^{-3} for adults (Chesapeake Bay Program website; Rose et al. 1999a). The summed total consumption over all fish larvae and ctenophore predators for each copepod life stage j , in layer i , at time t , was subtracted. Copepod movement was done the same way as for fish and adult ctenophores, based on proportional densities by layer and bottom water DO concentrations (Breitburg et al. 2003, Kolesar Chapter 2).

DISSOLVED OXYGEN EFFECT

Low DO directly affected modeled larval fish growth, adult ctenophore growth, and fish egg mortality. An equation formulated from larval fish growth in the laboratory at different DO concentrations by Zastrow et al. (unpubl.) was used to calculate reduction in larval fish growth. Both bay anchovy and naked goby larvae were used to formulate the equation because the 24 h LC50 of larvae of the two species is similar (Breitburg 1992), and because bay anchovy in the laboratory did not survive at DO concentrations below 4 $mg L^{-1}$ in three growth experiments (Zastrow et al. unpubl.):

$$GrLvDO = -0.00397 + 0.482 * DO^{0.389}$$

On each time step, the DO concentration in the layer for each modeled larval individual was used to determine GrLvDO, which was then multiplied by the predicted growth rate to obtain the realized DO-adjusted growth rate. GrLvDO was specified to obtain a value near one under high DO conditions.

The formulation of the DO adjustment to ctenophore growth was similar to that for larvae and was estimated from mesocosm experiments by Grove and Breitburg (2005):

$$\text{GrCtDO} = 0.1173 + 0.0104 * \text{DO}$$

As with the DO effect on larval fish growth, GrCtDO was applied to each modeled ctenophore growth rate based on the DO in their layer on each time step.

Model fish eggs were spawned in the high DO surface layer but can sink into the low DO bottom layer during development. Fish egg mortality due to low DO was calculated using an equation fit to data from Dorsey et al. (1996):

$$\text{MrtEggDO} = 95.77 / (1 + \exp^{-(\text{DO} - 2.35) / 0.95})$$

Fish egg mortality (MrtEggDO) at the DO in each layer was divided by MrtEggDO for high DO and multiplied by the fraction of fish eggs surviving for each time step. Other possible direct effects of low DO (e.g., swimming speeds, capture success, metabolism) were not included.

Low DO also had indirect effects on ctenophore and fish larvae predation rates. Differential effects of low DO on the vertical distributions of copepods, fish, and ctenophores affected their degree of vertical overlap and thus their encounter rates.

NUMERICAL CONSIDERATIONS

We used a super-individual approach for representing ctenophores and larval fish model individuals. The super-individual approach allows for a pre-determined number of model individuals to be in a simulation thereby preventing numerical coding problems associated with following thousand or millions of model individuals (Scheffer et al. 1995). In our model, ctenophore reproduction was simulated based on energy consumed.

However, adding a new model-individual for every new ctenophore introduced into the model could result in the computer code exceeding memory limitations. The super-individual approach addresses this by making each model individual worth some number of identical population individuals. Thus, a known number of model individuals can be added and their worth adjusted to reflect the population number added. Mortality is then simulated by decrementing the worth of the model individual to reflect the loss of population individuals represented by the model individual. In all model simulations, five ctenophore model individuals and five larval fish model individuals were introduced into each layer at the start of every time step ($5 \text{ layer}^{-1} 12 \text{ h}^{-1}$). The worth of ctenophore model individual (Ct Worth) and larval fish model individual (LvWorth) was calculated by dividing the number of population individuals introduced into each layer at each time step by 5.

Mortality and predation were imposed on model ctenophores and fish larvae by adjusting the population worth of model individuals. Mortality, either as a fixed mortality rate on either ctenophore or larval fish, or by ctenophore predation on a larval fish, resulted in a reduction of the population worth of the model individual. Because both the ctenophores (predator) and larval fish (prey) were both super-individuals, when a model ctenophore ate one or more of the population individuals of a model fish larva, we had to make adjustments to ensure mass balance. If the ctenophore worth times the number of population larva eaten was less than the worth of the larval fish, then the ctenophore model individual consumed the entire weight of the larval fish. The model ctenophore grew accordingly and the larval worth was reduced by the worth of the ctenophore times the number of larvae eaten. If the ctenophore worth times the number

of population larva eaten was greater than the worth of the model larva, then the ctenophore actually consumed the weight of the larval fish times the ratio of larval worth to ctenophore worth and the worth of the larva was set to zero. Ctenophore predation on larval fish and copepods, and larval fish predation on copepods, were accounted for after each ctenophore and larval fish evaluation as the predator. This was done to minimize the possibility of summed predation pressure over ctenophores or fish larvae exceeding the prey abundance in a layer on a time step. Because we updated the larval fish worths and copepod densities for predation after every predator, each time step the ctenophores and larval fish individuals were evaluated for growth and mortality in random order. Otherwise, modeled individuals evaluated first would always see higher prey densities.

Predation by ctenophores on fish eggs and yolk sac larvae were accounted for by the dynamic mortality term included in the estimation of the diagonal and sub-diagonal terms of their stage-based matrix projection model. Predation by ctenophores and larval fish on each of the three copepods stages was accounted for by inclusion of the mortality rate in each logistic production equation.

DESIGN OF MODEL SIMULATIONS

Three versions of the model were simulated under a high DO scenario and a low DO scenario for a total of six conditions (Fig. 4.3). All model simulations were for 100 days from May 25 (Ordinal Day 145) to early September. The objective was to separate the effect of predation of ctenophores on fish larvae from the effect of competition between ctenophores and fish larvae for copepods. The first version of the model was baseline and represented the full effects of intraguild predation (IGP): ctenophore consumption caused mortality of fish larvae, and ctenophore and fish larval consumption

caused mortality of copepods (Fig. 4.3a). The IGP version therefore included ctenophore predation on fish larvae and competition between ctenophores and larval fish for copepod prey. The second version of the model relaxed the ctenophore predation effects on fish larvae (Fig. 4.3b). Ctenophore consumption depended on their encounters with fish larvae, but eaten larval fish were not removed from the model, therefore ctenophores gained the appropriate prey resources but fish larvae were not affected. The third version of the model maintained the ctenophore predation effects on fish larvae but relaxed the competition between ctenophores and fish larvae for copepods.

Implementation of the relaxed competition version involved using output from other model simulations as input to recalibrate the model (Fig. 4.3c). First, the baseline model was run with only ctenophores and copepods (no fish larvae) and with ctenophore consumption causing mortality of copepods. The predicted copepod numbers by life stage and time step were recorded. We used these copepod densities as input back into the ctenophore-copepod only model but without ctenophore effects on copepods, and recalibrated ctenophore parameters so their dynamics closely resembled the IGP version. Finally, using the recalibrated ctenophore parameters, we ran the model with ctenophores only preying upon their own pool of copepods (the output from ctenophore-copepod model) and fish larvae consuming their own pool of copepods. In this relaxed competition version, ctenophore dynamics resembled the dynamics in the IGP baseline but with their consumption affecting fish larvae mortality and not affecting the availability of copepods to fish larvae. Consumption by larval fish did affect the pool of copepods specific to fish larvae, allowing for intra-specific competition, and ctenophore predation affected fish larvae. However, ctenophore consumption of copepods did not

affect the copepods available to fish larvae; thus, we was able to relax inter-specific competition between ctenophores and fish larvae for copepods, while still maintaining realistic ctenophore predation on fish larvae and realistic intra-specific competition of fish larvae for copepods.

We examined results from five replicate runs of the model for each of the three versions of the food web (three model scenarios) and two DO (low and high) concentrations. We first examined the full IGP version under both high and low DO conditions for general model behavior, corroboration with field data, and for the effects of low DO on model dynamics. Second, we compared the predicted larval fish survival and growth among the three model versions for the high DO condition to determine the importance of ctenophore predation versus ctenophore competition on larval fish survival and growth. The third comparison was between the three versions of the model for high DO versus low DO to determine whether low DO altered the importance of predation versus competition obtained under high DO in the second comparison.

Model output variables of number of larvae surviving and their average duration from first-feeding (introduced as model individuals) to 15-mm were compared among the six simulated conditions (3 versions of the food web and two DO conditions) for all five replicate simulations. Simple model corroboration consisted of comparing averaged densities over a single replicate simulation of the IGP version under high and low DO, and comparing these to field-measured densities for the Patuxent River estuary and Chesapeake Bay. Model corroboration also included coarse comparisons of larval fish and ctenophore growth rates, ctenophore egg production rates, and temporal patterns of copepod densities to reported values in the literature. The high and low DO IGP

simulations were used because the field data reflected a range of DO conditions. For simplicity we used a single replicate simulation for each of the six conditions and examined for every 12 hour time step over the 100-days of simulation: larval lengths and ctenophore weights over time for selected model individuals (every 50th model individual); time-series plots of larval, ctenophore, and adult-stage copepod densities by water layer; and time-series plots of larval, ctenophore, and adult-stage copepod densities summed for the entire water column. Diets of ctenophores and larval fish were summarized as the averaged proportion by biomass of nauplii, copepodites, and adult copepods over a single replicate simulation for each of the six conditions. Larval fish diets were further broken down by the size of the larvae (small: < 5 mm, intermediate: 5 – 10 mm, and large: > 10 mm). For contrasting the effects of low DO, we also report the fraction surviving the fish egg and yolk-sac larval stages because DO has a direct effect on fish egg mortality rate. Finally, as an aid for interpreting model results, we computed the average vertical overlap between ctenophores and fish larvae, ctenophores and copepods, and fish larvae and copepods for a single replicate simulation of each of the six conditions.

RESULTS

Baseline Model Behavior & Corroboration

Baseline Model Behavior

Survival of early life stages and larval fish growth to 15 mm in the high DO baseline IGP model were affected by ctenophore predation and competition for copepod prey. Total survival from egg production to hatching in the high DO baseline IGP food web simulation was 40 %. An average of 2.1 % of first feeding (~2 d post-hatch) fish larvae reached 15 mm, corresponding to a mean survival of 14.1 fish larvae to 15 mm

(Table 4.2). Average larval growth rate to 15 mm was 0.46 mm d^{-1} , which corresponded to an average duration of 26.0 days from first feeding to 15 mm (Table 4.2). In general, larval fish lengths during the middle period of simulations did not increase as rapidly as larval fish lengths during the early and late portions of the simulation (Fig. 4.4). Smaller increases in larval fish lengths during the middle of the IGP (baseline) version of the food web coincided with low copepod densities (Figs. 4.5a & b) and high ctenophore densities (Fig. 4.6a & b).

Larval fish diets in the baseline IGP food web simulation were composed mostly of copepodites with smaller proportions of copepod nauplii and adults (Table 4.3). Diets of larval fish with lengths greater than 5 mm contained mostly copepodites, and only larval fish longer than 10 mm contained adult copepods in their diets.

Weights of model individual ctenophores $\geq 400 \text{ mgdw}$ increased rapidly throughout the simulation in the high DO baseline IGP food web (Fig. 4.7). Weights of smaller ctenophores ($\leq 400 \text{ mgdw}$) increased rapidly early and late in the simulation, but their growth slowed during the middle time period of Ordinal Days 50 to 150 when copepod and larval fish prey densities were low (Figs. 4.5a & 4.8a). Copepods comprised 99 % of ctenophore diets on a dry weight basis in the baseline IGP food web, and the majority of the eaten copepods were nauplii (Table 4.4).

Densities of both larval fish and copepods in the high DO baseline IGP food web declined in the middle of simulations when ctenophore predator densities were highest (Figs. 4.5a, 4.6a, 4.8a). Larval fish densities reached their highest point early in the simulation ($\sim 6.0 \text{ individuals m}^{-3}$, Ordinal Day 160) as larval fish numbers accumulated from frequent spawning. Larval fish densities declined during the middle of simulations

and rebounded to a second, lower peak later in the simulation (~Ordinal Day 220; Fig. 4.8a). In the absence of ctenophore predation, a peak in density of larval fish ≤ 15 mm would be expected in the middle of simulations, as a result of repeated spawning events and growth out of the ≤ 15 mm size class. Ctenophore densities peaked around Ordinal Day 180 at 8.9 individuals m^{-3} , which followed the initial larval fish density peak (Figs. 4.5a & 4.8a). Adult-stage copepod densities in the baseline IGP food web scenario were high at the beginning and end of simulations, but declined during the middle of simulations coincident with the peak in ctenophore predator densities (Figs. 4.5a & 4.6a). Mean densities of copepodites and copepod nauplii in the baseline IGP food webs are reported in Table 4.5, and their temporal patterns in all food web scenarios mirrored those of adult copepods.

Effect of DO in the Baseline IGP Food Web

Survival of early life stages of fish was lower in the low DO baseline IGP food web than in the high DO simulation (Table 4.2), but the effect of DO varied among developmental stages. Survival of fish eggs to hatch was lower in the low DO simulations than in high DO due to direct mortality on eggs of low DO. Thirteen percent of spawned fish eggs hatched to reach the yolk sac larvae stage at low DO as compared to 40 % at high DO. Percent survival from hatch to first feeding was similar in both high and low DO food webs. In contrast, survival of larval fish from first feeding to 15 mm was higher in the low DO than in the high DO conditions (average of 4.4 % versus 2.1 %). Higher larval fish survival in the low DO baseline IGP food web is due to the effects of DO on vertical distribution of larval, copepods, and ctenophores. Such changes can affect larval fish diets and ctenophore predation on larval fish.

Larval fish growth rates were faster in the low DO simulations than in the high DO simulations. Growth rates of fish larvae from first feeding to 15 mm was 0.61 mm d⁻¹ in the low DO simulation, which corresponded to an average of 19.7 days; more than 6 days faster than in the high DO baseline IGP food web simulation (Table 4.2).

Larval fish diets differed between low and high DO simulations and among the larval fish size classes (Table 4.3). Small larval fish (length < 5 mm) ate only copepod nauplii. Larval fish in the intermediate size class (length of 5 to 10 mm) had a larger proportion of nauplii and a smaller proportion of copepodites in their diets at low DO compared with high DO. Larval fish longer than 10 mm had a roughly equivalent proportion of the 3 copepod life stages in their diets; proportions of nauplii and adults were larger and the proportion of copepodites was smaller at low DO than at high DO. As in high DO, adult copepods were only consumed by the large size class of larval fish in the low DO baseline IGP food web. An increase in the proportion of adult copepods in the diets of large larval fish in the low DO baseline IGP food web may account for increased growth rates.

Low DO did not affect the relative proportions of the 3 copepod life stages in ctenophore diets (Table 4.4). The temporal pattern of ctenophore growth was similar at high and low DO, although growth of smaller ctenophores slowed earlier at low DO than at high DO (Fig. 4.7).

Low DO affected average whole water column densities of larval fish and copepods but not ctenophore densities. Under low DO, the average larval fish density for the whole water column over the entire simulation was less than half that under high DO (Table 4.5). Ctenophore densities averaged for the whole water column over the entire

simulation were similar at high and low DO. In the low DO simulation, average copepod density for the whole water column over the entire simulation was 16 % lower than at high DO.

Temporal patterns of organism densities were generally the same under low and high DO conditions in the baseline IGP food web for larval fish (Fig. 4.9a), but differed for ctenophores and copepods. Ctenophore peak densities were higher and remained high longer before declining in the high DO baseline IGP food web than in the low DO simulation (Fig. 4.10a). In the low DO baseline IGP food web, ctenophore densities increased to a second, lower peak around Ordinal Day 210 following their initial peak and decline (Fig. 4.10a). Copepod densities declined to a lower abundance and remained low longer in the low DO simulation than in the high DO simulation (Fig. 4.11a). During the middle of the simulations there was a slight recovery in copepod density that corresponded to a decline in ctenophore density (Figs. 4.10a & 4.11a).

Changes in the vertical overlap between predator and prey in the low DO baseline IGP food web may explain higher larval fish survival and growth rates (Fig. 4.12). Fish larvae and copepods had a slightly higher overlap at low DO than at high DO during the day, which is when larval fish actively feed. Higher overlap between larval fish and copepods may result in the higher proportion of adult copepods in larval fish diets at low DO (Table 4.3), leading to the increase in larval fish growth rates (Table 4.2, Fig. 4.4). Overlap between ctenophores and fish larvae as well as between ctenophores and copepods was lower at low DO, resulting in less predation on larval fish as well as reduced competition for copepods prey at low DO, leading to higher larval fish survival and growth at low DO.

Model Corroboration

Average larval growth rates in both the high and low DO baseline IGP food web model were similar to bay anchovy growth rates reported from field studies. Average growth rates of larval fish surviving to 15 mm in the baseline IGP food web model were 0.46 at high DO and 0.61 mm d⁻¹ at low DO. Rilling and Houde (1999) reported field growth rates of larval bay anchovy ranging from 0.53 - 0.78 mm d⁻¹ in different regions of the Chesapeake Bay and at different times during the summer season, with fastest growth rates occurring during early summer. Bay anchovy larvae from North Carolina were estimated to grow exponentially at about 4 % d⁻¹, or equal to about 0.48 mm d⁻¹ (Fives et al. 1986).

Modeled ctenophore lengths and ctenophore egg production remained within bounds observed in field samples and laboratory studies. Ctenophore lengths in the IGP high DO model averaged 57.6 mm (range = 20.2 - 91.9 mm) as a result of metabolic and reproductive processes; lengths were not capped. Maximum ctenophore size attained in the model was slightly smaller than the largest ctenophore length observed in the Chesapeake Bay system (100 mm, personal observation). Ctenophore egg production in the IGP high DO model averaged 1056 eggs ctenophore⁻¹ d⁻¹. The range for ctenophore egg production in the model, 0 – 11,360 eggs ctenophore⁻¹ d⁻¹, is similar to the range reported in Purcell et al. (2001) of 0 - 14,000 eggs ctenophore⁻¹ d⁻¹.

Mean summertime densities of ctenophores, early life stages of fish, and adult copepods and copepodites from the mainstem Chesapeake Bay during July and August 1995-1998 (Purcell et al. 2001 see Table 6 and 7), and from the Patuxent River in the summers of 1992, 1993, 1999, and 2001 (Kolesar Chapter 2), as well as copepod nauplii from the Chesapeake Bay in June, July and August of 2000 and July 2001, and in the

Patuxent River in June, July and August of 1999 and July 2001 (Purcell et al. unpubl.), were compared with model output. Purcell et al. (2001) only report surface layer means for copepod densities. Mean whole water column densities of ctenophores and ichthyoplankton and mean surface densities of copepods in the high and low DO baseline IGP food web model simulations fell within the range of summertime means reported from field studies conducted in the Chesapeake Bay system (Table 4.5). Mean copepodite and adult copepod densities for the Patuxent River estuary water column were similar to mean model densities, but reported copepod nauplii densities were lower than model results (Chesapeake Bay Program Website). Reported densities of copepodites and adult copepods in the surface layer of the mesohaline Patuxent River in the summertime averaged around $10,000 \text{ m}^{-3}$, while nauplii densities occasionally approached $100,000 \text{ m}^{-3}$ in the surface layer of both the Patuxent River estuary (Heinle 1966) and the Chesapeake Bay (Purcell et al. 1994b), although average densities were typically lower ($\sim 10,000 \text{ m}^{-3}$).

The temporal pattern of modeled copepod life stage densities in the high and low DO baseline IGP food webs were similar to that observed in the Chesapeake Bay and Patuxent River. Purcell et al. (1994b) observed a summer period of low copepod densities similar to that seen in model output. Copepodite and adult copepod densities in the surface layer of the Chesapeake Bay during May were typically less than $10,000 \text{ m}^{-3}$, decreased in June and increased during July to densities approaching almost $100,000 \text{ m}^{-3}$ at some stations in August (Purcell et al. 1994b). Copepod densities in the Patuxent River were variable during the summer months (Heinle 1966).

Importance of Predation & Competition to Larval Fish Survival & Growth

Ctenophore predation had a greater effect on survival of the early life stages of fish than did competition under high DO conditions. Survival of fish eggs to hatch was 50 % in the relaxed predation food web compared with 40 % in both the baseline IGP and relaxed competition food webs. Likewise, the percent of larval fish surviving from hatch to first feeding in the relaxed predation scenario was 50 % compared with 16 % in the baseline IGP and relaxed competition scenarios. Larval fish survival from first feeding to 15 mm in the relaxed predation food web was 14.2 % compared with 6.4 % in the relaxed competition food web and 2.1 % in the baseline IGP food web. In relative terms, larval fish survival to 15 mm was 24 times higher in the relaxed predation model than in the baseline IGP food web, but only 2 times higher in the relaxed competition food web than in the baseline IGP food web (Table 4.2).

Larval fish growth rates to 15 mm under high DO conditions were fastest in the relaxed competition food web and slowest in the relaxed predation food web (Table 4.2). The number of days for a first feeding larval fish to reach 15 mm was 7 days shorter when competition was relaxed than in the baseline IGP food web, and 4 days longer when ctenophore predation was relaxed than in the baseline IGP food web. Average growth rate of larval fish survivors in the relaxed competition food web equaled 0.63 mm d⁻¹, compared with 0.46 mm d⁻¹ in the baseline IGP food web and 0.40 mm d⁻¹ in the relaxed predation food web. Increased larval fish growth rates in the relaxed competition food web is due to higher copepod densities, while slowed larval fish growth rates in the relaxed predation food web is due to high densities of larval fish.

The difference in growth rates between the three food webs under high DO conditions was also apparent in length trajectories of modeled individual larval fish. The

slopes of lines for larval fish length versus Ordinal Day, an indication of growth rates, were very high throughout the relaxed competition food web (Fig. 4.4e). But the slopes of lines for larval fish length in the baseline IGP and relaxed predation food webs did not increase or increased slowly during the middle portions of the simulations (Figs. 4.4a & c), which was when ctenophore densities were high (Figs. 4.6a & c) and copepod densities were low (Figs. 4.5a & c).

Competition by ctenophores had a noticeable effect on prey selection in larval fish diets but ctenophore predation did not affect larval fish diets (Table 4.3). Larval fish diet composition in both food webs that included ctenophore competition (baseline IGP and relaxed predation) were similar to each other. At least half of the diets of both large (length > 10 mm) and intermediate (length of 5 - 10 mm) larval fish in these two food webs were comprised of copepodites, and the diet of large larval fish contained only a small proportion (about 0.15) of adult copepods. In contrast, in the absence of ctenophore competitors (relaxed competition food web), adult copepods comprised the largest proportion of large larval fish diets, accounting for almost half of their prey. More adult copepods in the diets of large larval fish in the relaxed competition food web could account for higher growth rates observed in this food web than in the other two food webs (Table 4.3 & Fig. 4. 4). Intermediate-sized fish larvae ate a higher proportion of copepod nauplii and a lower proportion of copepodites in the relaxed competition food web than in the other two food web scenarios. Small larvae (< 5 mm) were constrained by the model to eat only nauplii in all food web and DO conditions.

Food web structure did not affect ctenophore growth rates or diets (Table 4.4 & Fig. 4.7). Ctenophore diet composition was similar for all three food webs. The slopes

of lines for ctenophore weight over the duration of simulations, an indication of growth rates, were also similar for all three food webs.

Predation was more important than competition to larval fish densities, but ctenophore densities did not vary among the three food webs. Larval fish densities were higher in the relaxed predation food web than in the two food webs with ctenophore predation; peak larval fish densities in the relaxed predation food web were 6.5 times higher than in the baseline IGP or relaxed competition food webs (Figs. 4.9b vs. 4.9a & c). Larval fish densities were similar in food webs that included ctenophore predation, and both the baseline IGP food web and the relaxed competition food web had peak densities around 6 individuals m^{-3} (Fig. 4.8a & e, Fig. 4.9a & c). Ctenophore densities were similar in all three high DO food web simulations, with densities peaking at 8.7 – 8.9 individuals m^{-3} (Figs. 4.6 a, c, e; & Fig. 4.10).

Ctenophore predation also had a large effect on copepod densities. Copepod densities in the relaxed predation food web were similar to copepod densities in the baseline IGP food web; adult copepod densities declined to below 3000 individuals m^{-3} in these two food web scenarios (Figs. 4.11a & b). Copepod densities in the relaxed competition food web barely declined as a result of larval fish predation and adult copepod densities did not fall below 9000 individuals m^{-3} in that food web (Fig. 4.11c).

Predation was more important than competition to the temporal density patterns of larval fish; the temporal pattern in the relaxed predation food web was different from the pattern in the other two food webs. In the relaxed predation food web, larval fish densities increased to a peak just prior to Ordinal Day 220 and declined for the remainder of the simulation (Figs. 4.8c & 4.9a). The temporal pattern of larval fish densities in the

relaxed competition food web was similar to the baseline IGP food web, and both were characterized by an initial peak followed by a decline and then a secondary peak around Ordinal Day 220 (Figs. 4. 8a & e, Figs. 4.9a & c). The temporal pattern of ctenophore densities was similar in all three food webs (Figs. 4.6a, c, e; & Fig. 4.10).

The relaxed ctenophore competition food web had a larger effect on copepod temporal patterns than did the relaxed ctenophore predation food web. When ctenophore competition with larval fish was relaxed copepod densities remained constant over time (Figs. 4.5c & 4.11c), although larval fish did prey on copepods (Table 4.3). In contrast, in the relaxed predation food web, the temporal pattern of copepod densities was similar to temporal patterns in the baseline IGP food web, with high copepod densities early and late in the simulations and lower densities during the middle of simulations when ctenophore densities were high (Figs. 4. 5a & c, Figs. 4.11 a & b).

Effect of DO on the Relative Importance of Predation & Competition

The much higher importance of ctenophore predation than competition to the survival of the early life stages of fish was not appreciably affected by low versus high DO conditions. In both high and low DO relaxed predation food webs, survival of early life stages of fish was about 24 times higher than in the baseline IGP food web (Table 4.2). At high DO, larval fish survival was 3 times higher in the relaxed competition food web than in the baseline IGP food web, but at low DO larval fish survival was only 2 times higher in the relaxed competition food web than in the baseline IGP food web.

The rank order of larval fish growth rates among the three food webs under high DO was not affected by low DO, but DO did influence the magnitude of effects of ctenophore predation and competition on larval fish growth. Under both high and low

DO conditions, larval duration was longest in the relaxed predation food web, intermediate in the baseline food web, and shortest in the relaxed competition food web. The difference in growth rates between the relaxed predation food web and the baseline IGP food web was 16 % at high DO and 21 % at low DO, even though the absolute difference in growth rates was 4.2 days for each (Table 4.2). The difference in growth rates between the relaxed competition food web and the baseline IGP food web was 37 % at high DO and 26 % at low DO, with an absolute difference in growth rates of 7 days at high DO and 4.1 days at low DO (Table 4.2). Slightly higher larval fish growth rates in the low DO versus high DO baseline IGP and relaxed predation food webs may be related to the decrease in ctenophore densities during the middle of low DO model simulations (Figs. 4.10a & b). The relatively smaller increase in larval fish growth rates in the low DO relaxed competition food web may be because growth rates in that food web were already relatively high (Table 4.2) or perhaps due to changes in diet composition (Table 4.3).

The effect of low DO on larval fish diets was different in the relaxed competition food web than in the other two food webs (Table 4.3). The proportion of adult copepods in larval fish diets declined in the relaxed competition low DO food web relative to the proportion under high DO conditions, although copepod nauplii remained the largest proportion of all larval fish diets. Higher proportions of copepod nauplii and lower proportions of adult copepods in larval fish diets in the low DO relaxed competition food web could account for the slower growth at low DO than at high DO (Fig. 4.4). In contrast, the proportion of larval fish diets comprised of adult copepods was higher at low DO than at high DO in the baseline IGP and relaxed predation food webs.

Ctenophore growth rates were not quantified, but qualitatively there did not appear to be a large effect of DO on the relative importance of predation and competition on ctenophore growth (Fig. 4.7). The temporal pattern of ctenophore growth was similar for both high and low DO for all food webs. Furthermore, low DO did not modify the affect of food web structure on ctenophore consumption of copepods (Table 4.4).

Although water column densities of all modeled organisms, except for copepods in the relaxed competition food web, averaged higher at high DO than at low DO, DO did not affect density differences among food webs (Figs. 4.9 - 4.11). Larval fish densities were similar in the baseline IGP and relaxed competition food webs, with peak densities equal to 6.9 – 6.0 individuals m^{-3} at high DO and 2.2 – 2.3 individuals m^{-3} at low DO (Fig. 4.9). Densities in both the high and low DO relaxed predation food web were much higher than in the other two food webs. Larval fish peak densities in the relaxed predation food web were 6.5 times higher in the high DO and 8.8 times higher in the low DO food webs relative to the other two food webs.

Low DO affected ctenophore densities similarly in all food webs. Ctenophore densities peaked at around 9 individuals m^{-3} under high DO in the three food webs and at about 8 individuals m^{-3} in the low DO food webs (Fig. 4.10). Low DO also affected copepod densities similarly in the baseline IGP and relaxed predation food webs at high and low DO, but copepod densities in the relaxed competition food web were similar for high and low DO conditions (Fig. 4.11).

For all modeled organisms the temporal pattern of abundances in the three food webs was maintained under high and low DO (Figs. 4. 9 - 4.11). Larval fish had two peaks in abundance in both the baseline IGP and relaxed competition food webs at both

high and low DO, and one peak in the relaxed predation food web at both high and low DO (Fig. 4.9). The pattern of ctenophore abundance for high and low DO in all three food webs was maintained. At high DO ctenophore abundance had one peak while at low DO there were two separate abundance peaks (Fig. 4.10). The temporal pattern of copepod abundance was maintained in the baseline IGP and relaxed predation food webs at both high and low DO (Fig. 4.11).

The interaction between DO and food web type affected the vertical overlap between predators and their prey (Fig. 4.12), and changes in vertical overlap can affect predation potential. Vertical overlap between ctenophores and larval fish was higher at high DO than at low DO in all three food webs during both day and night (Fig. 4.12). Vertical overlap between ctenophores and copepods was also higher at high DO than at low DO in all three food webs during the day and in the relaxed competition food web at night. But the overlap between ctenophores and copepods at high DO was relatively lower in the relaxed predation and baseline IGP food webs compared with the relaxed competition food web, which may reflect ctenophore predation on copepods in the baseline IGP and relaxed predation food webs. Vertical overlap between larval fish and copepod prey in the daytime, which is when larval fish feed, was slightly higher at low DO than at high DO in the relaxed predation food webs. Lower vertical overlap between fish larvae and copepods in high DO food webs during the day may be due to predation by ctenophores, which had higher overlap with fish larvae and copepods at high DO in all food webs during the day. Vertical overlap between larval fish and copepod prey was slightly higher in the relaxed competition food web compared to the baseline IGP food web at both high and low DO in the daytime. Higher overlap between fish larvae and

copepods in the relaxed competition food web may be due to higher copepod densities resulting from lack of ctenophore predation.

DISCUSSION

The ctenophore-fish larvae-copepod food web that typifies Chesapeake Bay and other temperate estuaries differs from more frequently examined IGP food webs in that the IGP predator (the ctenophore, *M. leidyi*) is a superior competitor to its prey. In our model food webs, survival of early life stages of fish was lower in the IGP food web that included the full effects of both predation and competition by ctenophores than when either of these interspecific interactions was relaxed. Simulations that relaxed predation or competition individually indicated that predation was far more important to survival of early life stages of fish than was competition, but that competition was more important to larval fish growth rates than was predation. Although low DO concentrations decreased survival of larval fish from first feeding to 15 mm by 47 -70%, larval fish growth rates were actually faster when the bottom layer of the water column was hypoxic, and there was only a minor effect of low DO on the relative importance of ctenophore predation and competition within the IGP food web. These results largely agree with theory that an IGP predator must be an inferior competitor in order to enhance persistence of its prey. The longer-term effects of the full IGP food web and hypoxia beyond the summer spawning and larval fish growth period to maintaining larval fish persistence in the food web remain unclear.

Ctenophore predation was more important than competition to survival of early life stages of fish in our modeled food webs. The high consumption rates of ctenophores coupled with their potential for rapid increase in biomass makes them voracious

planktonic predators (Monteleone and Duguay 1988, Cowan and Houde 1993, Purcell et al. 1994 a & b, Purcell and Decker 2005). Additionally, we found large vertical overlap between ctenophores and larval fish, especially in food webs at high DO. These model results support the importance of ctenophore predation to the survival of early life stages of fish suggested by experimental and field studies (Monteleone and Duguay 1988, Cowan and Houde 1993, Purcell et al. 1994 a & b, Purcell and Decker 2005).

Ctenophore competition was more important than ctenophore predation to larval fish growth and diets; larval fish growth rates were higher when ctenophore competition was relaxed than in either of the other two food webs. Copepod densities were highest in the relaxed competition food web. When ctenophores did not compete with larval fish for copepod prey, large larval fish also had a higher proportion of adult copepods in their diets. These large prey have higher caloric content than smaller copepod life stages. Higher prey densities and better quality prey may both have contributed to higher larval fish growth rates in the high DO relaxed competition food web relative to other high DO food webs that did contain ctenophore competitors. Larval fish growth rates were slowest in the relaxed predation food web, perhaps due to the combination of elevated intraspecific competition for prey at high larval fish densities as well as the presence of slow-growing larval fish that would otherwise be eliminated from the population by ctenophore predation.

Densities and survival of early life stages of fish were lower at low DO than at high DO for all three food webs, primarily due to higher mortality of fish eggs at low DO. Larval fish growth rates were faster at low DO than at high DO in all three food webs. The large degree of vertical overlap between ctenophores and larval fish in high

DO food webs may result in lower densities and smaller size classes of copepod prey available to larval fish.

DO had only a minor effect on the relative importance of ctenophore predation and competition to survival of early life stages of fish. Survival was highest in the relaxed predation food web regardless of DO, and the rank order of growth rates in the three food webs was not changed by DO. At both high and low DO, the growth rates were faster in the relaxed predation food web and slower in the relaxed competition food web compared to larval fish growth rates in the baseline IGP food web.

Ctenophore competition was slightly less important to survival of early life stages of fish and larval fish growth at low DO than at high DO. The relative difference in larval fish growth rates between the relaxed competition food web and the baseline IGP food web was smaller at low DO than at high DO. Vertical overlap between larval fish and copepods during the day, which was when fish larvae fed, did not differ between DO levels or among food web types and therefore should not have affected larval fish growth rates.

Predation is thought to be the largest source of mortality for the early life stages of fish (Bailey and Houde 1989). In the intraguild predation food web we modeled, competition between ctenophores and larval fish for shared copepod prey did not directly influence survival of early life stages of fish. But competition with ctenophores for copepod prey slowed larval fish growth rates, which should increase predation mortality. Slower growing larval fish are vulnerable to size-specific predation longer than are faster growing larval fish (Bailey and Houde 1989).

Low DO can also influence both survival of early life stages of fish and larval fish growth independent of food web structure. It was important to include a spatial component in the model because DO affects vertical overlap between predator and prey. Not only can the vertical distribution of organisms be influenced by physical factors such as DO, but also by biological factors such as prey capture or predator avoidance and these effects can act in concert. Spatial dynamics increase model complexity (Polis and Strong 1996), but including a spatial component can capture important features of food web interactions such as habitat refuges that increase food web persistence and reduce the likelihood of local extinctions (Keitt 1997, Fulton et al. 2004). Although overall survival of early life stages of fish to 15 mm larvae declined in low DO food webs, both larval fish growth rates from first feeding to 15 mm and survival of larval fish from first feeding to 15 mm increased at low DO, indicating that low DO was beneficial to larval fish survival and growth and contributed to persistence of larval fish.

Uncoupling the influence of a heterogeneous habitat from predation can be difficult (Anholt and Werner 1995). Spatial distributions of predators, competitors and prey in the environment may be important for food web persistence and species coexistence (Rosenheim et al. 2004), with habitat complexity leading to food web complexity (Angel and Ojeda 2001). The presence of a motile, omnivorous predator such as a ctenophore may stabilize complex food webs by increasing energy flow through weak links that promote species coexistence (McCann et al. 2005, Morris 2005). We attribute increased growth of larval fish in low DO food webs to decreased vertical overlap between larval fish and ctenophores at low DO.

Intraguild predation food webs are thought to persist due to the superiority of the IGP prey in exploiting shared resources, or because IGP prey have a resource subsidy unavailable to the IG predator (Polis 1984). In our modeled food web, and in the Chesapeake Bay system, ctenophores were both a predator on fish larvae and a superior competitor for copepod prey. Our result, that survival of early life stages of fish was lowest in the IGP food web provides evidence that this particular IGP food web would not facilitate persistence. Factors such as the age structure and seasonality of the food web, as well as the effects of DO on vertical habitat overlap, limit ctenophore predation on fish egg and larval stages to a brief period during the summer months. Temporal and spatial patchiness of ctenophores due to predation by medusae can also contribute to larval fish survival.

One reason to understand the behavior of IGP in food webs is to reconcile the sometimes conflicting goals of maintaining biodiversity and managing resources. Management of IGP food webs is complex due to the numerous species involved and the diverse trophic linkages of varying strengths (Polis and Holt 1992). In the Lake Kinneret food web, for example, herbivorous microzooplankton can control water clarity, but it was a predatory copepod that controlled the microzooplankton, not an omnivorous finfish as previously thought (Blumenshine and Hambright 2003). Finke and Denno (2004) found that reduction of arthropod species diversity in an IGP food web reduced consumption of a valued marshgrass while maintaining biodiversity was detrimental to primary productivity. Determining the importance of predation or competition in IGP food webs can be difficult.

Using a modeling approach to address questions about food web structure and the effects of low DO on trophic interactions had benefits as well as limitations. The individual-based, spatially explicit food web model enabled us to simulate the effects of ctenophore predation and competition with fish larvae; the ability to simulate competition was especially valuable since competition is difficult to isolate in either the field or laboratory. In constructing the food web model, we made certain simplifying assumptions (constant temperature, for example) as a tradeoff between practical model feasibility and precise real-world accuracy in order to produce valid model results. Next steps for the food web model include adding more trophic levels for both prey (for example, phytoplankton and microzooplankton) and predators (medusae) in order to increase complexity and realism of the interactions. Also, including changes in seasonality, such as later or earlier fish spawning, or including various levels of eutrophication that may increase or decrease water quality, such as more severe or more variable DO conditions, could expand the environmental questions that can be addressed with the food web model.

Ctenophores are more tolerant of low DO conditions than are fish larvae so the vertical distributions of both species in the Chesapeake Bay system change as duration or severity of low oxygen conditions in the Chesapeake Bay system change. Results from our modeled simulations of the Chesapeake Bay ctenophore-fish larvae-copepod food web suggest that ctenophore predation was most important for reducing survival of the early life stages of fish regardless of DO concentration. But low DO decreased vertical overlap between ctenophores and larval fish and increased growth of larval fish from first feeding to 15 mm. Increased occurrence of low DO in the Chesapeake Bay system would

favor tolerant ctenophore predators over larval fish and result in more predation, but the decrease in vertical overlap between ctenophores and larval fish at low DO might ultimately favor larval fish and food web persistence.

Table 4.1. Variable names used in the individual-based model.

Variable	Description	Units
LvWt	Larval fish weight	mgdw
LvLn	Larval fish length	mm
CtWt	Ctenophore weight	mgdw
CtLn	Ctenophore length	mm
LvCon	Larval fish consumption	mgdw
LvAsm	Larval fish assimilation	proportion
LvRsp	Larval fish total respiration per time step	mgdw 12h ⁻¹
j	Prey type (fish egg, yolk sac, or copepod life stage)	-
LvCmax	Fish larvae maximum consumption	mgdw 12h ⁻¹
ZZ _j	Number of each zooplankton prey type	number 12h ⁻¹
T	Temperature in the water column layer	°C
LvCap _j	Vulnerability of each copepod type to capture by larvae	proportion
KK _j	Half saturation constant of each copepod life stage	number m ⁻³
ZoopWt	Copepod weight	mgdw
LvRRsp	Larval fish routine respiration per time step	mgdw 12h ⁻¹
LvARsp	Larval fish active respiration per time step	mgdw 12h ⁻¹
CtCon	Ctenophore consumption per time step	mgdw 12h ⁻¹
CtAsm	Ctenophore assimilation	proportion
CtRsp	Ctenophore respiration	mgdw 12h ⁻¹
CtRpr	Fraction of unmetabolized assimilated energy for eggs	proportion
Fpp	Foraging rate	mm s ⁻¹
Fpred	Foraging rate used if ctenophore distance swum is greater	mm s ⁻¹
Fprey	Foraging rate used if larval fish distance swum is greater	mm s ⁻¹
DsPred	Distance swum by the predator per time step	mm 12h ⁻¹
DsPrey	Distance swum by the prey per time step	mm 12h ⁻¹
CtRd	Ctenophore reactive distance	mm
PrRd	Prey reactive distance	mm
E	Mean encounter numbers of encounters per time step	number 12h ⁻¹
PD	Number of prey available for encounter per layer	number m ⁻³
CtCap _j	Ctenophore capture success of prey	proportion
CtCapLv	Ctenophore capture success of individual fish larvae	proportion
CtConCal	Ctenophore consumption	calories
CtRprCal	Calories available for ctenophore reproduction	calories
CtEgg	Ctenophore egg production per time step	number 12h ⁻¹
ZProd _j	Copepod production rate	# ⁻¹ # ⁻¹ 12h ⁻¹
Ztot	Sum of all copepods over three layers	number m ⁻³
TotZ _j	Copepod equilibrium density	number m ⁻³
Vol	Water column volume	m ³
DO	Dissolved oxygen concentration	mg L ⁻¹
GrLvDO	Larval fish growth rate effect due to DO per time step	proportion
GrCtDO	Ctenophore growth rate effect due to DO per time step	proportion
MrtEggDO	Fish egg mortality due to DO per time step	number 12h ⁻¹

Table 4.2. Results from five replicate runs of model simulations in the baseline IGP, relaxed predation, and relaxed competition food webs at both high and low DO. Reported values are the random number seed, total number of fish larvae reaching 15 mm and total number of days for fish larvae to reach 15 mm during the 100-day simulation. No fish larvae less than 15 mm remain at the end of the simulations.

<i>Baseline IGP High DO</i>			<i>Baseline IGP Low DO</i>		
	<u># larvae to 15 mm</u>	<u>Days to 15 mm</u>		<u># larvae to 15 mm</u>	<u>Days to 15 mm</u>
Mean	14.1	26.0	Mean	9.9	19.7
Min - Max	13.8 - 14.5	25.5 - 26.4	Min - Max	9.7 - 10.2	19.3 - 20.1
<i>Relaxed Predation High DO</i>			<i>Relaxed Predation Low DO</i>		
	<u># larvae to 15 mm</u>	<u>Days to 15 mm</u>		<u># larvae to 15 mm</u>	<u>Days to 15 mm</u>
Mean	352.0	30.2	Mean	243.5	23.9
Min - Max	349.9 - 354.0	30.1 - 30.4	Min - Max	238.8 - 246.9	23.7 - 24.3
<i>Relaxed Competition High DO</i>			<i>Relaxed Competition Low DO</i>		
	<u># larvae to 15 mm</u>	<u>Days to 15 mm</u>		<u># larvae to 15 mm</u>	<u>Days to 15 mm</u>
Mean	41.5	19.0	Mean	19.4	15.6
Min - Max	38.1 - 44.8	18.9 - 19.0	Min - Max	14.6 - 24.4	15.4 - 15.9

Table 4.3. Values for the mean proportion of biomass (mgdw) of each copepod life stage in modeled larval fish diets for three size classes of larval fish. Larval fish size classes were large (larval fish length > 10 mm), medium (10 mm ≥ larval fish length ≥ 5 mm) and small (larval fish length < 5 mm) for all three food webs: baseline IGP, relaxed predation, and relaxed competition at both high and low DO.

	Large Fish Larvae Proportion in Diet		Medium Fish Larvae Proportion in Diet		Small Fish Larvae Proportion in Diet	
	High DO	Low DO	High DO	Low DO	High DO	Low DO
Baseline IGP						
Nauplii	0.26	0.38	0.13	0.36	1.00	1.00
Copepodites	0.60	0.35	0.87	0.64	0.00	0.00
Adult Copepods	0.14	0.27	0.00	0.00	0.00	0.00
Relaxed Predation						
Nauplii	0.26	0.44	0.15	0.35	1.00	1.00
Copepodites	0.59	0.34	0.85	0.65	0.00	0.00
Adult Copepods	0.15	0.22	0.00	0.00	0.00	0.00
Relaxed Competition						
Nauplii	0.32	0.49	0.26	0.88	1.00	1.00
Copepodites	0.25	0.15	0.74	0.12	0.00	0.00
Adult Copepods	0.43	0.36	0.00	0.00	0.00	0.00

Table 4.4. Copepods comprise the majority of ctenophore diets during the 100-day model simulation. Values reported are the mean proportion of biomass (mgdw) \pm SE due to zooplankton for each copepod life stage in ctenophore diets for all 3 food webs: baseline intraguild predation (IGP), relaxed predation (RP), and relaxed competition (RC) and under both high and low DO scenarios.

	High DO Proportion	Low DO Proportion
Baseline IGP (IGP)		
Copepod nauplii	0.78 \pm 0.01	0.81 \pm 0.01
Copepodites	0.08 \pm 0.01	0.07 \pm 0.01
Adult Copepods	0.14 \pm 0.01	0.12 \pm 0.01
Relaxed Predation (RP)		
Copepod nauplii	0.78 \pm 0.01	0.81 \pm 0.01
Copepodites	0.07 \pm 0.01	0.07 \pm 0.01
Adult Copepods	0.14 \pm 0.01	0.12 \pm 0.01
Relaxed Competition (RC)		
Copepod nauplii	0.78 \pm 0.01	0.81 \pm 0.01
Copepodites	0.08 \pm 0.01	0.07 \pm 0.01
Adult Copepods	0.14 \pm 0.01	0.12 \pm 0.01

Table 4.5. Comparison of model densities for ctenophores, fish eggs, yolk sac larvae, fish feeding larvae, and copepodites and adult copepods with field densities. Field densities were measured in the Chesapeake Bay in July and August 1995-1998 (data from the TIES project, summarized in Purcell et al. 2001 Tables 6 & 7) and the Patuxent River in June, July, and August 1992, 1993, 1999 & 2001 (Keister et al. 2000, Breitburg et al. 2003, Kolesar Chapter 2). Copepod nauplii field densities are reported for the Chesapeake Bay in June, July and August of 2000 and July 2001, and in the Patuxent River in June, July and August of 1999 and July 2001 (Purcell et al. unpubl.). Values presented are the minimum, maximum and mean \pm SE of the numbers entering each organism life stage from both the IGP high and low DO model scenarios and the range of summertime means for Patuxent River samples and from Chesapeake Bay data. Ctenophore and ichthyoplankton data are presented for the whole water column (W.C.), and copepod data are presented for the surface layer only (S), as this was the only data available for Chesapeake Bay TIES project samples. The number of stations is indicated by N. For field samples, yolk sac larvae and feeding larval fish, as well as copepodite and adult copepods, were combined.

Table 4.5.

Organism	Model IGP High DO		Model IGP Low DO		Field Samples Patuxent River (N = 43)	Field Samples Chesapeake Bay (N = 174)
	Min - Max	Mean \pm SE	Min - Max	Mean \pm SE	Range of Summertime Means (# m ⁻³)	Range of Summertime Means (# m ⁻³)
Ctenophores W.C.	0.01 – 8.7	3.8 \pm 0.2	0.02 – 7.9	3.7 \pm 0.2	0.03 – 6.83	2.8 – 12.7
Fish eggs W.C.	0 - 20	2.5 \pm 0.5	0 – 20	2.7 \pm 0.5	0 – 41.3	1.2 – 28.8
Fish yolk sac larvae W.C.	0 – 10	1.4 \pm 0.2	0 - 4	0.5 \pm 0.1	1.6 – 12.9	0.3 – 3.3
Post-yolk sac larvae W.C.	0 - 6	1.5 \pm 0.1	0 – 2.3	0.6 \pm 0.03		
Copepod nauplii SURFACE	92,052 – 399,590	226,865 \pm 7378	66,480 – 393,550	190,776 \pm 6064	36,350 – 38,284 (N = 13)	20,363 – 27,671 (N = 15)
Copepodites SURFACE Adult	3731 – 19,967	10,609 \pm 370	2620 – 19,666	8714 \pm 334	670 – 29,500	787.1 – 7503.8
Copepods SURFACE	1610 – 13,303	6291 \pm 256	976 – 13,099	4888 \pm 255		

Figure 4.1. The modeled mesohaline summertime Chesapeake Bay system food web. The food web includes intraguild predation (IGP) with ctenophores as the intraguild predators (IG predators) feeding on both the early life stages of fish (eggs, yolk sac larvae, and feeding larvae $\leq 15\text{mm}$) as well as three copepod life stages (nauplii, copepodites, and adults). Transitions from one life stage to the next are indicated with curved arrows. The relaxed predation model scenario eliminates ctenophores feeding on the early life stages of fish (dashed lines) and the relaxed competition scenario reduces ctenophore feeding on the 3 copepod life stages (dotted lines). Larval fish $\leq 15\text{mm}$ are the IG prey.

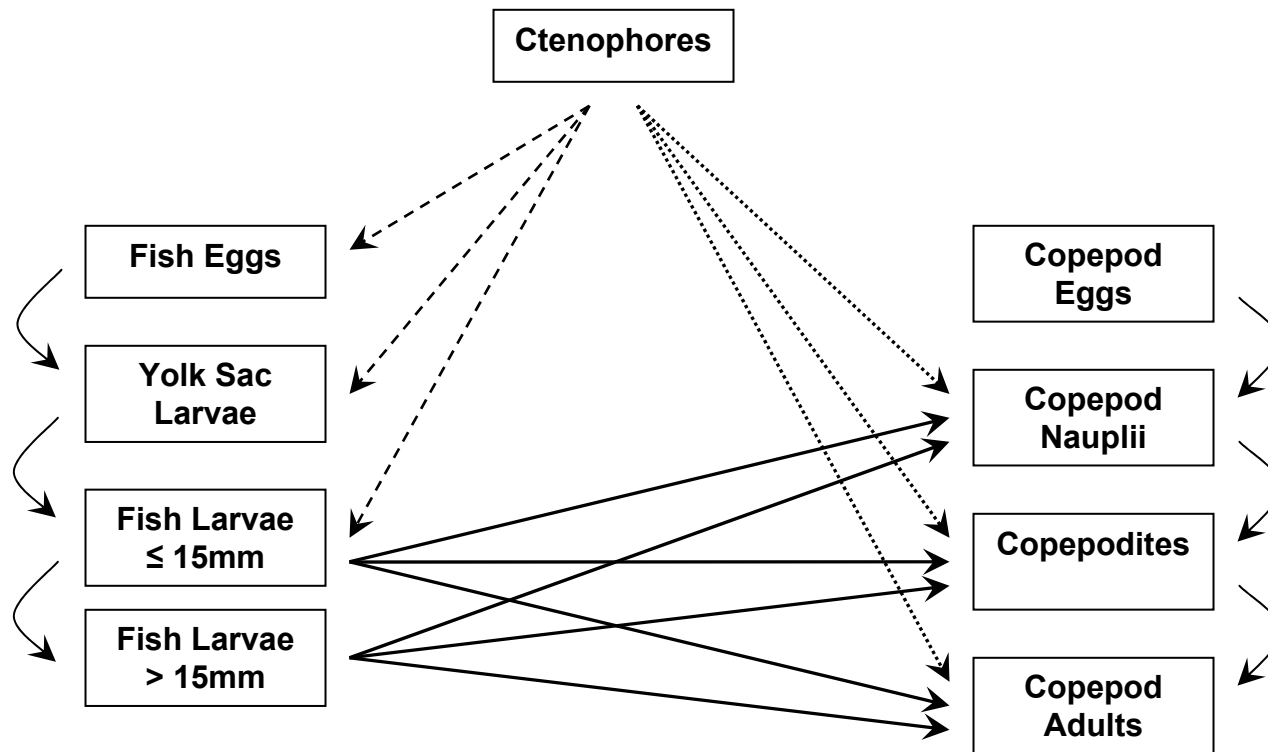


Figure 4.2. Equation for ctenophore assimilation used in the model determined from published data on ctenophore assimilation as well as information on ctenophore bioenergetics.

Ctenophore Assimilation

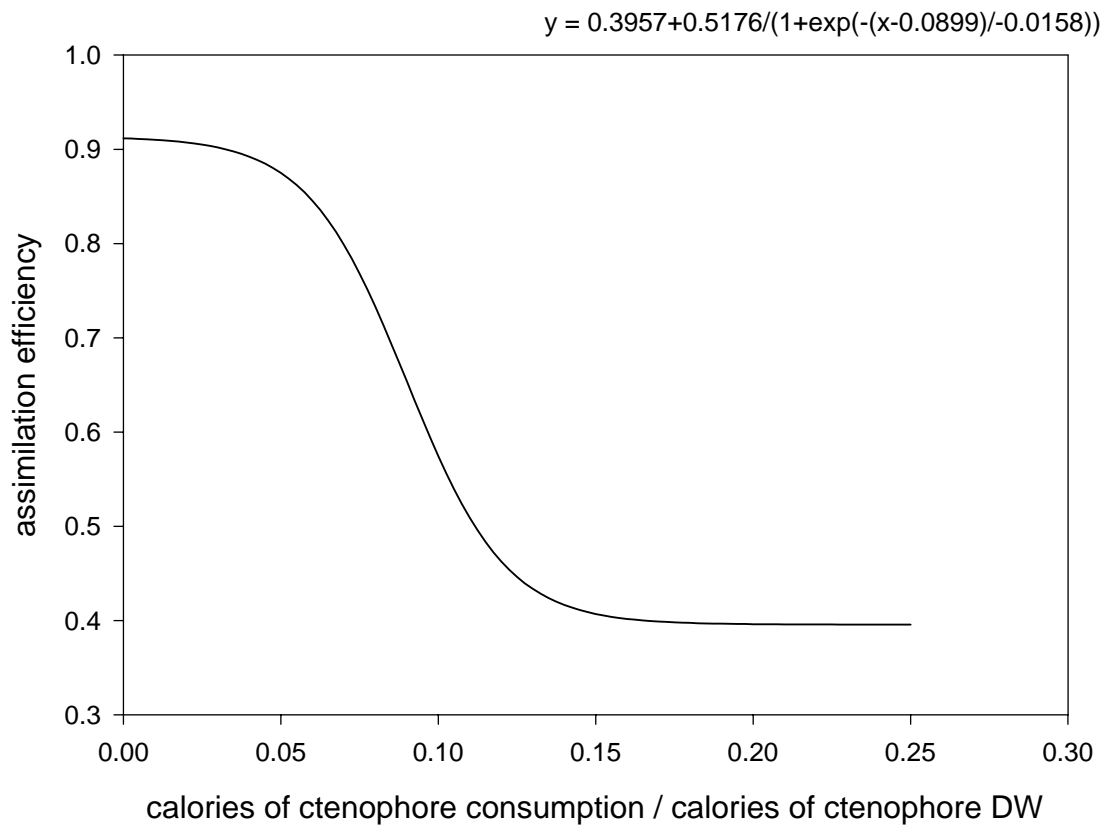
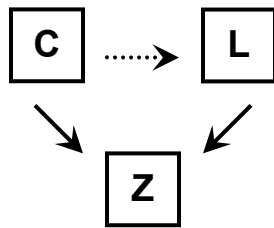
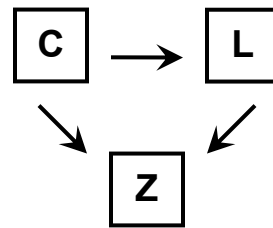


Figure 4.3. Modeled simulations included three food webs with five total simulations. a) The baseline intraguild predation (IGP) food web included ctenophores (C) as both predators on larval fish (L) and competitors for copepod prey (Z) (predation is designated by solid arrows), b) the relaxed predation food web (RP) included ctenophore predation on larval fish, but larval fish were not removed from simulations (represented by a dashed arrow), and ctenophores and larval fish were competitors for copepod prey, and finally c) the relaxed competition food web (RC) had separate prey pools for ctenophores and larval fish. In the RC food web, the zooplankton prey pool for ctenophores (Z_c) was generated from the ctenophore – zooplankton model (i), the fitted density-independent model was run to calibrate ctenophores to baseline conditions (ii), and the full RC model included two separate prey pools (iii).

a. Intraguild predation food web

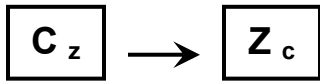


b. Relaxed predation food web

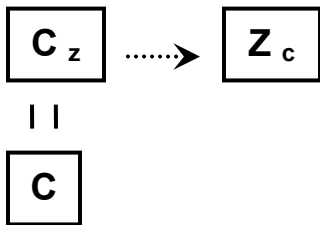


c. Relaxed competition food web (3 steps)

i.



ii.



iii.

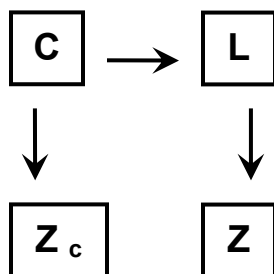


Figure 4.4. Larval fish length (mm) plotted against Ordinal Day for 6 different simulations: a) baseline IGP high DO, b) baseline IGP low DO, c) relaxed predation high DO, d) relaxed predation low DO, e) relaxed competition high DO, f) relaxed competition low DO. Each line represents a cohort of individual feeding fish larvae throughout the simulation with each cohort entering the model at a different timestep. The trajectory of size through time provides a representation of larval fish growth rates.

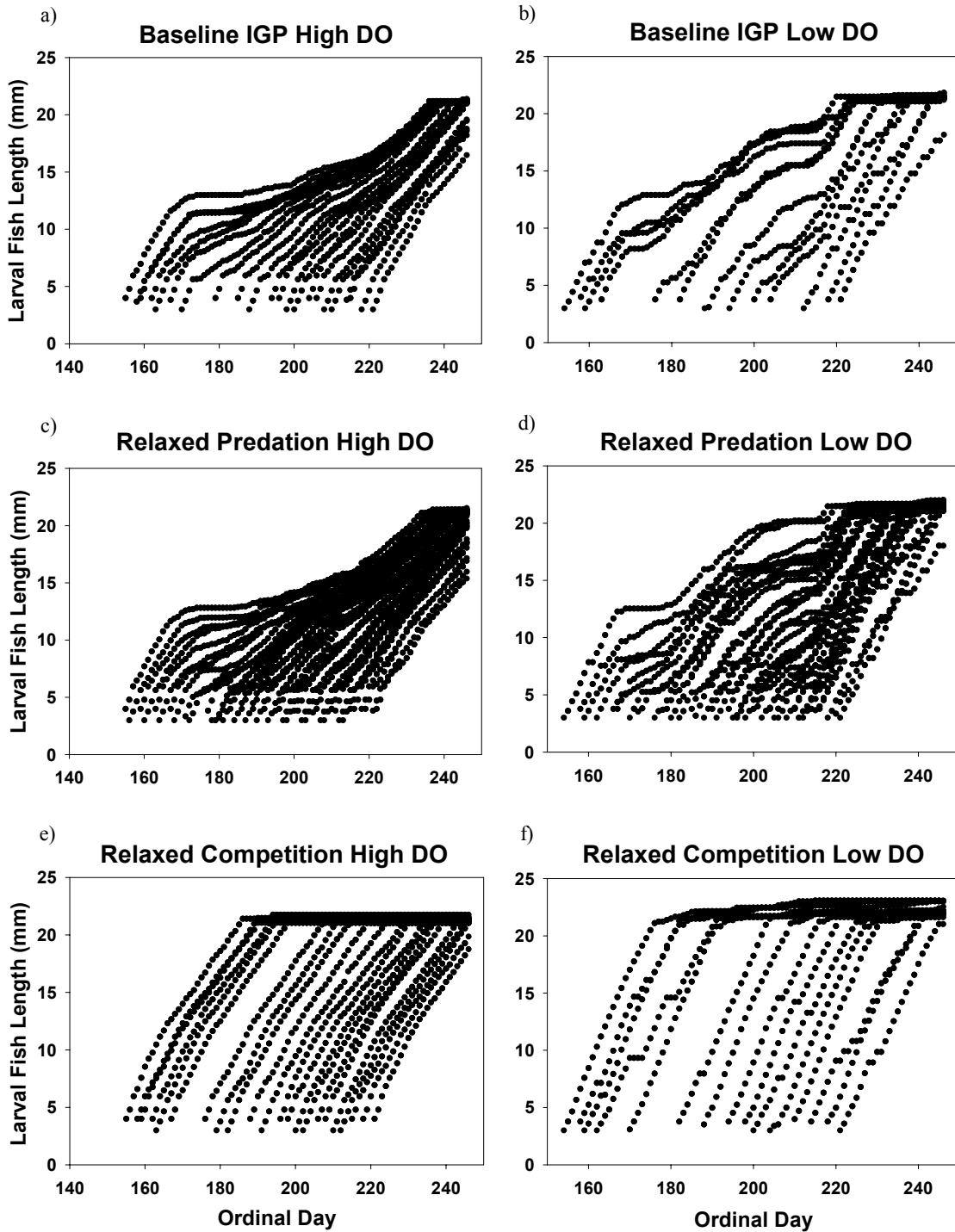


Figure 4.5. Copepod number m⁻³ by layer plotted against ordinal day for the adult life stage during both day (●) and night (x) for a representative simulation for each of 6 different food webs: a) baseline IGP high DO, b) baseline IGP low DO, c) relaxed predation high DO, d) relaxed predation low DO, e) relaxed competition high DO, f) relaxed competition low DO. Black dots denote the surface layer, red dots the pycnocline, and green dots the bottom layer. Mean densities of copepodites and nauplii are reported for the baseline IGP food web (Table 3.5) and distribution patterns are similar to those of adult copepods in all food web scenarios. Single dots on the first day of simulations are an artifact of the initial density.

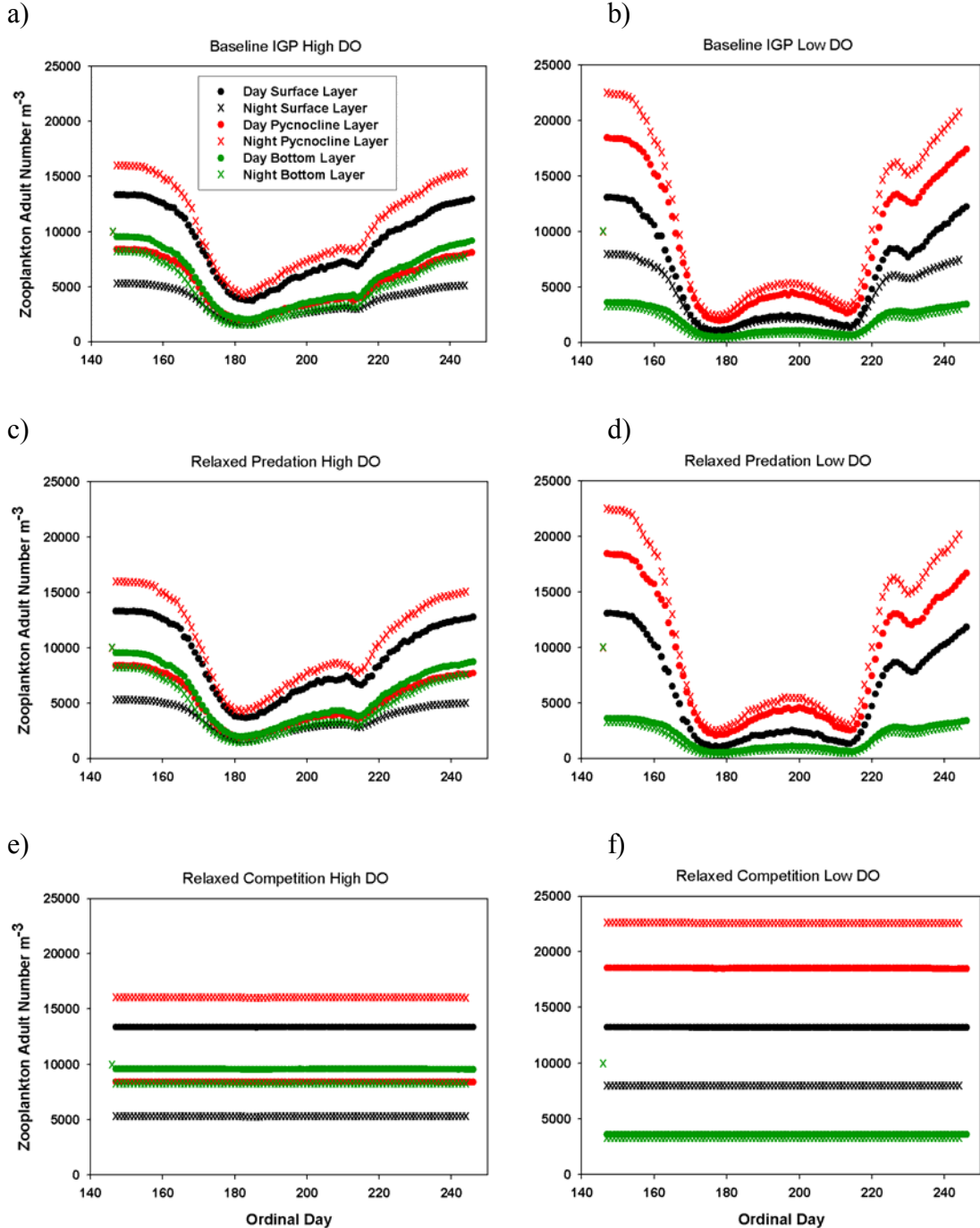


Figure 4.6. Ctenophore number m^{-3} by layer plotted against ordinal day during both day (●) and night (x) for a representative simulation for each of 6 different food webs: a) baseline IGP high DO, b) baseline IGP low DO, c) relaxed predation high DO, d) relaxed predation low DO, e) relaxed competition high DO, f) relaxed competition low DO. Black dots denote the surface layer, red dots the pycnocline, and green dots the bottom layer.

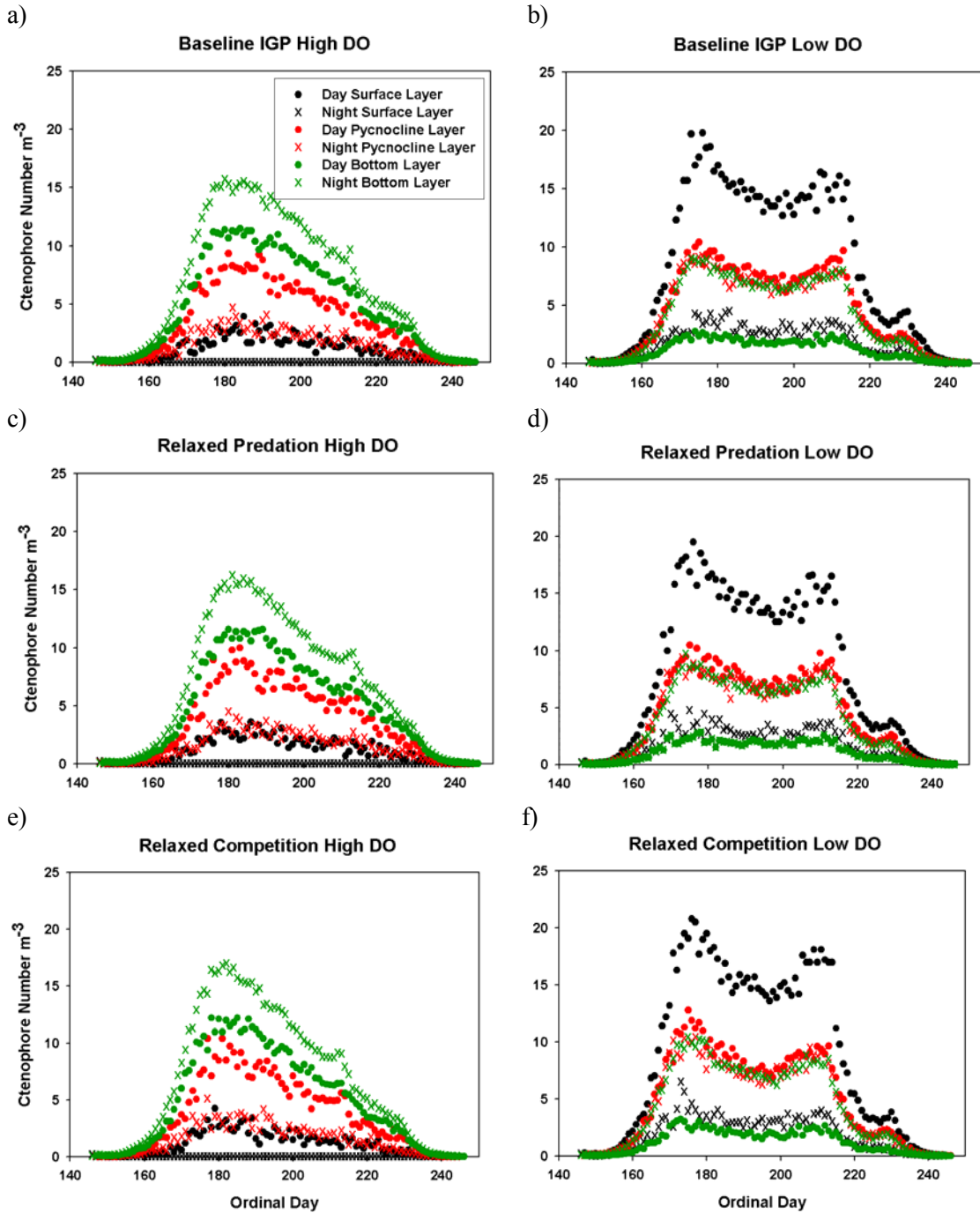


Figure 4.7. Ctenophore weight (mgdw) plotted against Ordinal Day for 6 different simulations: a) baseline IGP high DO, b) baseline IGP low DO, c) relaxed predation high DO, d) relaxed predation low DO, e) relaxed competition high DO, f) relaxed competition low DO. Each line represents a cohort of individual ctenophores throughout the simulation with each cohort entering the model at a different time step. The trajectory of weight through time provides a representation of ctenophore growth rates.

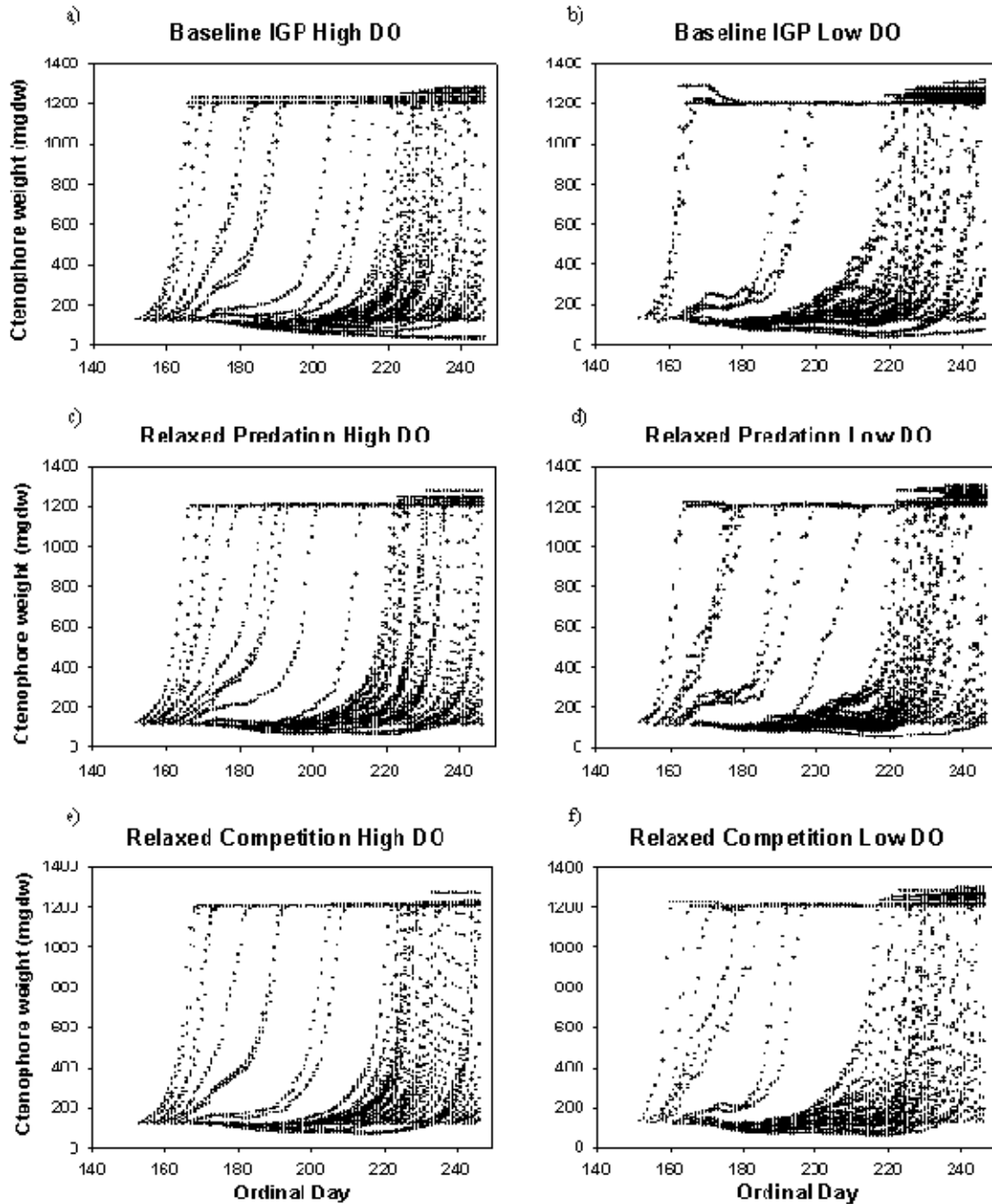


Figure 4.8. Fish larvae number m^{-3} by layer plotted against ordinal day during both day (●) and night (x) for a representative simulation for each of 6 different food webs: a) baseline IGP high DO, b) baseline IGP low DO, c) relaxed predation high DO, d) relaxed predation low DO, e) relaxed competition high DO, f) relaxed competition low DO. Black line denotes the surface layer, red line the pycnocline, and green line the bottom layer. Note different scales.

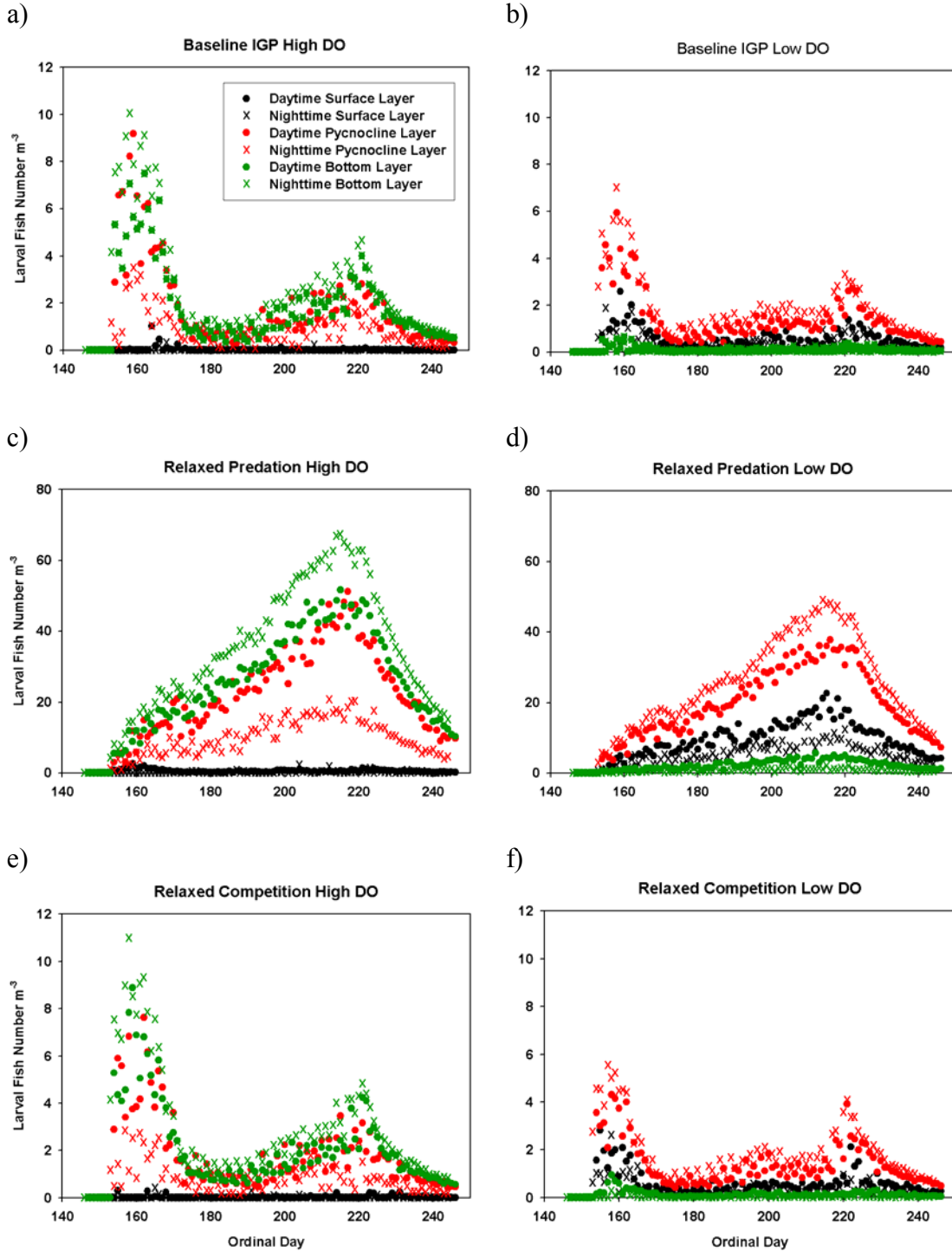


Figure 4.9. Mean daily larval fish average water column densities (number m^{-3}) for the high DO (blue circles) and low DO (black x's) a) baseline IGP, b) relaxed predation and c) relaxed competition food webs. Note different scales.

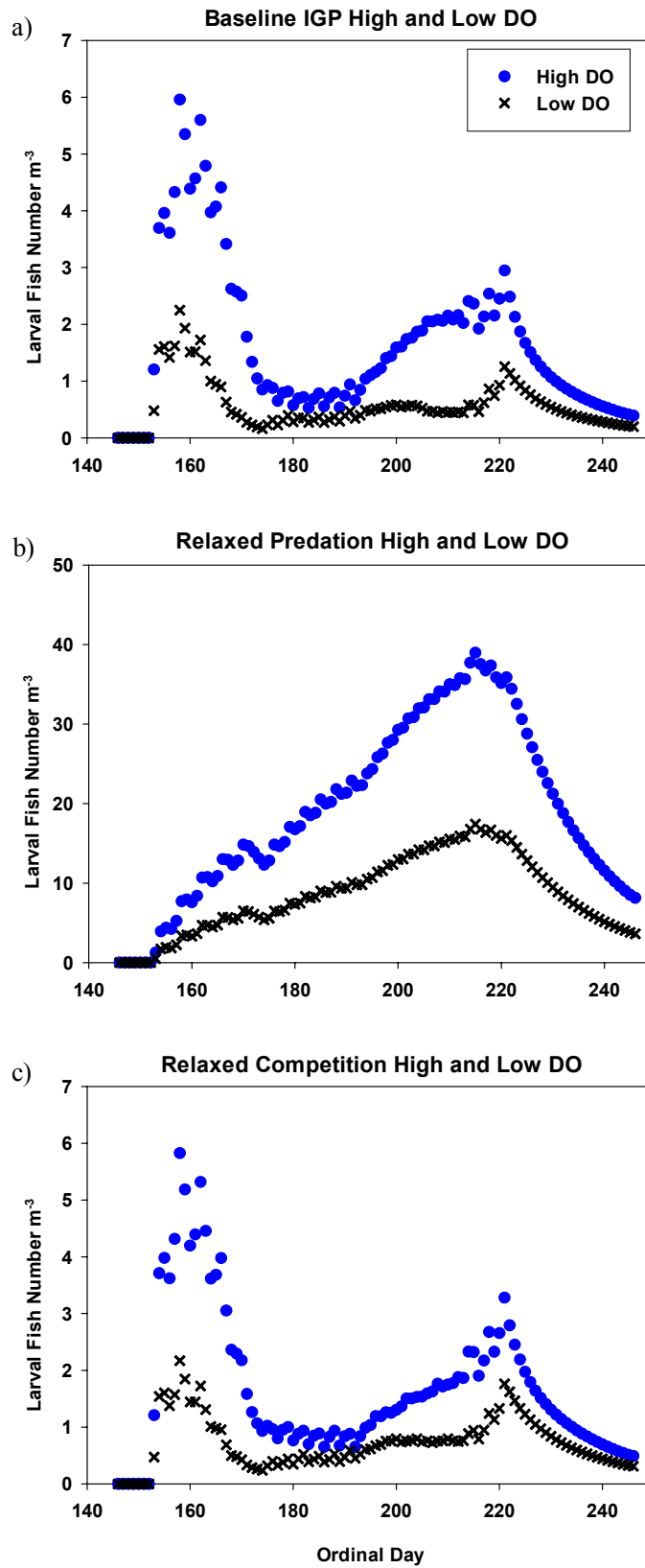


Figure 4.10. Mean daily ctenophore average water column densities (number m^{-3}) for the high DO (blue circles) and low DO (black x's) a) baseline IGP, b) relaxed predation and c) relaxed competition food webs.

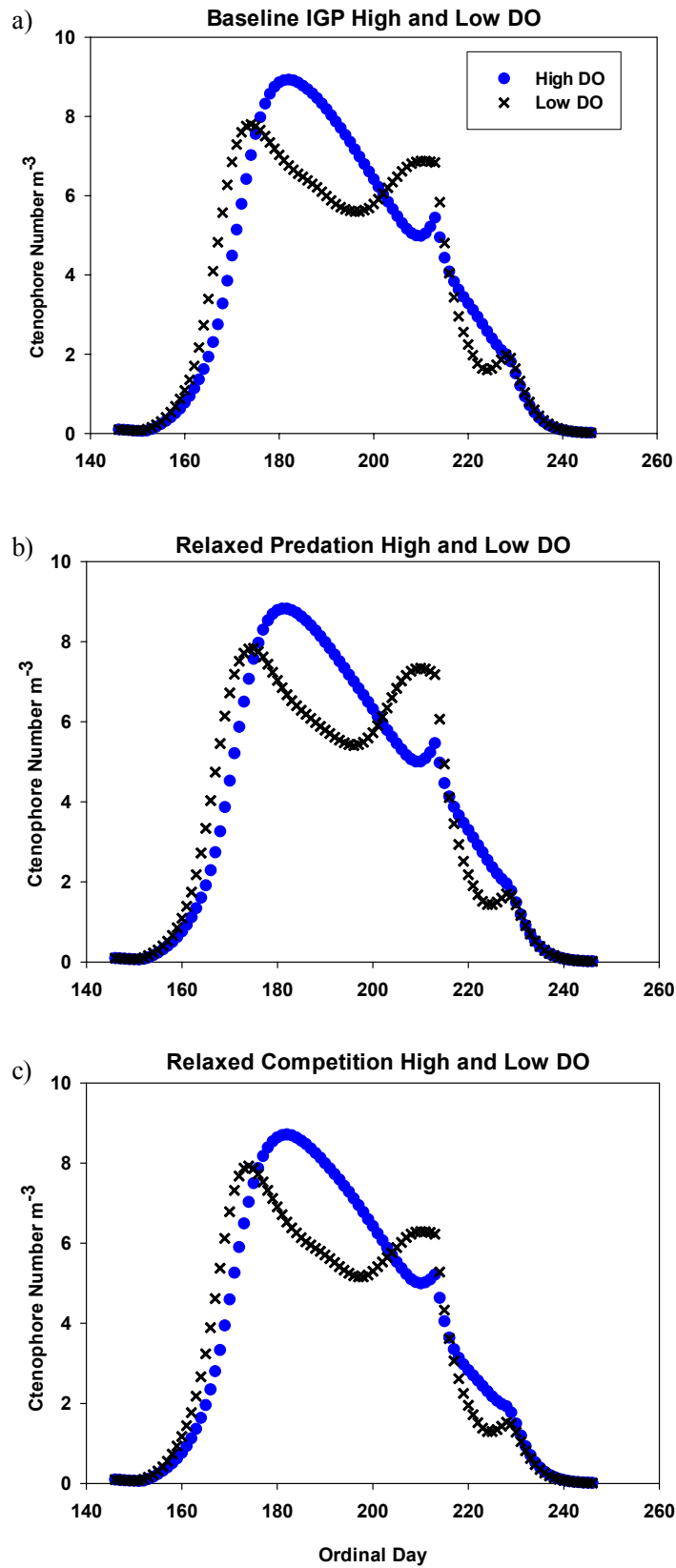


Figure 4.11. Mean daily adult copepod average water column densities (number m^{-3}) for the high DO (blue circles) and low DO (black x's) a) baseline IGP, b) relaxed predation and c) relaxed competition food webs.

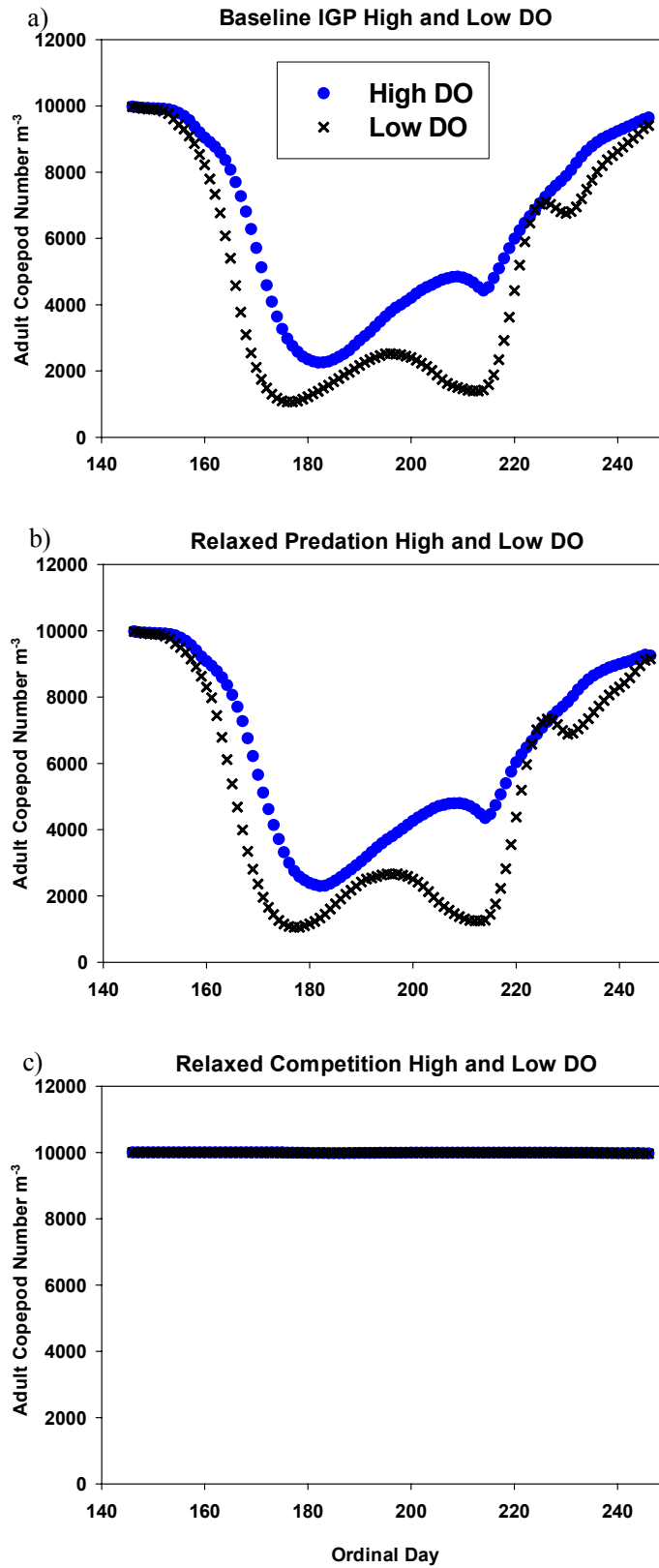
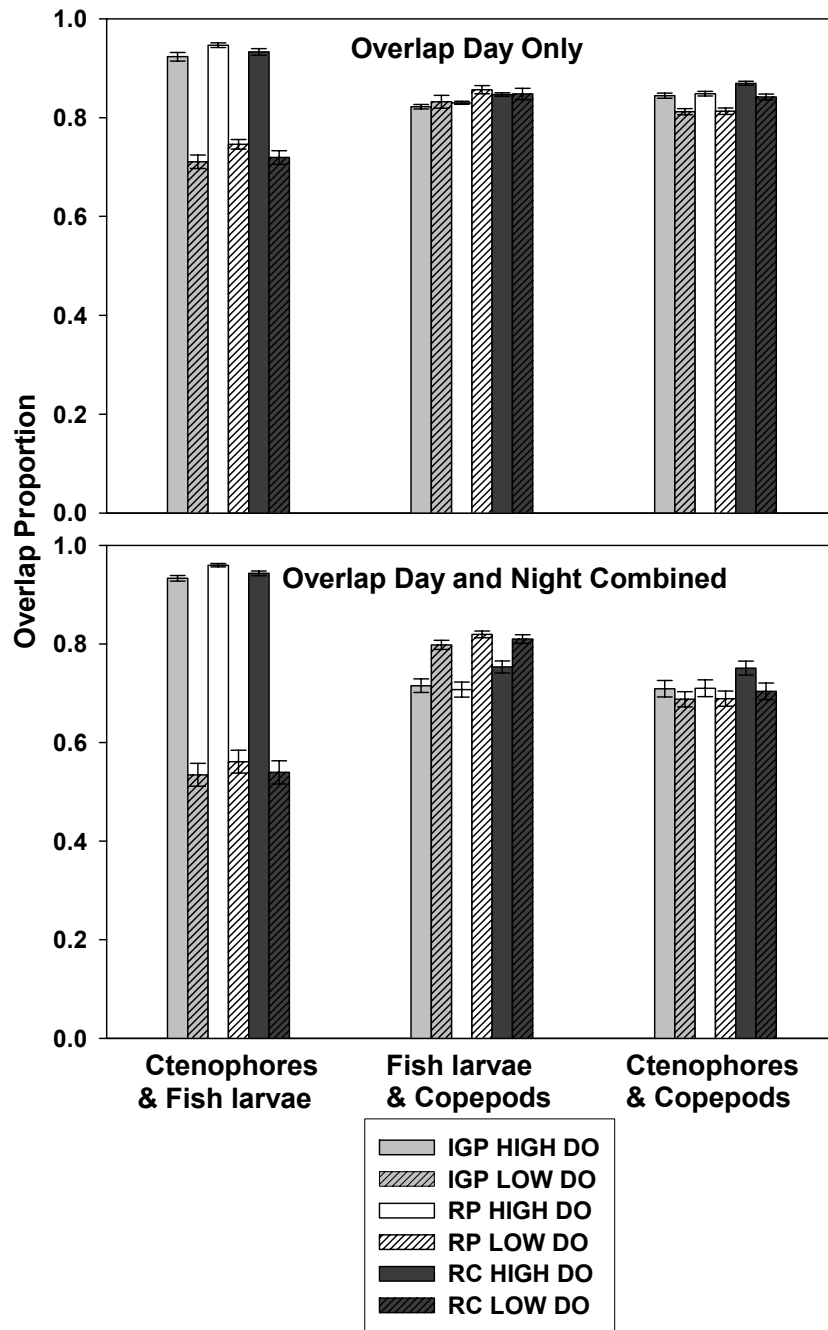


Figure 4.12. Vertical habitat overlap for three predator – prey pairs in the 6 different simulations: baseline IGP high DO (IGP HI DO, grey bars), baseline IGP low DO (IGP LO DO, grey striped bars), relaxed predation high DO (RP HI DO, white bars), relaxed predation low DO (RP LO DO, white striped bars), relaxed competition high DO (RC HI DO, dark grey bars), relaxed competition low DO (RC LO DO, dark grey striped bars). The three predator prey pairs are: ctenophores and fish larvae, fish larvae and copepods, and ctenophores and copepods. Overlap for all three copepod life stages (copepod nauplii, copepodites, and adult copepods) was combined since their vertical habitat distribution was the same. Daytime values are shown for larval fish predation and day and night combined are shown for ctenophores predators. Data are mean overlap \pm 95% confidence interval.



Chapter 5: Conclusions and Implications

My goal was to determine the effects of low DO on food web interactions between the ctenophore *Mnemiopsis leidyi* and Chesapeake Bay ichthyoplankton (bay anchovy *Anchoa mitchilli* and naked goby larvae *Gobiosoma bosc*). In Chapter 2, I conducted laboratory predation experiments that measured clearance rates of ctenophores feeding on fish eggs, yolk sac larvae, and feeding larvae at three different DO concentrations, and conducted field sampling to determine vertical habitat overlap of species in the Patuxent River planktonic food web under a range of DO conditions. Chapter 3 was comprised of small-scale observations of (1) ctenophore and larval fish swimming speeds at three DO concentrations, and (2) events leading from encounter to ingestion between a single ctenophore and fish larva at high and low DO. Finally, Chapter 4 combined results from laboratory experiments and field sampling with literature information to construct an individual-based predation model of the mesohaline Chesapeake Bay summertime ctenophore-fish larvae-copepod intraguild predation (IGP) food web under both high and low DO conditions.

My results indicate that different tolerances of low DO by predator and prey do not necessarily translate directly into differences in effects of DO on clearance rates, predation interactions, or swimming speeds. Experiments described in Chapter 2 suggest that hypoxia does not affect predation by ctenophores on ichthyoplankton. I found no significant DO effect on *Mnemiopsis leidyi* clearance rates of bay anchovy eggs, bay anchovy yolk sac larvae, or naked goby larvae in the laboratory; estimated predation rates were as high at low DO as they were at high DO. This result was unexpected as I anticipated differences in clearance rates due to DO based on different tolerances of low

DO between ctenophores and their prey (Purcell et al. 2001a, Breitbart et al. 2003, Decker et al. 2004), as well as the results of other predation studies (Breitbart et al. 1994, 1997, Decker et al. 2004).

Small-scale laboratory observations of predation interactions described in Chapter 3 revealed that DO does not have a significant effect on ingestion of fish larvae by ctenophores. But ctenophore swimming speeds were elevated under moderate hypoxia, which would be expected to increase encounter rates between predators and prey. Preliminary laboratory experiments did show a slight increase in larval fish ingestion by ctenophores under moderate hypoxia (Kolesar and Breitbart, unpubl.); however, this result was not observed in additional laboratory predation experiments (Kolesar Chapter 2).

Even though larval fish are sensitive to low DO, they may benefit from the effect of low DO on vertical habitat structure. The effect of DO on vertical distribution and overlap of predator and prey can either increase or decrease potential encounters, which can in turn affect predation. In the Patuxent River estuary, bottom DO affected the vertical distribution of each motile species I sampled and vertical overlap between species in the planktonic food web increased as bottom DO increased and all species utilized the bottom layer (Chapter 2). Greater vertical overlap with increasing bottom DO can increase encounters, leading to increased predation rates when DO concentrations are high in the bottom layer. Different tolerances to low DO of predator and prey resulted in different responses to low DO in bottom waters and decreasing vertical habitat overlap at low DO.

Competition for resources can also increase with increased vertical overlap of competitors in a well-oxygenated water column. My IGP food web model results from Chapter 4 indicated that the large degree of vertical overlap between ctenophores and larval fish in high DO food webs can result in lower densities and smaller size classes of copepod prey available to larval fish. In the low DO IGP food web model, overall survival of larval fish was less than at high DO but predation mortality was also less due to direct mortality of fish eggs due to hypoxia and changes in vertical overlap of ctenophores and fish larvae.

In IGP food webs, a species that is an inferior competitor to its prey can increase food web stability, but a species that is a superior competitor to its prey can decrease stability and eliminate prey. The ctenophore-fish larvae-copepod food web that typifies Chesapeake Bay and other temperate estuaries differs from more frequently examined IGP food webs in that the IGP predator (the ctenophore, *M. leidyi*) is a superior competitor to its prey. In Chapter 4, my simulation model of the IGP food web scenario resulted in fewer larval fish surviving than in either the relaxed predation or relaxed competition food web scenarios, signifying that larval fish persistence is not favored in the IGP food web.

Model simulations that relaxed predation or competition individually also indicated that predation was far more important to survival of early life stages of fish than was competition, but that competition was more important to larval fish growth rates than was predation. Larval fish survival was much higher when ctenophore predation was relaxed than in either the baseline IGP or relaxed competition food web, while larval fish

growth rates were higher when ctenophore competition was relaxed than in either of the other two food webs.

In my food web model, DO had only a minor effect on the relative importance of ctenophore predation and competition to survival of early life stages of fish. Larval fish survival was highest in the relaxed predation food web regardless of DO, and the rank order of growth rates in the three food webs was not changed by DO. At both high and low DO, larval fish growth rates were faster in the relaxed predation food web and slower in the relaxed competition food web compared to growth rates in the baseline IGP food web.

The longer-term effects of the full IGP food web and hypoxia beyond the summer spawning and larval fish growth period to maintaining larval fish persistence in the food web are unclear. Additional modeling that incorporates multiple years of food web interactions is necessary to determine effects of IGP on persistence of the Chesapeake Bay system planktonic food web. Expanding the model food web to include multiple levels of predators and prey (such as predatory scyphomedusae or microzooplankton prey) can provide a more robust simulation of trophic interactions. In addition, my individual-based food web model can be used to explore how factors affecting food web dynamics such as changes in spawning, overall species number and abundance, and environmental conditions might influence IGP food webs both in the Chesapeake Bay system and in other, similar habitats.

Understanding the interaction among trophic linkages and environmental stressors is important for sustainable resource management, and detrimental effects of a stressor on organisms may not directly translate into food web effects. Food web complexity can

make it difficult to predict environmental effects on species interactions. In my IGP food web model, an environmental perturbation such as low DO had a larger effect in a less complex food web (relaxed competition) than in the full IGP food web. Although these results look interesting, I interpret them with caution due to the low number of larval fish survivors. Further simulations with the IGP food web model are necessary to adequately address questions concerning environmental perturbations and food web stability.

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