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Mnemiopsis leidyi (Agassiz, 1865) on Ichthyoplankton in
Narragansett Bay, Rhode Island**

Angela R. Allen
University of Rhode Island

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AN ASSESSMENT OF PREDATION BY THE LOBATE CTENOPHORE
Mnemiopsis leidyi (Agassiz, 1865) ON ICHTHYOPLANKTON IN NARRAGANSETT
BAY, RHODE ISLAND

BY
ANGELA R. ALLEN

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
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MASTER OF SCIENCE THESIS

OF

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2004

ABSTRACT

I investigated the importance of predation on fish eggs and larvae by the lobate ctenophore, *Mnemiopsis leidyi*, in Narragansett Bay, RI, USA, by measuring the abundance and distribution of *M. leidyi* and its ichthyoplankton prey at five stations in the East and West Passages of the bay from May to August, 2002. During early-June, the *M. leidyi* population reached an abundance of 682 m^{-3} in the mid-bay, while fish egg densities were 3.2 m^{-3} and fish larvae were absent. In late June, a maximum larval fish density of $34 \text{ } 100\text{m}^{-3}$ was observed, and ctenophore abundance was $<33 \text{ m}^{-3}$ at all stations. These data confirm that predator and prey co-occur in the bay, but there is not a substantial amount of temporal overlap. Coincident with the ctenophore abundance measurements, I conducted *in situ* gut content analyses of 1,031 *M. leidyi* during the period of highest ichthyoplankton abundance. This revealed that 6.9% of the ctenophore guts examined contained at least one fish egg and one fish larva was observed from May-August. During June, 14.6% contained at least one fish egg. These data provide evidence that fish eggs are consumed by ctenophores in the bay. There was no evidence for frequent predation on fish larvae. Individual feeding rates ranged from 0.04 to 0.6 fish eggs ingested per ctenophore h^{-1} . Predation rates on fish eggs were calculated from the numbers of ichthyoplankton prey found in *M. leidyi*, temperature-specific digestion times determined in the laboratory, and the field densities of predator and prey. Accordingly, estimates of predation on fish eggs in Narragansett Bay ranged from $<1\%$ to 330% of the standing stock of the fish eggs ingested h^{-1} during periods of low and high ctenophore abundance, respectively. Predation on fish eggs was not detected in samples taken after June 26. An electivity

analysis was performed to compare the proportions of fish eggs versus other prey in the diet of *M. leidyi* and that found in the environment. Electivity of *M. leidyi* was examined at the Fox Island station and was found to be positive 23% of the time with respect to fish eggs and negative 8% of the time. All positive and negative values were significantly different from 0 ($p < 0.0005$). The date of peak abundance of ctenophores in the bay coincided with positive electivity for fish eggs. Also, the predators were found to have no selection 69% of the time with respect to fish eggs. Electivity was also examined at Dutch Island and was positive 42% of the time with respect to fish eggs and negative 16% of the time. No selection occurred 42% of the time. All positive and negative values were significantly different from 0 ($p < 0.01$). These results support that *M. leidyi* preys upon fish eggs in Narragansett Bay.

M. leidyi, zooplankton, fish eggs, and fish larvae abundances were sampled through the summer of 2002 in Narragansett Bay. These data were combined with literature values of microzooplankton abundance and physiological processes and a bioenergetics model was developed to simulate seasonal ctenophore biomass from June to July at Dutch and Fox Island. The goal of the model was to examine which prey groups were most important in supporting the observed *M. leidyi* biomass during the initiation or rapid population growth. The magnitude, rate of biomass increase, and timing output by the model was compared with field estimates of *M. leidyi* biomass. The model simulations clearly show that the carbon present in copepod biomass alone could account for the magnitude and high rate of increase of the ctenophores in early to mid-June. Later in the season after the copepods have been depleted, it appears that other sources of carbon become increasingly important to *M. leidyi*.

ACKNOWLEDGMENTS

I offer many thanks to my advisor, Dr. Barbara Sullivan-Watts, for imparting her knowledge of gelatinous zooplankton during my time at the Graduate School of Oceanography. Behind every well-run laboratory is an ever-resourceful person like my friend, Donna Van Keuren. I am deeply indebted to her for the support, patience, and genuine kindness that she extended to me. As a member of my committee, Dr. Scott Nixon has not only been steadfast in his enthusiasm, helpfulness, and commitment to making me a better scientist, but has offered many words of encouragement and for these things I am truly grateful. The title of this thesis includes the word “ichthyoplankton” and without the expertise of Dr. Grace Klein MacPhee, I would have been lost. Thank you for your time and knowledge. Dr. Mark Brush has been an invaluable source of help with the model and he truly deserves the nickname “golden boy.” To you, Mark, I extend many, many heartfelt thanks and wish you all the best with future projects.

Many other people at GSO have offered their help, advice, and have taken a genuine interest, not only my science, but in my well-being...so to Dr. Candace Oviatt, Dr. Edward Durbin, “The Fantastic” Meredith Clark, and countless others...Thank you so very much!

I also thank Dr. Pat Kremer for her constructive comments and the work that she did on *Mnemiopsis leidyi* in Narragansett Bay in the 1970's.

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To my parents, John and Debbie Allen; my brother, John; and my grandmother, Nena...I love you so very much and dedicate this thesis to you.

PREFACE

The primary goal of this research is to determine the degree to which the ctenophore, *M. leidy*, can reduce ichthyoplankton in Narragansett Bay, Rhode Island. The research presented in this thesis was supported by NOAA-CMER and NSF. The thesis is presented in manuscript format, with 2 manuscripts and 9 appendices.

The first manuscript will be submitted to Marine Biology with the authors Allen, A.R., B.K. Sullivan, G. Klein-MacPhee, and S.W. Nixon. This paper is the result of combining laboratory and field data to determine the predatory impact of *Mnemiopsis leidy* on ichthyoplankton in Narragansett Bay, RI. Important evidence includes digestion rates of fish eggs and larvae and ranges of ingestion and % clearance rates for *M. leidy* on both fish eggs and larvae. Another important component was determining to what extent predator and prey overlap both spatially and temporally in Narragansett Bay.

The second manuscript will be submitted to Ecological Modelling with authors Allen, A.R., M.J. Brush, and S.W. Nixon. This paper presents the application of a mechanistic population model, which provides insight into the amount of carbon necessary to support the observed changes in ctenophore biomass in Narragansett Bay. The model provides a first order approximation of the extent to which the ctenophore's metabolic demands can be met with mesozooplankton, microzooplankton, fish eggs, and fish larvae.

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CHAPTER 1: *Mnemiopsis leidyi* and ichthyoplankton: predator-prey dynamics in Narragansett Bay

INTRODUCTION

Predation on the early life history stages of marine fish is an important contributor to their overall mortality (Bailey and Houde 1989). Marine scientists noticed the importance of ichthyoplankton predation by invertebrates early in the 20th century (Mayer 1917; Joubin 1924; Bigelow 1926: all cited in Alvarino, 1985). Recent research has continued to focus on mortality due to predation because starvation appears to account for only a minor fraction of ichthyoplankton mortality (Bailey and Houde 1989). One study estimated that predation losses can range up to 95% over the duration of the egg stage (Hunter 1976).

Unfortunately, in spite of this long history, progress in this field has been slow due to the experimental difficulties associated with in situ predation studies (Bailey and Houde 1989; Purcell 1985). Previous studies have examined predation by gelatinous zooplankton on fish eggs and larvae using a variety of methods such as laboratory observations, quantification of digestion rates, gut content analyses, and modeling of predator-prey dynamics.

Among the known gelatinous predators of ichthyoplankton, cnidarians and ctenophores have substantial predatory potential because of high population densities and ingestion rates. Numerous studies have shown that pelagic cnidarians and some ctenophores prey on fish eggs and larvae (Burrell and Van Engel 1976; Purcell 1985; Purcell 1989; Arai and Hay 1982; Fancett and Jenkins 1988; Bailey and Houde 1989; Purcell 1994). Most studies that have reported predation by ctenophores on

ichthyoplankton targeted the total diet of the predator and the majority found that fish eggs comprised only a small portion of the diet. For example, Burrell and Van Engel (1976) observed that, out of 3,300 *M. leidy* guts examined, only 1% had ingested a fish egg and 0.4% had ingested a fish larva. Similarly, investigations that examined the role of larval fish in the diet of ctenophores found that they made up a relatively small portion of the total. Van der veer (1985) suggested that *Pleurobrachia pileus* was a significant predator of flounder larvae, despite finding only 9 larvae in 15,000 ctenophores guts. Purcell (1989) found 3 fish larvae out of 3,566 *Pleurobrachia bachei* guts examined in Kulleet Bay, Vancouver Island, British Columbia. These studies, however, examined tentaculate ctenophores, which may not be as effective at capturing fish larvae as their lobate counterparts.

The lobate ctenophore, *Mnemiopsis leidy*, may be an important predator in coastal systems given its high population densities and ingestion rates, and multiple feeding strategies such as lobe or auricular capture. *Mnemiopsis leidy* consumes a wide range of prey, including: crustacean larvae and copepods (Waggett and Costello 1999), Annelid larvae (Burrell and Van Engel 1976), and fish eggs and larvae (Cowan and Houde 1993). The mechanisms used by *M. leidy* to capture prey include the creation of a low-velocity current with the auricles and use of the oral lobes (Waggett and Costello 1999). The ctenophore's ability to use both lobes and auricles in concert for prey capture makes it an effective predator (Costello et al. 1999). A laboratory study by Cowan and Houde (1992) indicated that *M. leidy* preyed on Chesapeake Bay goby larvae, *Gobiosoma bosci*, from 2.7-9.4 mm SL, and that the ctenophore's slow

swimming speed resulted in lessened escape responses by larger fish larvae. However, there is little supporting evidence from field studies to confirm this laboratory finding.

A study of *M. leidy* in the Chesapeake Bay (Purcell et al. 1994) provides in situ clearance rates of fish eggs of $128 \pm 58 \text{ l d}^{-1} \text{ predator}^{-1}$ and predation estimates of 0-38% of the prey consumed d^{-1} . Large ctenophores were collected for gut content analysis and data for 75 individuals were reported. Of those, 51 contained no fish eggs, 24 contained one or more fish eggs, and none contained fish larvae. However, this study focused on one fish species, *Anchoa mitchilli*, and was limited by a small sample size and use of only large ctenophores for gut content analyses.

Because of container effects, studies which determine the predatory potential of ctenophores from laboratory feeding experiments should be considered with caution. Three laboratory feeding experiments and one mesocosm study have been conducted that used both 40-l and 20 to 25-l vessels (Kremer 1975), 5-l vessels (Tsikhon-Lukanina et al. 1994), 15 liter containers (Monteleone and Duguay 1988) and 3.0 m^3 enclosures (Cowan and Houde 1993), respectively. An experiment to determine the effect of container volume on the feeding rates of *M. leidy* demonstrated that small containers (<50 l) significantly reduce ctenophore feeding behavior (Monteleone and Duguay 1988). Unfortunately, the one large enclosure study only provided one experiment in which alternate prey were available and predation on only one species, *Anchoa mitchilli*, was investigated (Cowan and Houde 1993). Thus, more field estimates of predation rates are needed to compare with existing estimates of predation from laboratory studies.

Mnemiopsis sp. was first reported in large “rafts” in northern coastal waters in 1881 (Fewkes 1881). However, surprisingly little was known about the ecology of ctenophores because they are difficult to sample using conventional methods such as plankton nets, and they do not preserve well. Large-scale quantitative studies involving *M. leidyi* in New England waters did not begin until the 1970s (Kremer 1975). Since the 1970s, *M. leidyi* has been reported in large concentrations in Narragansett Bay, Rhode Island (Kremer and Nixon 1976, Deason and Smayda 1982, Sullivan et al. 2001), where the ctenophore population is typically larger than in warmer southern waters (Kremer 1994). The timing and maintenance of such immense growth events (“blooms”) has substantial trophic effects on zooplankton and, potentially, ichthyoplankton populations, as well as indirect impacts on phytoplankton. For example, Deason and Smayda (1982) observed diminished copepod abundance in Narragansett Bay following an increase in ctenophore abundance. The relaxation of grazing pressure by copepods then allowed a summer phytoplankton bloom in the bay.

In Narragansett Bay, a temporal shift in peak abundance of *M. leidyi* has been documented concurrent with increasing water temperatures (Sullivan et al 2001). Potential ecological consequences of this shift include a spatial-temporal overlap of *M. leidyi* and fish eggs and larvae during warm years, decreased survival of larval fish due to competition with *M. leidyi* for their zooplankton food source, and a decrease in overall ichthyoplankton abundance due to the top-down control exerted by the ctenophores. I speculate that the latter is potentially supported by a documented 2-4 fold decrease in ichthyoplankton abundance since the 1970’s (Keller et al. 1999) which

coincides with a significant increase in *M. leidy* abundance from the same time period (Sullivan et al 2001) (Fig. 1-1).



Figure 1-1. Nitrogen (µg/L) concentration in the Kalamazoo River, Michigan, from 1974 to 2005. The data shows a general increase in nitrogen concentration over time, with a notable dip around 1985 and another around 1995. The concentration reaches approximately 1300 µg/L by 2005.

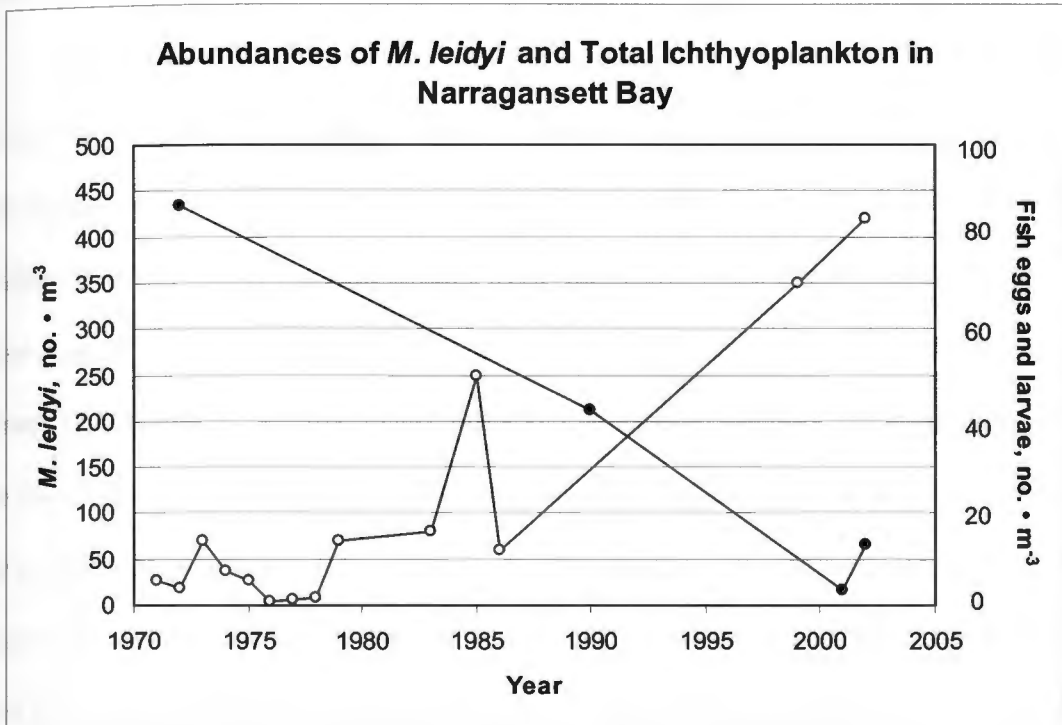


Figure 1-1. A 30 year comparison of *M. leidyi* and ichthyoplankton abundance in Narragansett Bay, RI. Open circles represent *M. leidyi* and closed circles are ichthyoplankton. *M. leidyi* data from Sullivan et al., 2001 and ichthyoplankton from Keller et al., 1999. Unpublished 2001-2002 *M. leidyi* and ichthyoplankton data are courtesy of B. Sullivan and G. Klein-MacPhee, respectively. Ichthyoplankton sampling frequency and site location was similar in all studies, but the sampling frequency of *M. leidyi* and sites sampled varied among studies. Mesh sizes used to determine *M. leidyi* abundances were as follows: 6 mm, 1971-72, 1974 (Kremer 1975); 153 μm , 1973 and 1974-76 (Hulsizer 1976) and (Deason and Smayda 1982); 1.8mm (summer and fall) and 153 μm (winter), 1975 (Deason 1982); 1 mm, 1983, 1985-86 (MERL, unpublished); 505 μm , 1990 (Keller et al. 1999); 500 and 1000 μm (Sullivan et al. 2001). Mesh sizes used to determine ichthyoplankton abundances were as follows: 505 μm , 1972, 1990, and 2001 (Bourne and Govoni 1988), (Keller et al. 1999), and (Klein-MacPhee, unpublished), 333 μm (this study).

METHODS

Field Sampling

Narragansett Bay is a temperate, relatively well-mixed estuary on the northeast coast of the United States (Hicks, 1959). The lower region of the bay is divided into two passages, East and West, by Prudence and Conanicut Islands. Ctenophores, ichthyoplankton, and mesozooplankton were sampled at 5 stations in the bay during May-August 2002. The stations: Warren River, Greenwich Bay, Prudence Island (East), Dutch Island, and Fox Island, were located in both the East and West passages of the Bay. The northernmost station was located at the mouth of the Warren River and the southernmost at Dutch Island (Fig. 1-2). The depths of the stations ranged from 13 meters at Dutch Island to 5 meters at Greenwich Bay. Two stations, Dutch Island and Fox Island, were sampled weekly throughout the entire sampling season. The remaining three stations were sampled weekly in June and then approximately bi-weekly during July and August. Sampling stations were positioned where fish eggs were most abundant during a 2001 ichthyoplankton survey in the bay (MacPhee, pers. comm.).

Ctenophore densities and sizes

I measured ctenophore abundance using a 1-mm mesh plankton net with a 0.5-m diameter opening equipped with a flowmeter. The net was slowly towed vertically from the bottom to the surface (2 tows per station) and the collected animals were placed in a cooler. The organisms were returned to the laboratory where they were counted and measured to the nearest centimeter with a ruler.

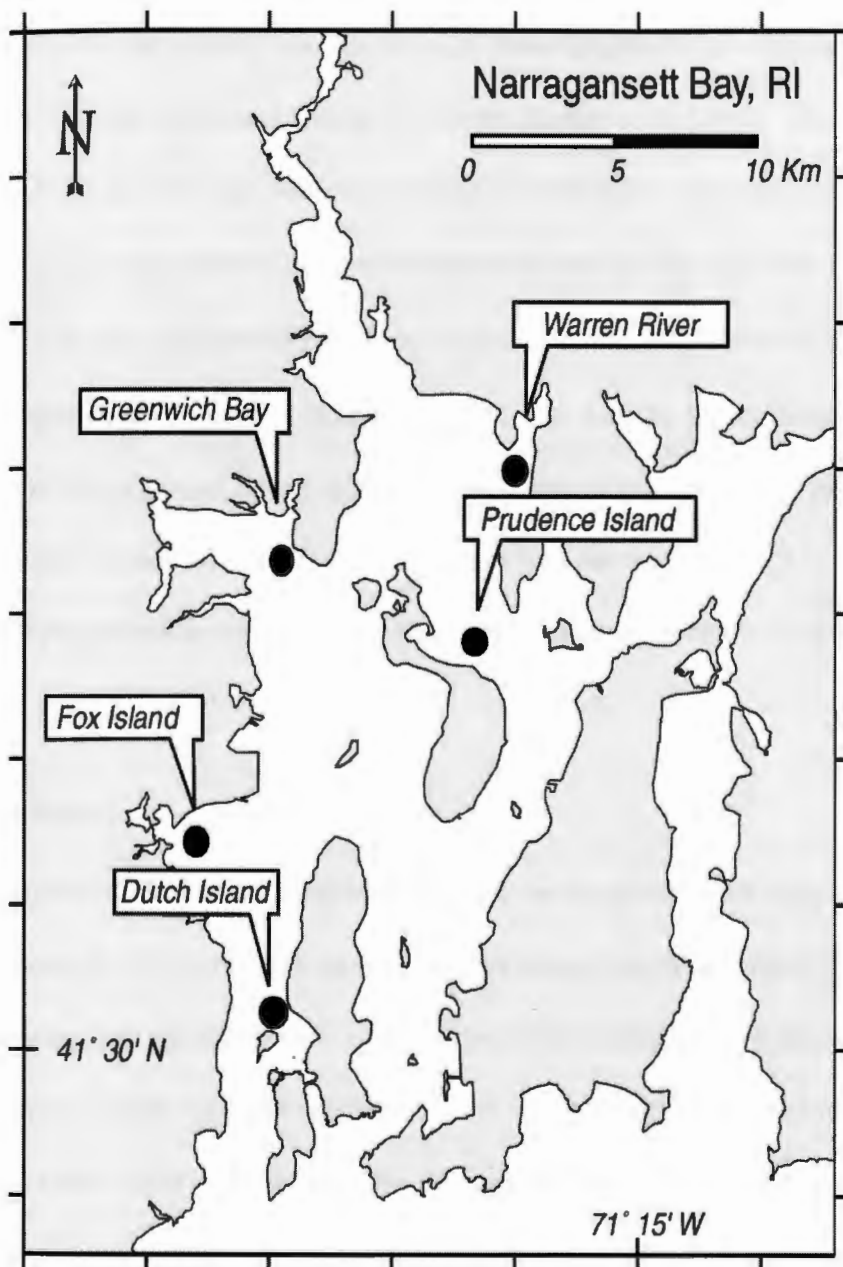


Figure 1-2. Station location in Narragansett Bay, RI where ctenophore, ichthyoplankton, and mesozooplankton abundances were sampled.

Fish egg and larvae densities

Ichthyoplankton density was determined from three replicate oblique tows, each at 3.7 km h^{-1} (Herman 1958) and lasting 2 minutes (Keller et al. 1999). The samples were collected using a $333\text{-}\mu\text{m}$ mesh net with a 0.5-m diameter opening equipped with a flowmeter. The average amount of water filtered per tow was 50 m^3 . This mesh size is a mid-sized mesh and was chosen based on a range of sizes, 280 to $505\mu\text{m}$, used in previous ichthyoplankton surveys (Keller et al 1999) as well as its suitability for capturing both fish eggs and larvae in Narragansett Bay (Klein-MacPhee, pers. comm.). One sample was counted live and the ichthyoplankton removed and used in laboratory digestion rate experiments, while the remaining two were preserved in 37% buffered formalin.

Zooplankton densities

Other constituents of the zooplankton (such as copepods, crab zoea, and veliger larvae) were sampled by vertical tows taken with a $64\text{-}\mu\text{m}$ mesh net with a 0.25-m diameter opening also equipped with a flowmeter. The chosen mesh size is appropriate for both larval and adult stages of members of the zooplankton in Narragansett Bay (Durbin and Durbin 1978). These samples were preserved in 37% buffered formalin and the contents enumerated. Data from these tows was used for calculation of selectivity of prey and was provided by Sullivan and Van Keuren (unpublished).

Gut Content Analyses

I also collected ctenophores at each station using a long-handled bucket and a plankton net. I immediately examined their gut contents under a dissecting microscope.

Shipboard microscopy is the most direct method to determine the actual diet of the predators. This method avoids the artifacts of over-handling, especially the ejection of gut contents, which have plagued laboratory studies. Fish eggs and larvae were identified to species level and enumerated in the ctenophore gut contents. As many ctenophores as possible were examined at each station with the target number being a minimum of 30 organisms from each of two size classes (<1 cm, >1 cm). This target number was selected based on desired confidence intervals for statistical significance. This was not always possible due to time constraints or lack of organisms.

Digestion Times

It is important to accurately determine the length of time a fish egg or larva can be identified in the predator's gut (D), so that those values can be used in combination with frequency of prey per predator (G) to calculate predation rates from the equation $I = G/D$, when I = ingestion predator per hour. Laboratory studies were performed to determine the digestion times of *M. leidyi* of multiple size classes. Freshly collected ctenophores were placed in 8-l containers with 20- μm mesh filtered seawater in an environmental chamber and held overnight to clear their guts. The temperature was set within 1-2°C of the temperature of ambient seawater in the bay at the time ctenophores were collected. Prior to measurements, the ctenophores were maintained in the environmental chamber at the same temperature and light/dark cycle as they would encounter naturally. Two temperature treatments, a low range of 7.5-13°C and a high range of 21.5-24°C, were chosen based on the observed temperature range in Narragansett Bay during 2002. Approximately the same temperature ranges were used in previous *M. leidyi* predation experiments on zooplankton of Narragansett Bay

(Kremer 1979). Eight-liter containers were used in the digestion experiments, because container effects were not important as these studies were concerned with ctenophore digestion time and not feeding behavior. The prey consisted of net-collected zooplankton and net-collected and cultured ichthyoplankton. Fish egg sizes used in the determination of ctenophore digestion rates ranged from 0.74-1.15 mm in diameter and fish larvae used were 2.78-3.0 mm in total length (Table 1-1). Five species of fish eggs, cunner (*Tautoglabrus adspersus*), tautog (*Tautoga onitis*), searobin (*Prionotus sp.*), summer flounder (*Paralichthys dentatus*), and winter flounder (*Pleuronectes americanus*) were used in the digestion rate experiments as well as summer flounder and winter flounder larvae from aquaculture.

I dyed fish eggs and larvae by adding full-strength Neutral Red (1 g/ 1.5 L water) to an aqueous solution that contained the prey. This procedure did not alter the behavior of either component during the feeding period, nor did it effect the digestion time (Appendix H). Coloring the otherwise translucent fish eggs was an experimental innovation which served three purposes: first, it allowed the eggs to be easily observed in the transparent ctenophore gut; second, it decreased the amount of handling of the ctenophore during the experiment; and third, it allowed for more frequent observations of gut contents. Live prey items were added to the experimental container and the ctenophore was allowed to feed until 1-2 prey were detected in the gut. The ctenophore was then removed from the prey container, placed into another 8-liter container with filtered seawater and no prey items. I examined the ctenophore at 2-3 minute intervals to determine a functional digestion time (the time when an ingested prey item could no longer be positively identified) and an actual digestion time (the time when the prey was

completely digested). An interval of 2-3 minutes allowed for observation of several ctenophores at the same time.

Table 1-1. : Ichthyoplankton prey used in digestion rate experiments. One asterisk denotes egg diameter and two asterisks indicate total larval length.

Taxon	Common Name	Prey type	Prey size, mm	Demersal or pelagic egg
Triglidae	Searobin	egg	*0.94-1.15	pelagic
<i>Priontus spp.</i>				
Labridae				
<i>Tautoga onitis</i>	Tautog	egg	*0.97-1.00	pelagic
<i>Tautogolabrus adspersus</i>	Cunner	egg	*0.84-0.92	pelagic
Pleuronectidae				
<i>Pleuronectes americanus</i>	Winter flounder	larva	**3.0	
		egg	*0.74-0.85	demersal
Bothidae				
<i>Paralichthys dentatus</i>	Summer flounder	larva	**2.78	
		egg	*1.02	pelagic

Digestion times of fish eggs reported in the literature range from 10-45 minutes with fish larvae being digested in as few as 15 minutes, so the 2-3 minute observation intervals resulted in more tightly constrained digestion rates than in previous studies (Monteleone and Duguay 1988).

Ingestion Rates and Predatory Impact

For each sampling time, ingestion rates of the ctenophores were calculated from the average number of eggs or larvae per ctenophore from 30 or more organisms in each size class in field collections and digestion time measured in the laboratory. The ingestion model used was: $I = G/D$, where I = number of eggs ingested per ctenophore per hour, G = number of fish eggs or larvae per ctenophore (from field collections), D = egg or larvae actual digestion time (h) (from laboratory study). The actual digestion time was used instead of the functional time because actual digestion times were available for all experiments. This technique of using the model $I = G/D$, described by Purcell (1997), reduced laboratory artifacts and revealed the actual diet of the ctenophore by relying on gut content data from field collected ctenophores. However, this equation assumes that there is steady-state feeding by the predators and that food identified from gut content analysis (G) is the same food that will be used in the measurements of digestion times (D). In addition, this method assumes that the animals collected for gut contents are representative of the population at that location. A % clearance rate was calculated from the ingestion rate and densities of prey in the water column ($I/\text{egg or larvae density}$). These ingestion rates were multiplied by the number of predators to estimate the percent of the prey population that could potentially be

consumed. The calculation of % clearance rate relies upon "I" or the calculated ingestion rate and is therefore dependent on the gut content approach.

Statistical Analysis

Descriptive statistical analyses such as mean and standard deviation of *M. leidy* and ichthyoplankton abundances were performed using the Microsoft® Excel 2000 software package. I used the Sigmastat® statistical software package to perform one way ANOVAs to determine the variability of both ctenophore and fish egg and larval abundance by station and date. Because there was a significant difference among stations for ctenophore abundance, I used Sigmastat® to perform an All Pairwise Multiple Comparison Test or Tukey Test. In order to examine if digestion times of fish eggs and larvae were affected by independent variables such as ctenophore size, date, prey size, and temperature, a multiple linear regression analysis was performed using Sigmastat® software. Pearre's (1982) electivity index, C, was used to assess *M. leidy*'s prey-selectivity in situ at Fox Island and Dutch Island. Electivity analysis could not be performed at the other stations, because total gut content data was not collected, only ichthyoplankton data.

RESULTS

Seasonal Abundance of Predator and Prey

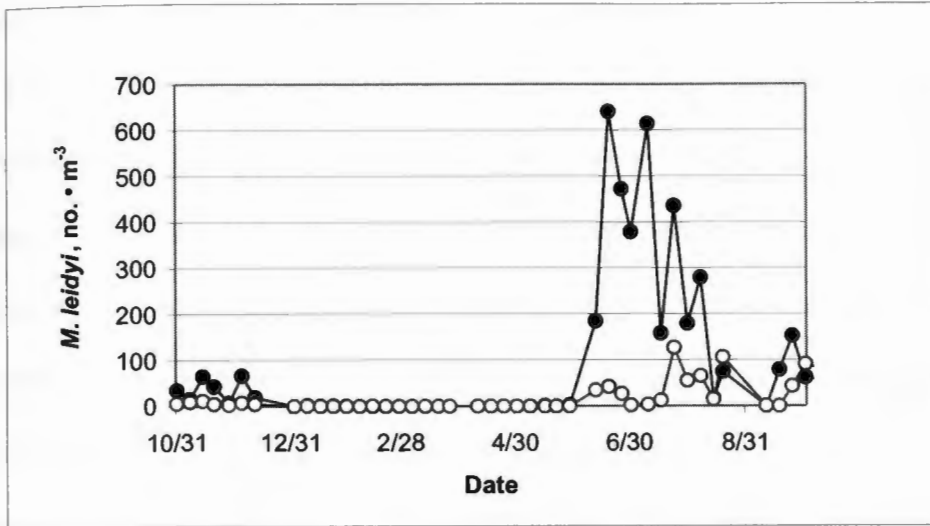
Mnemiopsis leidy was the most abundant gelatinous predator collected in Narragansett Bay during the study period. The *M. leidy* population in Narragansett Bay was characterized by a rapid increase in abundance which spanned several orders

of magnitude and then a steep decline in late summer through early fall (Fig. 1-3). The change in ctenophore abundance in Narragansett Bay was significantly related to both



Figure 1-3
Standard deviation
Closed circles
January 1998

A.



B.

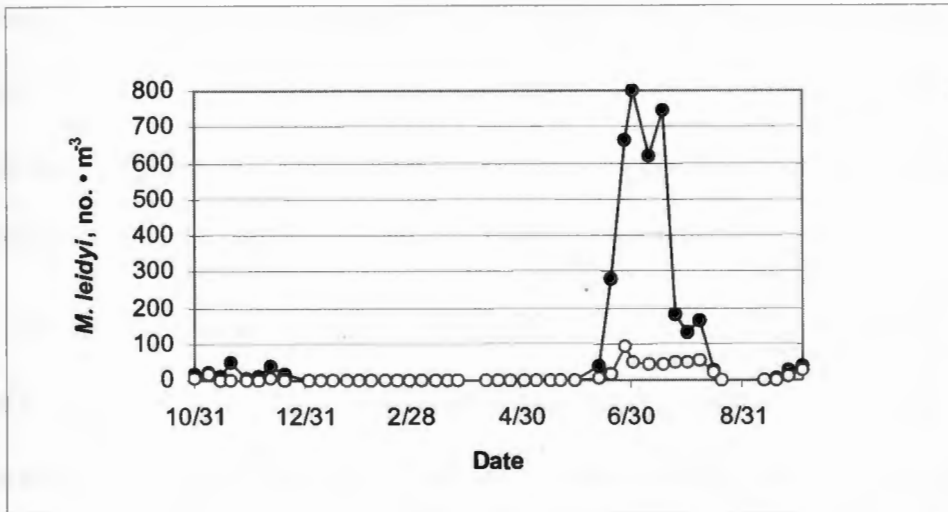


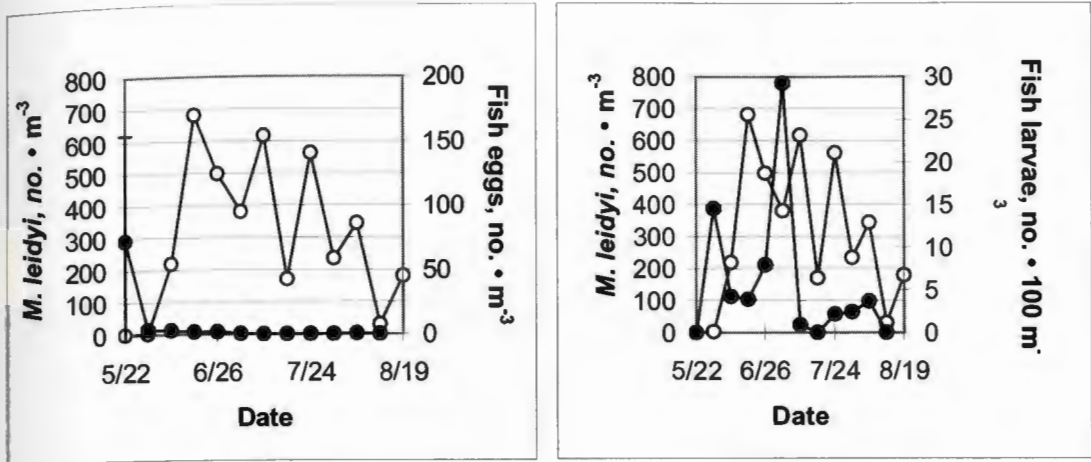
Figure 1-3. Abundance of *M. leidyi* in Narragansett Bay, RI, 2001-2002. A. *M. leidyi* abundance at Fox Island station. B. *M. leidyi* abundance at Dutch Island station. Closed circles represent ctenophores =1cm total length and open circles >1cm in total length. Data courtesy of B. Sullivan, unpublished.

sampling date and station (one-way ANOVA, $p < 0.001$ and $p < 0.05$, respectively). The increase in volume of *M. leidy* spread down-bay; beginning in March in the Providence River and progressing southward throughout the summer and fall (Appendix A).

Total predator densities were $< 100 \text{ m}^{-3}$ until mid-June, when a dramatic increase in total ctenophore abundance was observed at both stations (Fig. 1-3). The *M. leidy* population experienced a rate of increase of $22.5\% \text{ d}^{-1}$ during this time, which coincided with the time that was previously identified as the spawning period of numerous local fish species, including cunner (*Tautoglabrus adspersus*), tautog (*Tautoga onitis*), butterfish (*Peprilus triacanthus*), atlantic menhaden (*Brevoortia tyrannus*) and searobin (*Prionotus spp.*) (French 1991). But the maximum egg population appears to have occurred earlier at Fox Island and Dutch Island than the time of increase of Mnemiopsis (Fig. 1-4a). Of the 14 identified species of fish eggs and larvae in the ichthyoplankton samples, the species composition was dominated by butterfish, cunner, tautog, and searobin eggs (Fig. 1-5A). The same four species were the dominant eggs found in the gut contents of *M. leidy* during the sampling period (Fig 1-5B).

The highest total mean fish egg density (of three tows), $73.2 \pm 82.2 \text{ m}^{-3}$, was recorded on May 29 at Fox Island when mean ctenophore abundance (of duplicate tows) was low at 2.9 m^{-3} (Fig. 1-4A). Fish larvae reached a peak average abundance (of three tows) of $34.1 \pm 59.8 \text{ 100m}^{-3}$ larvae on June 18 at Prudence Island and were inversely related to ctenophore abundance at 3 out of 5 stations. Prudence Island and Warren River did not exhibit this pattern and ctenophore abundance and fish larvae increased simultaneously (Appendix B). Abundance of fish eggs and larvae was not significantly different among stations during the survey (one-way ANOVA, $p = 0.318$).

A.



B.

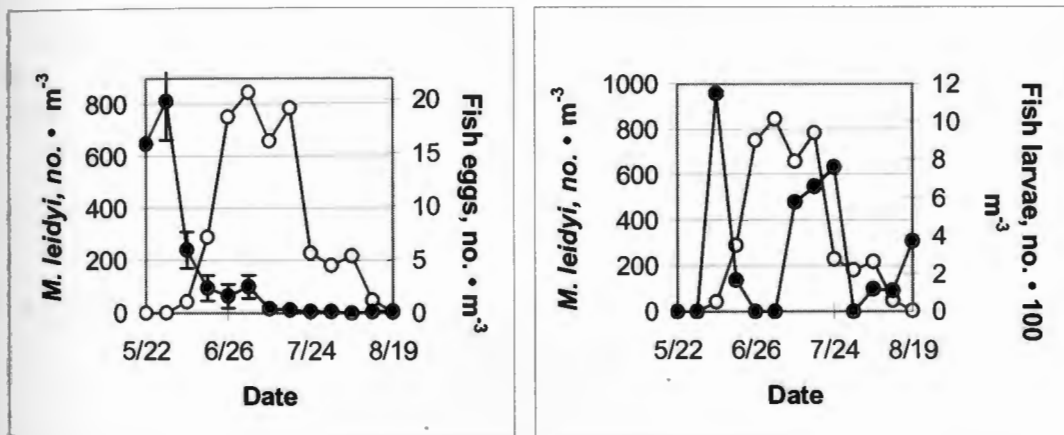
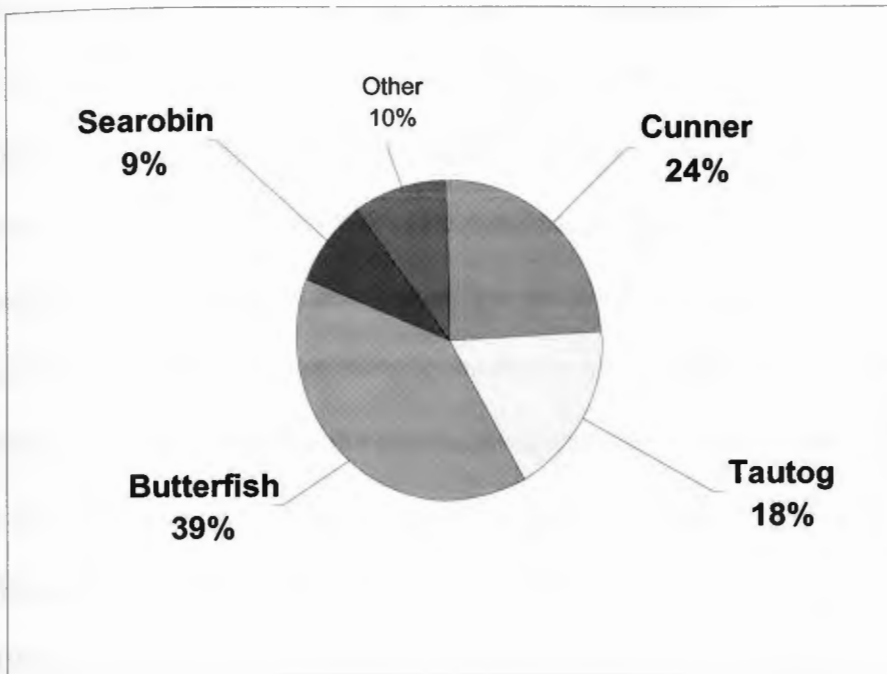


Figure 1-4. Mean abundance of all sizes of *M. leidyi* and fish eggs and larvae at two stations in the West Passage of Narragansett Bay during the summer of 2002. Open circles represent all sizes of *M. leidyi* and closed circles are fish eggs or larvae. A. Fox Island, B. Dutch Island. The standard deviations for fish egg and larvae mean abundances are included. Error bars are not visible when the standard deviation approaches zero. See Appendix F for standard deviation and coefficient of variation values of ctenophore abundance estimates.

A.



B.

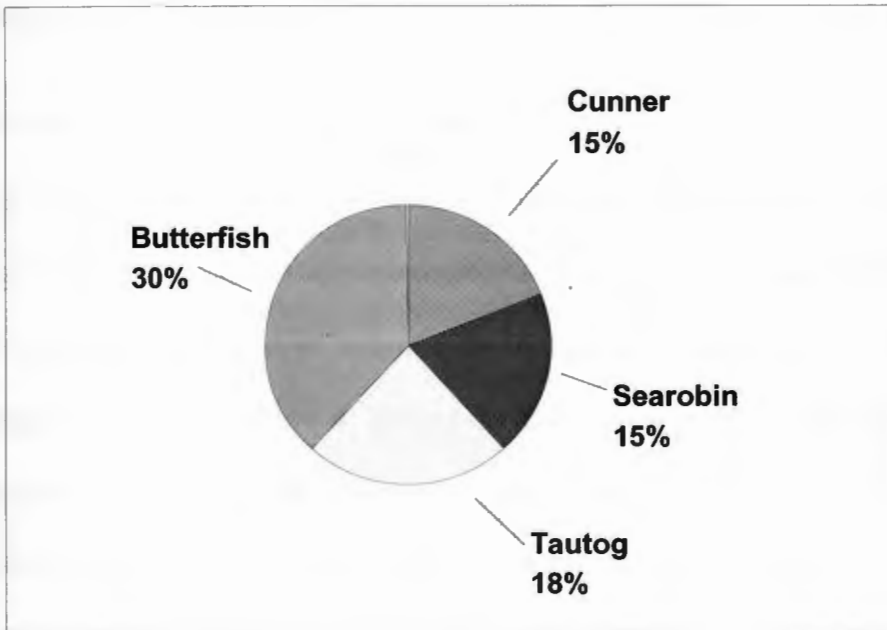


Figure 1-5. A. Percent composition of fish eggs determined from enumerated weekly ichthyoplankton tows taken at 5 stations in Narragansett Bay, RI from May-August 2002. B. Percent composition of fish eggs identified in the gut contents of >1,000 *M. leidyi* at the same 5 stations from May-August 2002.

Further analysis of the abundance patterns of fish eggs and *M. leidyi* at each station was performed during the period characterized by the greatest fish egg decline (Table 1-2). Based on % clearance rate calculations for this time period (Table 1-3), I determined the percentage of the fish egg decline per day that could be attributed to predation by *M. leidyi*. At every station except Prudence Island, the values obtained indicated that over 100% of the fish egg decline could be explained by *M. leidyi* predation. However, these values are not consistent with the observation that the timing of *M. leidyi* peak abundance was not synchronous with the period of greatest fish egg decline. Therefore, the decline was further examined in terms of tidal flushing from the lower West passage to Rhode Island Sound at a rate of 20-40% per day (Kremer and Nixon 1978). This revealed that the decline in fish eggs can be completely explained by physical flushing at all stations.

Digestion rates of M. leidyi on fish eggs and larvae

M. leidyi digestion times increased with increasing egg size, but the effect of differing larval sizes could not be evaluated because all larvae were approximately equal lengths. Digestion rates of *M. leidyi* for fish eggs and larvae decreased with increasing temperatures (Table 1-4; Table 1-5). In both temperature treatments, mean fish egg digestion times, 1.5 ± 0.6 hrs. (13°C) and 1.1 ± 0.4 hrs. (21.5°C) were longer than those for fish larvae, 1.2 ± 0.2 hrs. (7.5°C) and 0.4 ± 0.05 hrs. (24°C). A Q_{10} of 0.7 was calculated for fish egg digestion by *M. leidyi* using the following equation:

$$Q_{10} = \frac{\ln k_1 - \ln k_2}{\Delta T} * 10 \quad (1)$$

Table 1-2. : Results of the analysis of the period of greatest fish egg decline. The exponential model, $N_t = N_0 e^{-kt}$, was applied to determine the percent fish egg decrease d^{-1} , where N_0 = initial number of prey, N_t = number of prey at time, t , e = base of natural logarithm, t = time in days, and k = the fraction of the standing stock of prey removed d^{-1} . The loss rate of 20-40% due to flushing is based on a tidal mixing model for the lower West Passage of Narragansett Bay (Kremer and Nixon 1978).

Station	Period of egg decrease	N_0 , # m^{-3}	N_t , # m^{-3}	Decrease d^{-1} , %	Loss due to flushing d^{-1} , %	Maturation or mortality d^{-1} , %
FI	5/29-6/12	73	3.7	21.3	20-40	60-80
DI	5/29-6/12	19.8	5.9	8.6	20-40	60-80
PI	6/11-6/18	18.2	3.6	23.1	20-40	60-80
WR	6/4-6/25	8.2	4.7	2.6	20-40	60-80
GB	6/11-6/19	7.4	1.8	17.7	20-40	60-80

Table 1-3: Data for $I = G/D$ and % clearance rate calculations. A digestion time of 1.1 hours was used in all the calculations.

Station/ Date	I, # of fish eggs or larvae ingested h^{-1}	G, # of eggs or larvae <i>M. leidyi</i> gut $^{-1}$	N, # of <i>M.</i> <i>leidyi</i> guts	P, proportion with eggs in gut	% of fish eggs cleared h^{-1}	I * # of cteno. >1cm m^{-3}	I * # of cteno. <1cm m^{-3}	# of <i>M.</i> <i>leidyi</i> >1cm m^{-3}	# of <i>M.</i> <i>leidyi</i> <1cm m^{-3}	# of fish eggs m^{-3}
FI, 5/29/02	0.1	0.1	18	0.12±0.16	0.01	0.01	0	0.1	2.9	73
WR, 6/4/02	0.4	0.48	40	0.475±0.155	15.8	1.3	0	3	0.7	8.2
PI, 6/4/02	0.06	0.08	26	0.08±0.11	0.1	0.007	0	0.1	2.6	6.9
GB, 6/4/02	0.6	0.7	17	0.71±0.22	17.9	2.1	0	3.2	7	11.5
GB, 6/11/02	0.56	0.6	13	0.62±0.27	7.3	0.8	0	1.5	23	11.5
PI, 6/11/02	0.2	0.25	16	0.25±0.21	0.02	0.005	0	0.02	20.4	18.2
FI, 6/12/02	0.1	0.1	41	0.15±0.11	330.7	4.6	0	34.8	185.3	1.4
PI 6/18/02	0.17	0.2	21	0.19±0.17	1.4	0.1	0	0.3	33.8	3.6
WR, 6/18/02	0.1	0.1	55	0.11±0.08	20.4	1.3	0	13.4	68.9	6.5
DI, 6/19/02	0.16	0.2	34	0.18±0.13	125.7	2.3	0	14.1	277.1	1.8
FI, 6/19/02	0.05	0.1	35	0.06±0.08	68.2	21.8	0	42.0	640.6	3.2
GB, 6/19/02	0.04	0.06	81	0.05±0.05	8.3	0.1	4.4	2.6	97.6	1.4
WR, 6/25/02	0.09	0.1	20	0.1±0.13	3.8	0.2	0	1.7	171.1	4.1
FI, 6/26/02	0.05	0.06	35	0.06±0.08	70.1	1.4	0	27	472.3	2

Table 1-4. Digestion rates of *M. leidyi* on fish eggs and larvae at low temperatures, 7.5-13 degrees Celsius. ND denotes "no data."

Date	Prey type	Temp., °C	<i>M. leidyi</i> total length, cm	Functional digestion time, h	Actual digestion time, h	Prey number	Other prey in gut
5/23/02	Searobin egg	13	4.2	ND	1.2	1	
5/23/02	Tautog egg	13	4.1	1.1	1.1	1	
6/10/02	unidentified eggs	13	5.3	2	2.8	2	
6/10/02	Cunner egg	13	2.9	ND	2.3	1	
6/10/02	Cunner egg	13	3.3	ND	1.3	1	14 <i>Acartia tonsa</i> copepodites
6/24/02	Cunner egg	10	4.8	1.5	2.5	1	1 <i>Acartia tonsa</i> , 7 <i>A. tonsa</i> copepodites
1/27/03	Winter flounder larva	7.5	2.5	ND	1.1	1	4 Podon
1/27/03	Winter flounder larva	7.5	1.6	ND	1.0	1	3 Podon, 1 <i>Crepidula</i>
1/28/03	Winter flounder larva	7.5	2.9	0.7	1.4	2	1 <i>Crepidula</i>
1/28/03	Winter flounder larva	7.5	3.4	0.65	1.4	2	

Table 1-5. Digestion rates of *M. leidyi* on fish eggs and larvae at high temperatures, 21.5-24 degrees Celsius. ND denotes "no data."

Date	Prey type	Temp., °C	<i>M. leidyi</i> total length, cm	Functional digestion time, h	Actual digestion time, h	Prey number	Other prey in gut
8/7/03	Tautog egg	24	3.8	1.0	1.2	1	11 <i>Acartia tonsa</i> adults, 1 crab zoea, 8 ovoid bodies
8/7/03	Tautog egg	23	4.1	ND	0.6	1	1 <i>A. tonsa</i> adult, 1 crab zoea, detrital mass
8/20/03	Summer flounder egg	21.5	ND	ND	0.7	1	
8/20/03	Summer flounder egg	21.5	1.8	1.0	1.2	2	
8/20/03	Summer flounder egg	21.5	5.3	1.2	1.5	4	
8/20/03	Summer flounder larva	21.5	4.5	0.4	0.6	1	
8/21/03	Summer flounder larva	24	5.2	0.3	0.4	1	
8/21/03	Summer flounder larva	24	3.1	0.2	0.3	1	

where k_1 is the rate at temperature t_1 and k_2 the rate at temperature t_2 . Multiple linear regression analysis indicated that the length of digestion time in ctenophores depends on both temperature and prey size (Table 1-6).

Table 1-6. Multiple regression ^a analysis of ctenophore digestion time in relation to prey size and temperature.

Variable	Range	Mean	P-value
X ₁ , prey size (mm)	0.94-3.0	1.8	0.004
X ₂ , temperature	7.5-24.0	15.9	0.002
Y ₁ , digestion time (h)	0.32-2.75	1.2	—

^a Regression equation: $Y_1 = 2.972 - (0.386 * X_1) + (0.0661 * X_2)$, $r^2 = 0.580$; ANOVA $F = 10.375$, $p = 0.001$, SE of estimate = 0.475.

Gut Content Analyses

In situ gut content analyses of *M. leidyi* during the period of highest ichthyoplankton abundance (May 22- June 7) revealed that 19.6% of the ctenophores examined had consumed at least one fish egg with a range from 0-71% over the sampling season. Of 1,031 ctenophore guts examined from May to August, 6.9% contained at least one fish egg, with one having 5 in the gut. This study shows that a broad size range of ctenophores are capable of ingesting fish eggs. The largest ctenophore to have ingested a fish egg was 10.1 cm total length, the smallest was 0.5 cm, and the mean ctenophore size that ingested a fish egg was 5.2 cm. Only 2 ctenophores < 1 cm consumed a fish egg and the median size of *M. leidyi* that ingested an egg was 5.4 cm and the mean size was 5.2 cm total length. The size distribution of the % of ctenophores that consumed fish eggs revealed that the percentage of *M. leidyi* that ingested fish eggs was roughly 5 times higher when the predators were larger than 4 cm total length (Figure 1- 6). The percent composition of fish eggs in the ichthyoplankton diet of *M. leidyi* consisted of butterfish eggs (39%), tautog (23%), cunner (19%), and searobin (19%).

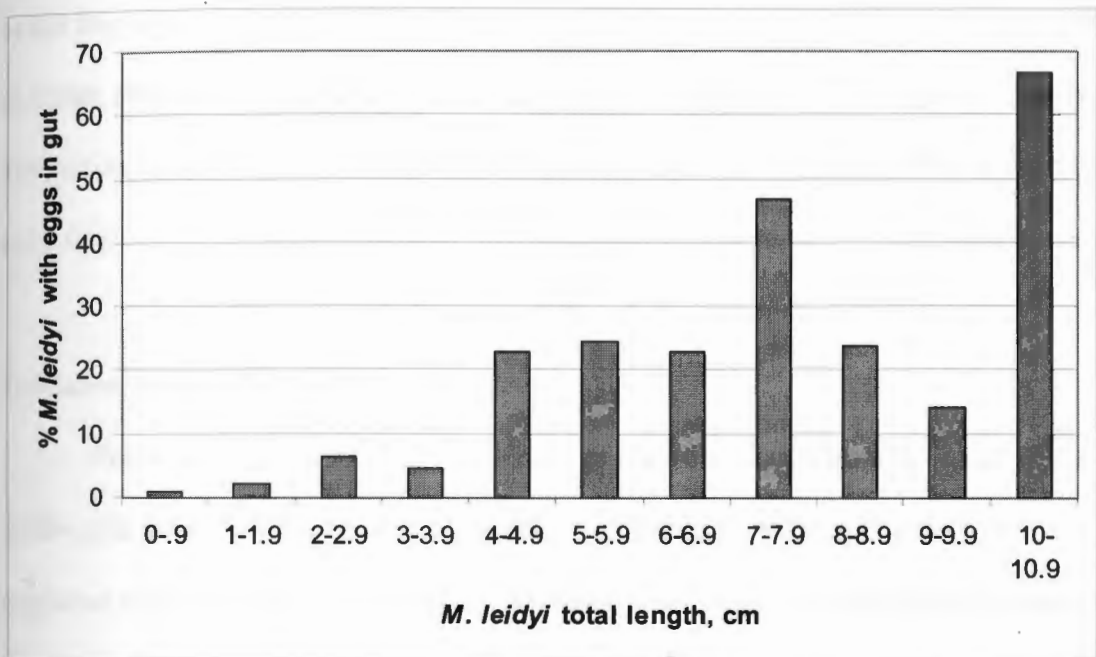


Figure 1-6. Size distribution of the % of *M. leidyi* that consumed fish eggs at all stations from May-August 2002

Only one fish larva was observed in gut contents during the study. An electivity analysis was performed to compare the proportions of fish eggs versus other prey in the diet of *M. leidy* and that found in the environment. Electivity of *M. leidy* was examined at the Fox Island station and was found to be positive 23% of the time with respect to fish eggs and negative 8% of the time. All positive and negative values were significantly different from 0 ($p < 0.0005$). The date of peak abundance of ctenophores in the bay coincided with positive electivity for fish eggs. Electivity was also examined at Dutch Island and was positive 42% of the time with respect to fish eggs and negative 16% of the time. All positive and negative values were significantly different from 0 ($p < 0.01$).

Predation rates on fish eggs

Predation rates by *M. leidy* on fish eggs were calculated from the numbers of ichthyoplankton prey found in the predator's gut contents, the temperature-specific digestion times, and the field densities of predator and prey. Accordingly, estimates of predation on fish eggs in Narragansett Bay ranged from <1 to $111 \text{ eggs consumed m}^{-3} \text{ d}^{-1}$. These values are comparable to previous estimates that range from 0 to 14.7 and 21 to 174 (Monteleone and Duguay, 1988) and 10 to 79 $\text{eggs m}^{-3} \text{ d}^{-1}$ (Purcell, 1994). The percent clearance ranged from less than 1% to over 300% h^{-1} during periods of low and high ctenophore abundance, respectively (Table 1-3). Predation rates on eggs were highest at Dutch and Fox Island stations where *M. leidy* reached the highest densities while prey densities were low. On June 4, Greenwich Bay was the station where the most fish eggs were found in ctenophore guts. Thus, individual feeding rates on eggs

were highest in Greenwich Bay, even though fish egg densities were higher at other stations. The stations were divided into upper-bay and lower-bay based on results of a Tukey all-pairwise comparison test of % clearance rates. Accordingly, Warren River, Greenwich Bay, and Prudence Island were placed into the upper-bay category and were characterized by % clearance rates between 0.5-13.4% h⁻¹. Dutch Island and Fox Island were grouped in the lower-bay and had % clearance rates of 70.1-330.7% h⁻¹. Predation on fish eggs was not detected in samples taken after June 26. Variability in the estimates of predator abundance was examined by calculating the coefficient of variation for replicate tows and these values ranged from 0-84% with a mean of 28% (Appendix D).

Temperature and Salinity

The year 2002 was unusually warm and had the second highest mean annual water temperature (12.5°C) since 1956 (Hawk 1998) (Fig. 1-7). The seasonal temperature pattern in Narragansett Bay is characterized by a spring increase, a peak in early fall, and an autumnal decline (Fig. 1-8).

The temperature during the sampling period, May-August 2002, ranged from 13-25°C at all stations and *M. leidy* was present across the entire temperature range. Salinity ranged from 25.4-31.3 psu among stations, with lower salinities recorded at the

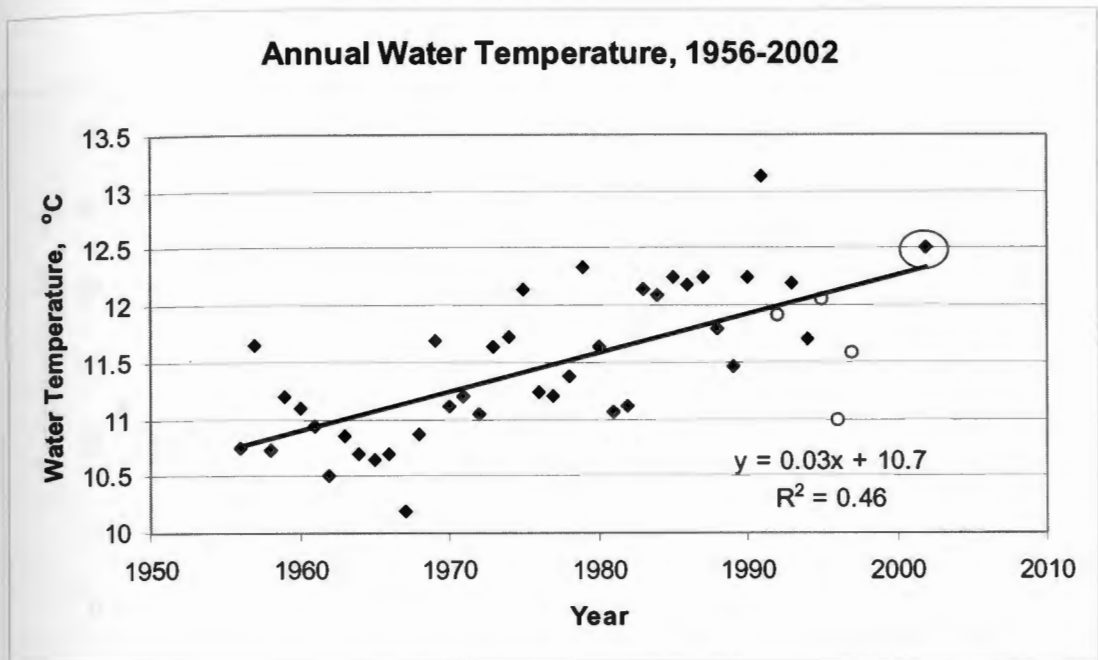


Figure 1-7. Mean annual, near surface, water temperature at Newport, RI, in the lower East passage (1955-94) calculated from monthly means of hourly readings from the National Oceanic and Atmospheric Administration (NOAA) station #8452660 (closed diamonds) and at Fox Island in the middle of the West Passage measured once each week (1992, 1995-98) (open circles) (Hawk 1998) and 2002. The measurements for 2002 are surface samples collected using a Yellow Springs Instruments 600XLM multi-parameter water quality monitor at Fox Island (D. Gifford, unpublished). The annual mean for 2002 is circled on the graph.

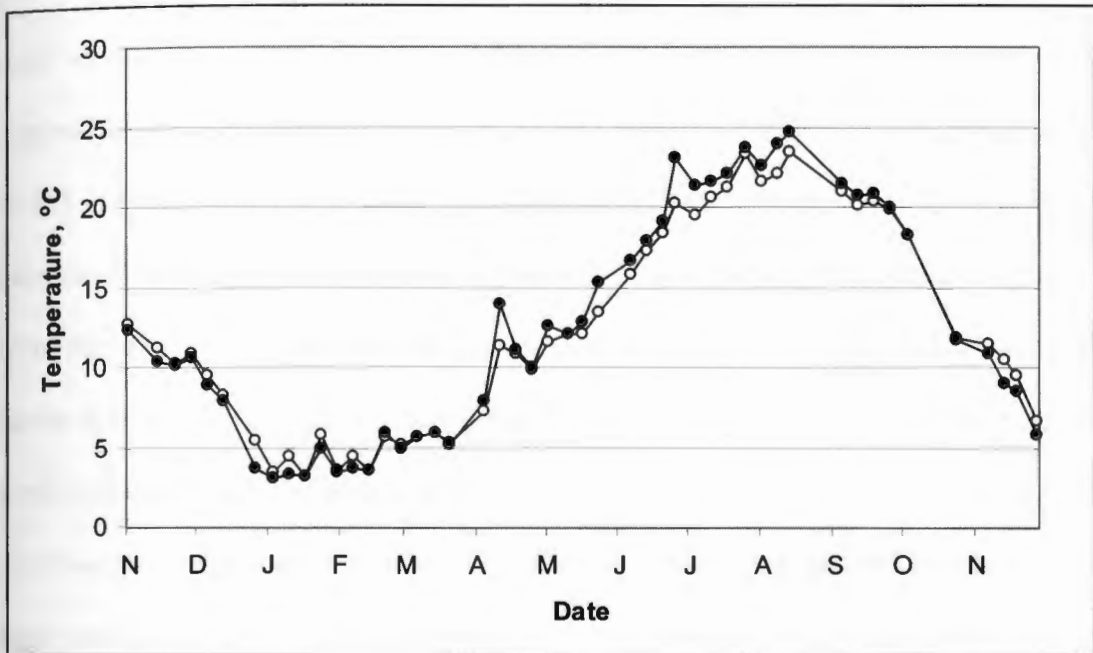


Figure 1-8. Annual near surface water temperature for 2001-2002 at Dutch Island and Fox Island stations. Measurements were taken weekly using a Yellow Springs Instruments 600XLM multi-parameter water quality monitor. Open circles represent Dutch Island and closed circles are Fox Island. Labels for the months (i.e. "N" for November) start at the beginning of the month. Data courtesy of D. Gifford, unpublished.

Warren River station and in the West Passage at Fox Island. The highest salinity, 31.3 psu, occurred at Dutch Island on July 1, 2002. Ctenophores were found throughout the entire salinity range.

DISCUSSION

Predation on the early life history stages of marine fish is potentially the single most important source of mortality. A likely result of predation is the regulation of fish egg and larvae abundances, which may, in turn, affect recruitment (Bailey and Houde, 1989). To affect fish recruitment, ctenophore predation must remove a significant number of fish eggs, which prevents maturation into larvae and the escape of ctenophore predation. *M. leidy* has been shown to prey successfully on fish eggs and larvae in both laboratory and field studies. In the field, timing of fish spawning and explosive ctenophore population growth dictate the extent to which *M. leidy* can decrease the ichthyoplankton in Narragansett Bay. If most of the fish spawn and the eggs mature into larvae before ctenophores become abundant, then the fish are not subjected to intense predation because of their timing relative to the ctenophore abundance. Therefore, perhaps the most important factor to consider when examining predation of fish eggs and larvae by ctenophores is the degree of spatial-temporal overlap of predator and prey (Frank and Leggett 1982).

The degree of temporal overlap was considered by examining the predator-prey abundance patterns that show that the peak of *M. leidy* occurred at the end of the period of highest fish egg density. In other words, ctenophore abundance was relatively low during the period of the greatest decrease of fish eggs at each station. Although, gut content analyses revealed that *M. leidy* consumed fish eggs at all stations, eggs were

only present in 6.9% of the ctenophore guts examined. This data supports the conclusion that *M. leidyi* preys upon fish eggs. However, the low percentage of ctenophores that ingested fish eggs combined with the lack of temporal overlap between predator and prey means that *M. leidyi* did not substantially diminish fish eggs at the stations sampled. Other fish egg predators such as fish and crustacean larvae, fish egg maturation, and flushing from the bay might explain the decline observed in the bay during early-mid June.

Another important result of the gut content analyses was that very small *M. leidyi* (0.5 cm) can consume fish eggs, but do so very infrequently. The former differs from the findings of a previous laboratory study that stated “larval tentaculate ctenophores (<0.9 cm) did not consume bay anchovy eggs” (Monteleone and Duguay, 1988). Ctenophores larger than 4 cm had higher feeding rates, particularly in the first two weeks of June, but all sizes did sometimes consume fish eggs contrary to the findings of previous studies (Appendix C). Specifically, gut content data from the present study show that 2 ctenophores < 1 cm consumed a fish egg. The mean size of *M. leidyi* that ingested an egg was 5.2 cm. Of the 1,031 ctenophores examined for gut contents, 36% were <1 cm total length, so there was not an equal representation of smaller ctenophores.

Gut content data also suggest that the decline in fish larvae does not appear to be due to ctenophore predation. Only one fish larva was found out of 1,031 ctenophore guts examined. The lack of predation on fish larvae agrees with findings of Purcell et al (1994) as they failed to find any fish larvae in the gut contents of *M. leidyi* (n=75) in Chesapeake Bay. Plausible explanations for this include: rapid digestion times of *M.*

leidyi for fish larvae found in this study 0.4 ± 0.05 hrs. (24°C), low *in situ* densities of fish larvae also observed in the present study ($<35 \text{ } 100\text{m}^{-3}$), and/or low swimming speeds of the ctenophores which may have resulted in fewer encounters with fish larvae (Cowan and Houde 1992). Also, if the escape response of a fish larva can be assumed to approximate that of an adult *Acartia tonsa*, then the larva may be strong enough to escape an initial contact with the ctenophore (Costello et al. 1999). Given the numerous factors that may prevent researchers from finding larvae in field-collected ctenophores, it seems that alternate approaches warrant consideration. I propose that a laboratory experiment to compare *M. leidyi*'s ability to capture fish larvae with its capture of other prey types (e.g. copepods) would be useful in addressing this issue.

In recent literature, the application of immunological techniques has been suggested as a method with which to identify highly-digested fish larvae in ctenophore guts (Purcell 1985). A preliminary assessment of the Ouchterlony Immunoassay technique was conducted in conjunction with the present study ($n=50$) and it was unable to detect fish eggs or larvae in ctenophores that had ingested each prey type (Feller et al. 1979). This was likely due to extreme dilution caused by the high water content of *M. leidyi* (96%) (Kremer 1975). Therefore, this approach does not appear to be sufficient to further our understanding of *M. leidyi* predation on ichthyoplankton.

Ctenophore predation was quantitatively estimated by calculating individual ingestion rates using the ingestion model, $I = G/D$. I calculated a range of ingestion rates from 0.04 to 0.6 eggs h^{-1} . Based on the small degree of temporal overlap of *M. leidyi* and fish eggs, I conclude that results obtained using the ingestion model should

not be extrapolated over a 24-hour period as the steady state feeding assumption is most certainly violated in this case.

I also calculated individual clearance rates and percent clearance rates, which were highly variable. This is because they respond to changes in both predator and prey densities. For example, the range of individual clearance rates for *M. leidyi* >1cm total length was 10.6-578.1 liters d⁻¹ g wet weight⁻¹. A laboratory study by Kremer (1975) examined *M. leidyi* clearance rates on copepods and reported a range of 0.61-2.03 liters g wet weight⁻¹ for ctenophores larger than 8g wet weight. Individual clearance rates from this study differ greatly from those Kremer observed and this can likely be attributed to the patchiness of fish eggs in Narragansett Bay. At Dutch Island and Fox Island, the % clearance rates ranged from 70-330.7% of the eggs cleared h⁻¹, whereas values in the upper-bay were 0.5-13.3% of the eggs cleared h⁻¹. A recent study in Narragansett Bay estimated percent clearance of *M. leidyi* on fish eggs between 4.6-62.5% h⁻¹ (Sullivan unpublished). The peak abundance of ctenophores in the study by Sullivan et al (2001) was 350 m⁻³. In the present study, *M. leidyi* obtained a maximum abundance of 846 m⁻³ at Fox Island, which is 2.5 times higher than the peak abundance recorded in Sullivan's survey. Tow-derived estimates of predator abundance were characterized by small amount of variability (Appendix D), which is incorporated into the % clearance estimates. As such, the extremely high % clearance values in the lower-bay are attributed to very high densities of predators and relatively low densities of prey. Abundance data from the lower bay stations show that the period when fish eggs are abundant does not coincide with the period of peak ctenophore abundance (Figure 1-4). As a result, my predation estimates seem too high to be reasonable in

Narragansett Bay given the small amount of temporal overlap between predator and prey.

Furthermore, the percent of ctenophores with fish eggs present in their guts was greater in the upper bay despite higher % clearance rates from lower bay stations (Table 1-3). The discrepancy between observed ctenophore ingestion and the predation impact estimated by the ingestion model using the predator and prey densities is evidence that the latter is not appropriate in this type of application. As a result, a mechanistic numerical model of *M. leidyi* biomass was developed as an alternate approach for examining ctenophore predation on ichthyoplankton in the bay (manuscript #2).

Numerous factors determine the extent to which *M. leidyi* can impact ichthyoplankton stocks in coastal ecosystems. Some factors that were not addressed in the present study include diel periodicity in ichthyoplankton as Govoni and Olney (1991) observed peak densities of fish eggs in the Chesapeake Bay from dusk to dawn and vulnerability of fish larvae to predation (Paradis et al. 1996). So, these estimates may be conservative or underestimates of both fish egg density and ingestion by ctenophores. Also, an on-going study in Narragansett Bay is addressing diel differences in *M. leidyi* predation. The findings of this study may provide important information concerning *M. leidyi* predation on ichthyoplankton. It is likely that interannual variation of predation is considerable.

This study has shown that *M. leidyi* is a predator of fish eggs in Narragansett Bay, but did not considerably reduce their standing stocks during this year. *M. leidyi* predation on fish larvae is rare.

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CHAPTER 2 : A Carbon Budget Model of the Seasonal Biomass of the ctenophore *Mnemiopsis leidyi*

INTRODUCTION

At the outset of marine ecosystem modeling, Riley (1946) described “two opposite approaches” used to test hypotheses in the field of oceanography. The first method was “descriptive” and relied on measurements analyzed with statistics, while the other was an assumption-based, synthetic approach that sought the “mathematical derivation of relationships” (Riley 1946). In manuscript 1, I used a traditional descriptive approach to examine the possible predatory impact of the secondary consumer, *Mnemiopsis leidyi*, on ichthyoplankton by calculating their ingestion and % clearance rates based on gut content analyses coupled with laboratory-determined digestion times and predator and prey densities. The conclusion was that *M. leidyi* is a predator of fish eggs in Narragansett Bay, but does not considerably reduce their standing stocks and that predation on fish larvae is rare.

The present study is representative of the alternative approach, whereby a carbon budget model was developed to examine the amount of prey carbon necessary to support the observed changes in ctenophore biomass in Narragansett Bay. The model output is a first order approximation of the extent to which *M. leidyi*'s metabolic demands can be met by invoking individual and then collective prey categories. The goal is to determine if ichthyoplankton play an important role in supporting the observed biomass. Few, if any, studies have attempted to compare these two methods and their results, which is key to determining how well the observed phenomena are understood.

Recently, it has been suggested that climatic warming is increasing water temperatures in Narragansett Bay and that this allows *M. leidyi* to experience explosive population growth during the spawning season of local fish species (Sullivan et al 2001). This suggests that *M. leidyi* may have a better opportunity to reduce ichthyoplankton stocks in the bay if there is sufficient spatial-temporal overlap between predator and prey and *M. leidyi* eat a significant number of fish eggs. In other words, the carbon in fish eggs and larvae may be contributing to the rapid population increase of *M. leidyi* in June.

One condition that allows ctenophores to increase their populations rapidly is suitable food (in terms of quantity and quality). Understanding the nutritional value of the prey present in the environment and how efficiently the predator uses the procured nutrients can give researchers insight into the causes of massive population growth events.

Carbon comprises 1.7% of the ctenophore's dry weight. This is equivalent to 4% of the organism's wet weight, which is a large amount given the high water content of the ctenophore (Kremer 1975). Based on the body composition of the organisms, carbon is the most important constituent and plays a key role in overall protein metabolism, the major energy source for ctenophores (Kremer 1975). Therefore, a carbon budget model can provide important information about the increase in ctenophore biomass observed in the summer in Narragansett Bay.

Numerical models of gelatinous zooplankton have been developed for a variety of estuarine systems (i.e. the Black Sea, the Chesapeake Bay, and Narragansett Bay) to examine population dynamics and the factors that control seasonality of the organisms.

For example, a population model of the carnivorous ctenophore, *M. leidyi* in Narragansett Bay showed that food availability was the main factor controlling the predator's abundance rather than predation, as had been previously suggested (Kremer 1975). Also, the model indicated that predation brought about the decrease of the biomass of ctenophores in the fall, but it did not limit the maximum seasonal abundance.

Over the last decade the Black Sea ecosystem received a great deal of attention from biologists as the invasive ctenophore, *M. leidyi*, reportedly destroyed stocks of commercially important species such as anchovy and the Mediterranean horse mackerel (Mutlu 1994; Shiganova 2001). More recently, models of the Black Sea ecosystem suggest that gelatinous zooplankton may play a much smaller role in the documented fish stock decline than previously reported and that over-fishing may have led to the fisheries crash (Gucu 2002). In this case modeling was used to successfully address tropho-dynamics within a complex ecosystem

METHODS

Field Sampling

Narragansett Bay is a temperate, relatively well-mixed estuary on the northeast coast of the United States (Hicks, 1959). The lower region of the bay is divided into two passages, East and West, by Prudence and Conanicut Islands. Ctenophores, ichthyoplankton, and mesozooplankton were sampled at Dutch Island and Fox Island during May-August 2002. The stations were sampled weekly throughout the entire sampling season. Sampling stations were positioned where fish eggs and larvae were

most abundant during a 2001 ichthyoplankton survey in the bay (MacPhee, pers. comm.).

Carbon Budget Model of M. leidy Population Biomass

A dynamic numerical model was developed to simulate the seasonal biomass of *M. leidy* in Narragansett Bay (Figure 2-1) and I compared the model results with those of a previous study, which suggest that fish eggs are a small component of the ctenophore's diet and fish larvae are rarely consumed (manuscript 1). Field-generated model inputs include: temperature and biomass data for the following forced compartments: *M. leidy*, mesozooplankton (*Acartia sp.* was used as a proxy for this category), fish eggs, and fish larvae. Microzooplankton biomass was based on abundance data from the literature (Verity 1984). Carbon composition of the mesozooplankton and microzooplankton was estimated using values obtained from the literature (Durbin et al. 1992; Verity 1984) while values for fish eggs and larvae were calculated based on the size of the prey item and the assumption that 50% of the dry weight is carbon (Kremer and Nixon 1978).

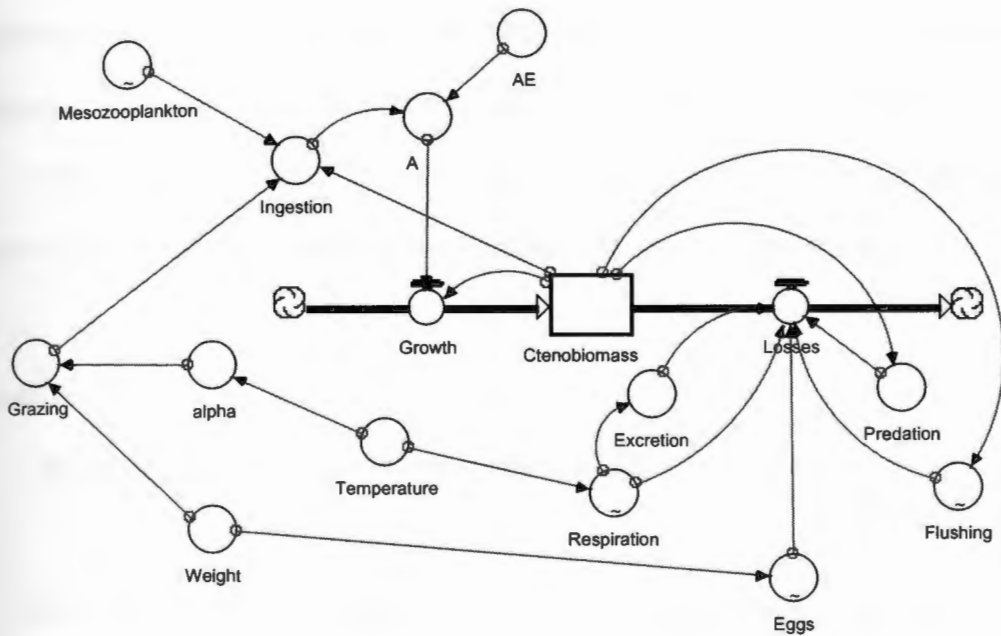


Figure 2-1. A schematic representation of the ctenophore biomass model for Narragansett Bay. This version of the model includes mesozooplankton as the only prey compartment. A time step (dt) of one day was used for all runs of the model.

As a large amount of data was available from the 2002 Narragansett Bay *M. leidy* survey, data and equations in the literature, and the author's experiments, many components of the model were forced seasonally rather than simulated (Table 2-1).

Only seasonal biomass of the *M. leidy* population was computed mechanistically using the software package Stella®, Version 6. The in situ amount of ctenophore carbon at Dutch and Fox Island was examined using both the mean size of ctenophore present and the size frequency data of the population (Figure 2-2).

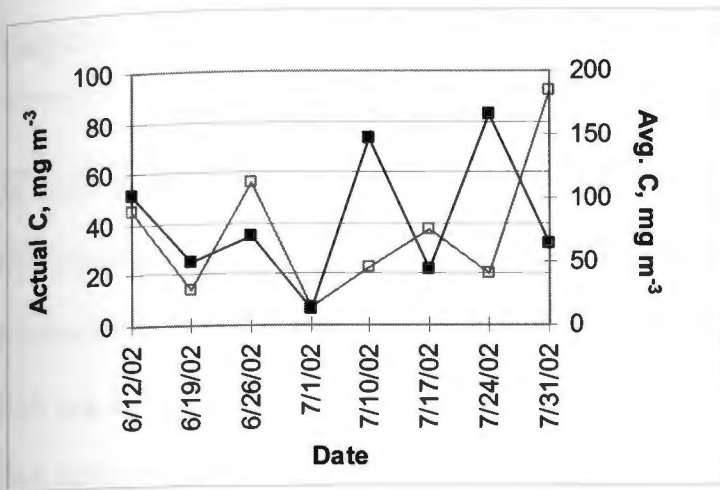
Biomass was simulated at Dutch and Fox Island, because the time series were extensive at these stations and mesozooplankton data were also available.

Growth Terms

Ingestion rates were calculated according to the following equation:

$$I (\text{mg C m}^{-3} \text{ d}^{-1}) = (\text{prey biomass}) * (1 - \exp(-\text{Grazing} * M. leidy \text{ biomass} * dt)) \quad (1)$$

A.



B.

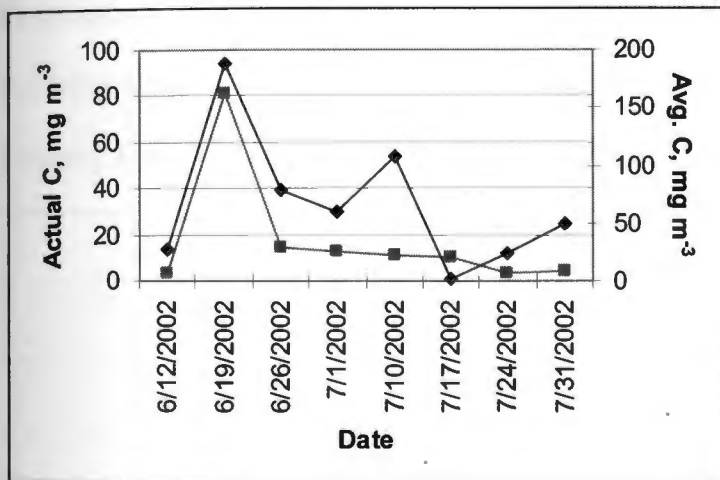


Figure 2-2. *M. leidyi* carbon derived from size frequency of the in situ ctenophore population versus *M. leidyi* carbon based on mean ctenophore size for A. Fox Island and B. Dutch Island. Open squares represent actual carbon from size frequency and closed squares are based on mean ctenophore size.

Table 2-1. Sources of data used in the carbon-based model of ctenophore ingestion.

Data	Source
<i>M. leidy</i> density	B. Sullivan, unpublished (2002)
Mesozooplankton density	B. Sullivan, unpublished (2002)
Microzooplankton density	P. Verity (1984)
Fish egg density	Author's data (2002)
Fish larvae density	Author's data (2002)
Temperature	D. Gifford, unpublished (2002)
Respiration and excretion	P. Kremer (1975)
Predation Rate	C. Oviatt and P. Kremer (1977)
Flushing Rate	J. Kremer and S.W. Nixon (1978)

where prey biomass is equal to one or more of the following prey types:

mesozooplankton, microzooplankton, fish eggs, and fish larvae (mg C m^{-3}). An assimilation efficiency (AE) of 75% was input into the model and is based on findings for the congener of *M. leidyi*, *M. mccradyi* (Kremer 1975). In the schematic diagram of the model, $A = \text{Ingestion} * \text{AE}$ and $\text{growth} = A * \text{Ctenobiomass}$. Ctenophore grazing (G) was computed as in Kremer (1975):

$$G = (a * M. leidyi \text{ weight}^{-0.5}) \quad (2)$$

Kremer's formulation is based on prey removal experiments conducted in 20-25 liter tanks over forty-eight hours. Kremer's feeding rate model is used despite the results of a study by Monteleone and Duguay (1988), which show that small containers (<50 l) significantly reduce ctenophore feeding behavior. The container size used in Kremer's study ranged from 20-40 liters and was deemed sufficient given that studies in which larger containers are used may encounter problems with patchiness of prey during the experiments.

Alpha (a) in equation 2 is represented by the following exponential equation:

$$a = a_0 e^{KT} \quad (3)$$

where $a_0 = 0.04 \text{ L/mg day}$ $K = 0.05 \text{ C}^{-1}$ are constants based on Kremer's calculations (1975) and T is temperature in °C. The temperature equation used in the model was formulated based on surface sample measurements for 2002 collected using a Yellow Springs Instruments 600XLM multi-parameter water quality monitor at Dutch Island

and Fox Island (D. Gifford, unpublished, Figure 1-7, manuscript 1). The observed temperature pattern during the sampling period can be described with the equation:

$$\text{Temp } (^{\circ}\text{C}) = 13.5 - 10 * \cos [2\pi (\text{day} - 50) / 365] \quad (3)$$

where 13.5°C is the mean and the amplitude is 10°C.

As a first order approximation, an assumed organism size of 5 grams wet weight was input into the model. This weight represents a mid-range value as determined in Kremer's (1975) *M. leidy* population model.

Loss Terms

The loss terms in the model are predation by butterfish, flushing from the bay, respiration and excretion, and egg production. A constant loss due to predation by the butterfish, *Peprilus triacanthus*, of 10% of the ctenophore biomass per day was used in the initial runs of the model (Oviatt and Kremer 1977). A range of 20-40% was determined appropriate for the amount of hydrodynamic exchange between the lower West Passage of Narragansett Bay and Rhode Island Sound in a model developed by Kremer and Nixon (1978). As such, a flushing rate of 20% of the ctenophore biomass per day was used in the initial model simulation. Respiration was determined to be a function of temperature only and was input into the model according to Kremer (1975): $R = 4.4 \exp^{0.15T}$, where R is weight-specific respiration and T is temperature in degrees Celsius. Excretion was calculated as in Kremer (1975), $\text{Exc} = 0.67 * R$, where R = respiration. The equation input into the model for loss due to egg production is based

on Kremer's formulation (1975) and is as follows: $E = 0.01 \exp^{0.115W}$, where E is the fraction of unmetabolized assimilation put into reproduction and W is the organisms wet weight in grams.

Sensitivity Analysis

The model's sensitivity to variations in various parameters was examined. *M. leidy* weight was varied to determine how important the value was in the model runs. In the sensitivity analyses, a logical array of values was tested based on approximate ranges of each from Narragansett Bay. For example, ctenophore weights of 1 and 10 grams wet weight were tested and temperature values of 11.5, 15.5, and 20.5 °C. Other parameters were tested with a sensitivity analysis similar to that of Kremer and Nixon (1978) where the model was run with ½ and 2 times the initial values from the standard run.

RESULTS

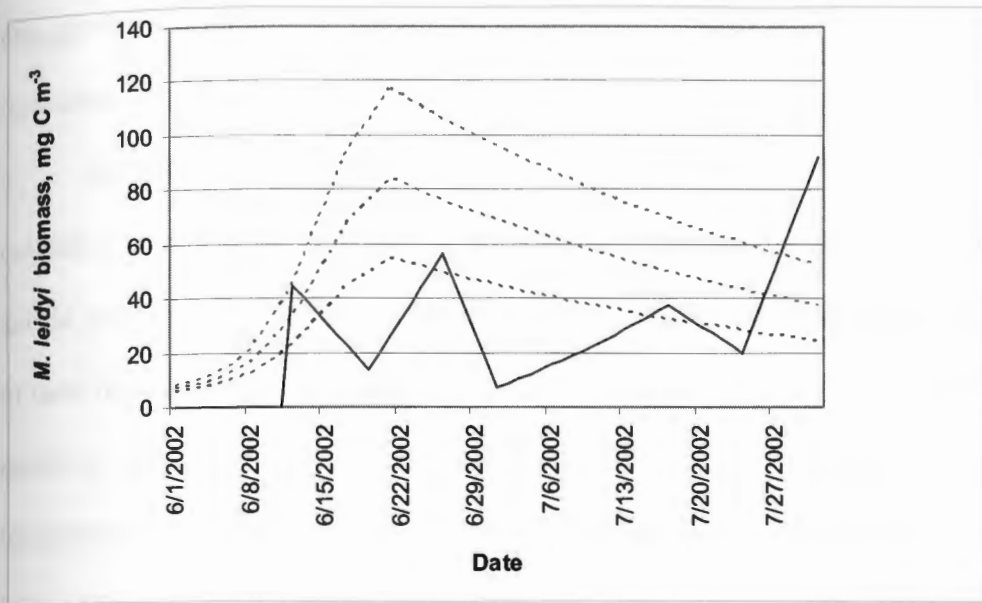
Simulations for Dutch Island were initiated on June 1 with an initial *M. leidy* biomass of 25 mg C m⁻³ whereas for Fox Island, the initial biomass was 7 mg C m⁻³. These initial model biomass values were based on a range of field biomasses observed from June to July. The field biomass of *M. leidy* at Fox Island was characterized by oscillatory patterns of peaks and valleys during June and July (Figure 2-3A). At Dutch Island, the pattern was dominated by one, large peak in the beginning of the season (Figure 2-3B). The overall patterns of ctenophore biomass predicted by the model at both stations show little agreement to the field data. The model output at Dutch Island captured the initial peak observed in the field data, but the timing and magnitude of the model output was later than the field data (Figure 2-3B). The magnitude of ctenophore

biomass observed in the field fell below the range of values predicted by the model (Figure 2-3). The results at both stations are based on simulated ctenophore biomass when only mesozooplankton was forced as a prey source.



Figure 2-3
Comparison of observed and simulated biomass. The observed biomass (open circles) is consistently lower than the simulated biomass (open squares) across the entire period shown. The simulation is based on mesozooplankton as the only prey source for ctenophores.

A.



B.

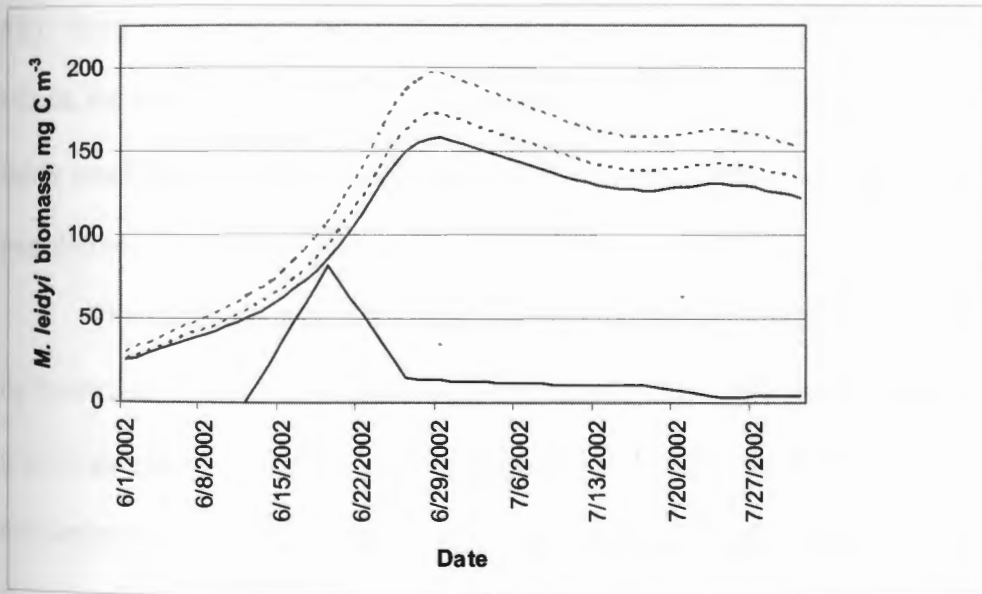


Figure 2-3. Field estimates of *M. leidy* biomass versus modeled *M. leidy* biomass from June-July 2002 at A. Fox Island and B. Dutch Island. The solid line is the field data and the dotted lines represent model outputs. The range covered by the model simulations results from varying the initial ctenophore biomass.

M. leidyi biomass was also simulated when all prey categories were available, but the change was negligible in the beginning of the season and increased throughout the remainder of the season (Figure 2-4).

Sensitivity analyses were run to test the sensitivity of the model to initial conditions and changes in model parameters. In the sensitivity analysis of temperature and *M. leidyi* weight, a logical array of values was tested based on approximate ranges of each from Narragansett Bay. Varying the temperature by ± 2 °C resulted in a relatively small change in the estimated ctenophore biomass. Increasing the temperature from an initial 13.5°C to 20.5°C resulted in a difference of 46.5% at Dutch Island (Table 2-2). It appears that the model is fairly robust to temperature changes within the range that is typical of the summer months in Narragansett Bay (Figure 2-5B). Also, when the weight of *M. leidyi* was decreased to 1 g at Fox Island and Dutch Island, the difference was 28.6% at each station. These results indicate that the model is fairly insensitive to changes in the weight of the ctenophores that make up the population.

The model appears to be very sensitive to mesozooplankton biomass, predation by butterfish, and choice of flushing rate (Figure 2-5A). The mesozooplankton results are not surprising as Kremer (1975) observed that “the exact choice of food concentration proved to be the most critical parameter of all.” This was attributed to forcing the compartment with no daily feedback from predation by the ctenophores to the mesozooplankton biomass (Kremer 1975).

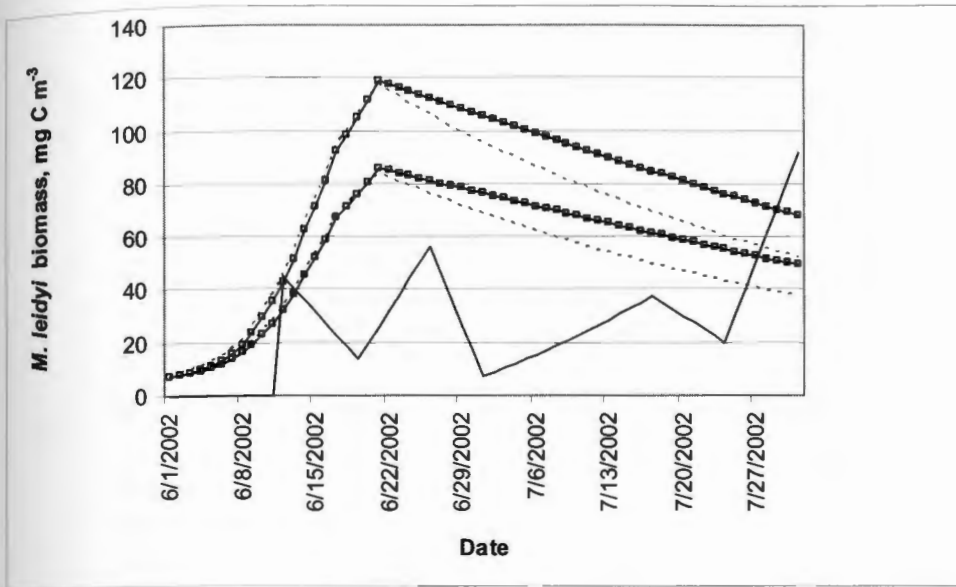
The sensitivity of the model to predation is attributed to the fact that it was formulated as a constant loss per day instead of as a function of predators in the

environment. Butterfish are the only documented predator of *M. leidyi* still present in Narragansett Bay, but it likely that there are other fish that feed on the ctenophores.



Figure 1. A. Abundance of *M. leidyi* in Narragansett Bay, RI, from 1998 to 2002. B. Abundance of *M. leidyi* in Narragansett Bay, RI, from 2003 to 2007.

A.



B.

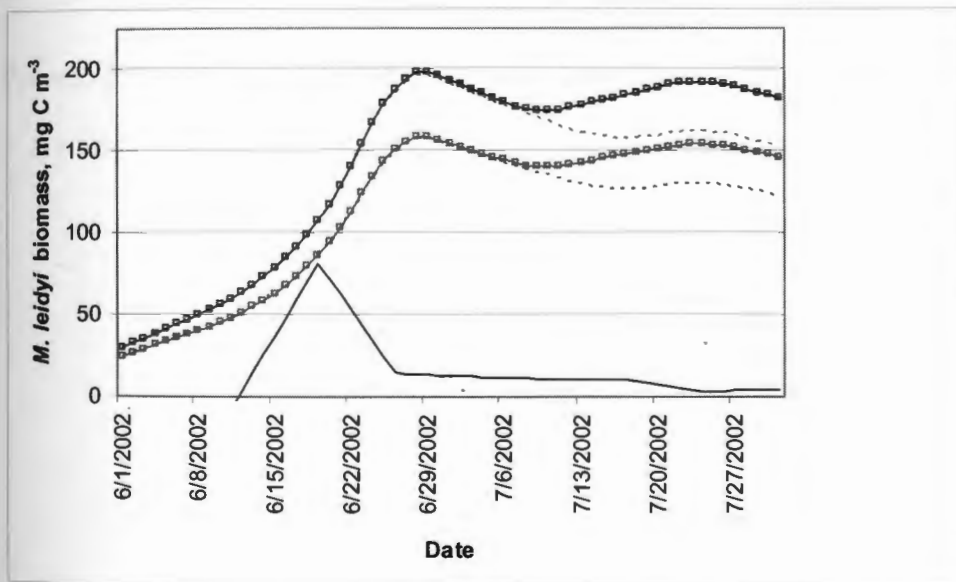


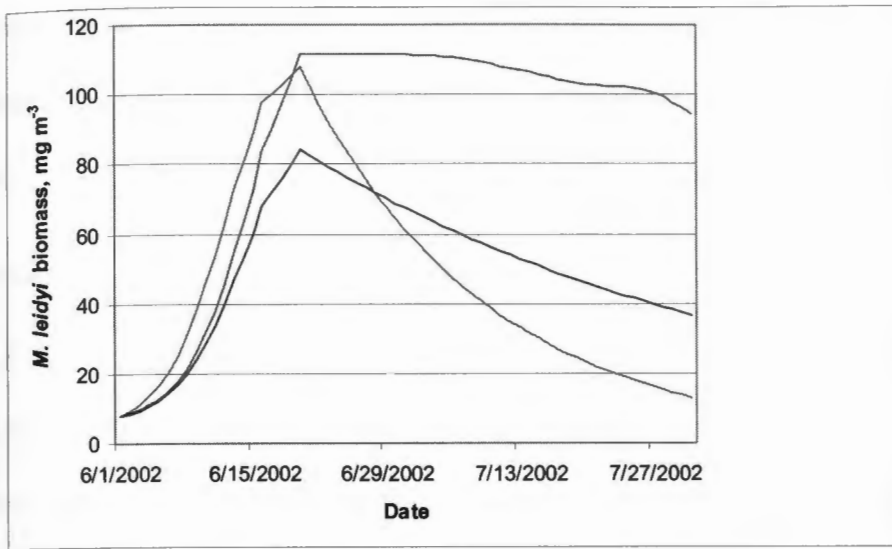
Figure 2-4: A. *M. leidyi* biomass at Fox Island from the field data (solid line) and two runs with mesozooplankton prey (dashed lines) and with all prey categories (squares). B. Ctenophore biomass at Dutch Island from the field data (solid line) and two runs with mesozooplankton prey (dashed lines) and with all prey categories (squares).

Table 2-2: Results of sensitivity analyses for various model parameters are shown with the percent difference (% D) from the initial run of the model. Both Dutch and Fox Island are included in the table.

Model input varied	Scenario	% D, DI	% D, FI
None	Initial		
Temperature	11.5°C	12.6	5.9
Temperature	15.5°C	11.8	4.7
Temperature	20.5°C	46.5	14.9
<i>M. leidy</i> wet weight	10g	33.0	23.4
<i>M. leidy</i> wet weight	1g	28.6	28.6
Mesozooplankton biomass	2X	483.1	128.3
Mesozooplankton biomass	½	69.7	63.9
Predation	15%	42.7	41.1
Predation	5%	22.8	48.0
Flushing	10%	70.2	157.7
Flushing	40%	88.7	69.8

Percent difference was calculated using the following equation: $\% D = \frac{|C_{\text{standard}} - C_{\text{sensitivity}}|}{C_{\text{standard}}} \times 100\%$

A.



B.

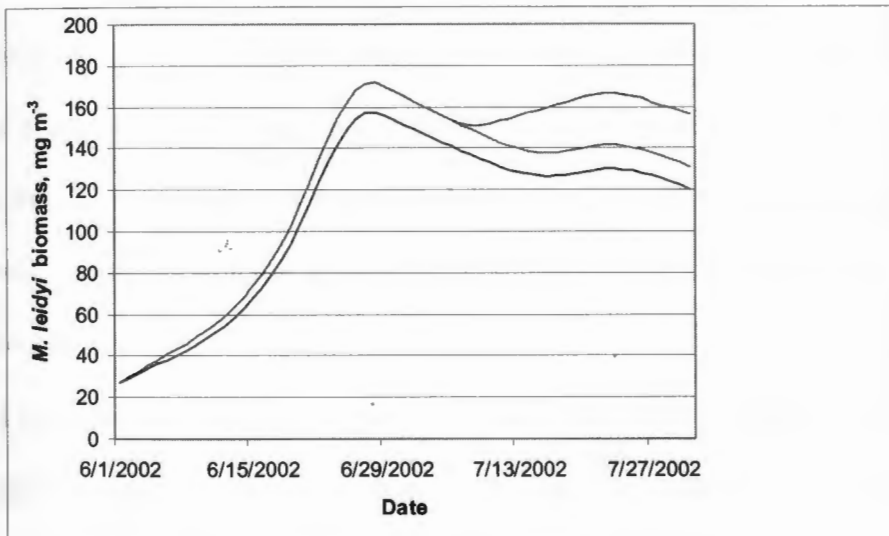


Figure 2-5. A. Sensitivity analyses of mesozooplankton at Fox Island, where the uppermost line is 2X the mesozooplankton, the middle is the standard run, and the lower is $\frac{1}{2}$ the standard run. B. Sensitivity analyses of temperature at Dutch Island, where the upper line is 20.5°C, the middle line is 15.5°C, and the lower line is 13.5°C.

The flushing rate was set at a mid-range value, 20%, which may not be appropriate for the summer months in Narragansett Bay. However, in this case, the mid-range value was deemed sufficient as a first order approximation was the goal of the model.

DISCUSSION

A numerical model of *M. leidy* seasonal biomass was developed and has been applied to two mid-bay stations, Dutch and Fox Island, in Narragansett Bay. In preliminary runs of the model, an average ctenophore biomass was input into the model and the model output agreed with the field data. However, when I compared the average ctenophore biomass with ctenophore biomass based on size frequency of the in situ population, I found that the biomass based on the size frequency data was different from the average (Figure 2-2). As a result, all runs of the model presented herein use the size frequency ctenophore biomass and do not agree well with the field data. Future efforts will focus on re-parameterizing the model to the size frequency based ctenophore biomass.

I also compared the model predictions with field data to examine the extent to which mesozooplankton, fish eggs, fish larvae, and microzooplankton could support the observed ctenophore biomass. Plankton studies show that initiation of the summer increase of *M. leidy* coincides with a rapid decline in the copepod population in Narragansett Bay (Deason and Smayda 1982). Based on these results, the model was run with mesozooplankton as the lone prey source and these runs show that copepods would be an adequate carbon supply for the field biomass estimates in magnitude and the rate of biomass increase. However, the timing of the peak ctenophore biomass was

not as well captured at Fox Island or Dutch Island. The model was re-run at both stations with mesozooplankton, microzooplankton, fish eggs, and fish larvae as carbon sources and the results did not change in the beginning of the season. I conclude that the initiation of rapid ctenophore population growth in the bay is primarily supported by copepods and that fish eggs, fish larvae, and microzooplankton are not an important source of carbon during this time. Later in the season when the copepods are diminished, however, there seems to be an increase in ctenophore biomass due to the addition of these alternate prey sources.

Sensitivity analysis of the model showed that mesozooplankton biomass, predation, and choice of flushing rate had the largest effects on the ctenophore biomass estimates. This indicates the need for more detailed mesozooplankton population information and a better-constrained estimate of predation by accounting for the fluctuation in predator populations.

The ability of *M. leidyi* to exploit its prey environment is crucial to its success in Narragansett Bay. The ctenophore is a generalist and it feeds primarily on the prey type that is most abundant in the water column. During June 2002, mesozooplankton dominated the prey assemblage and therefore, supported the observed increase in ctenophore biomass.

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APPENDICES

APPENDIX A

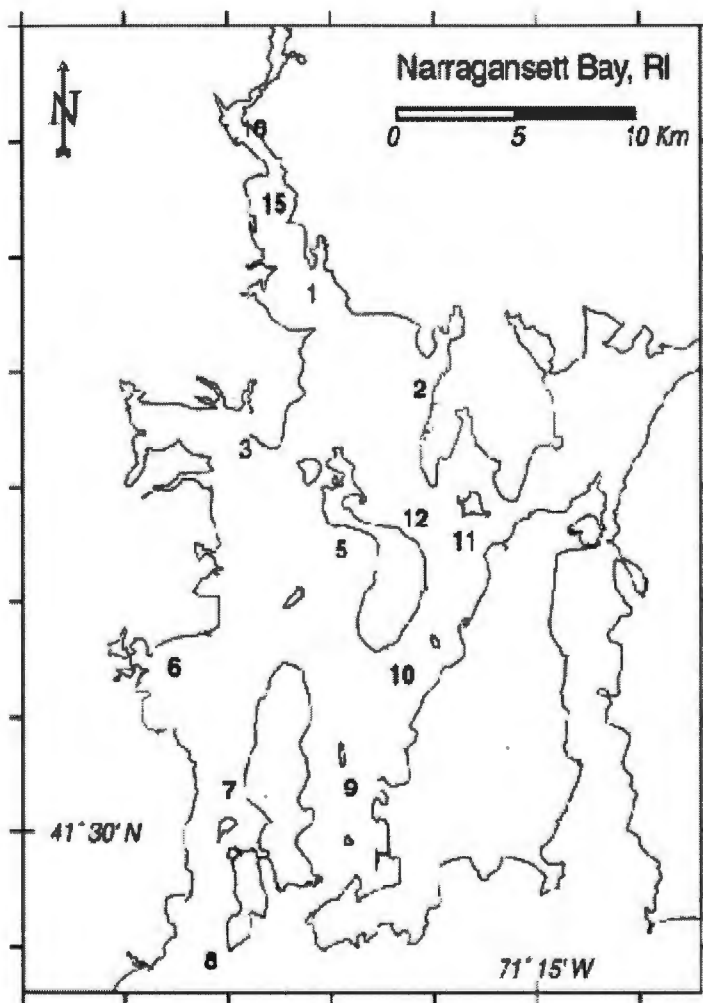
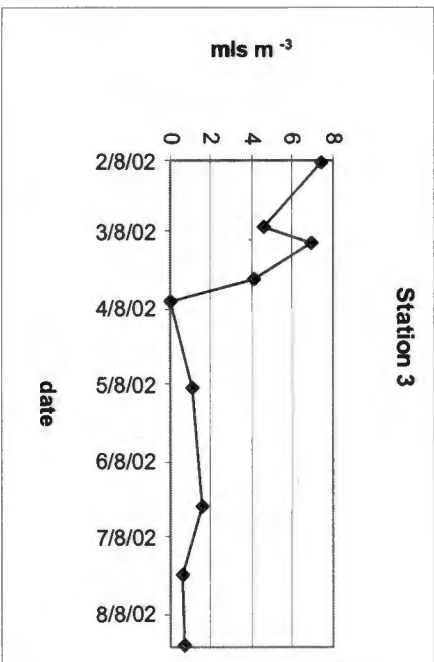
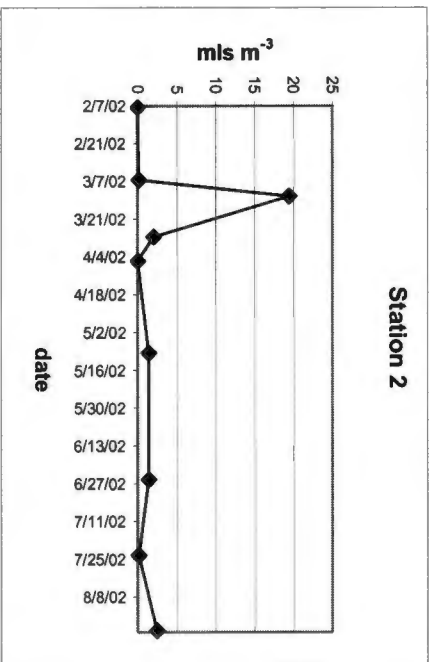
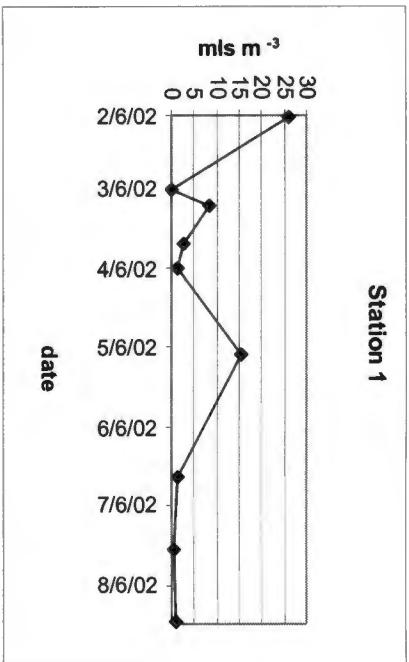
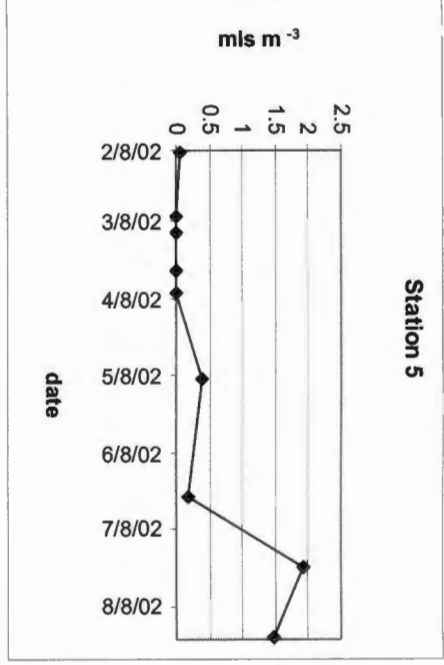
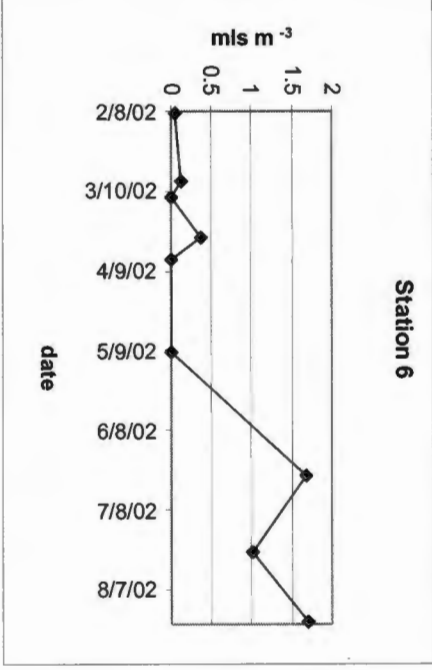
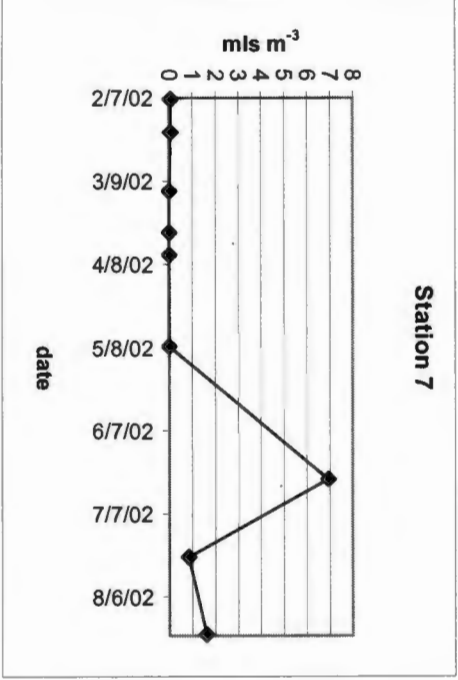
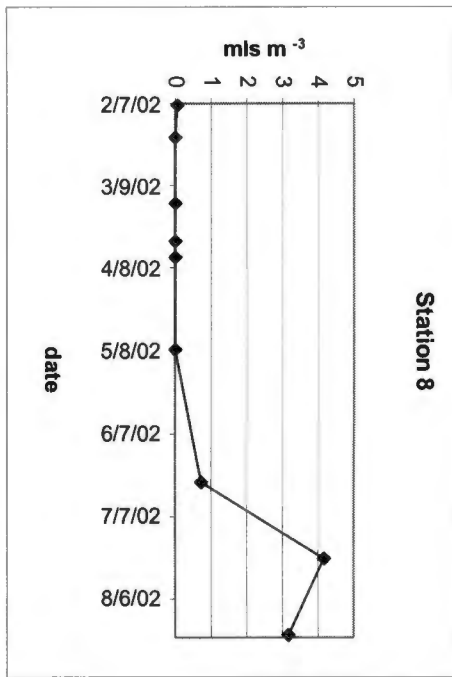
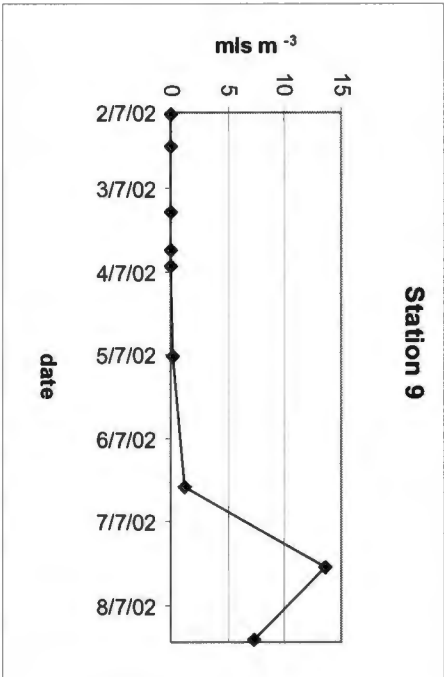
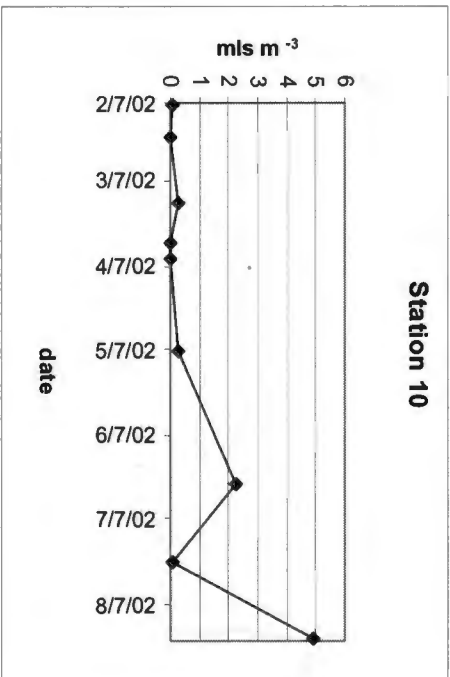
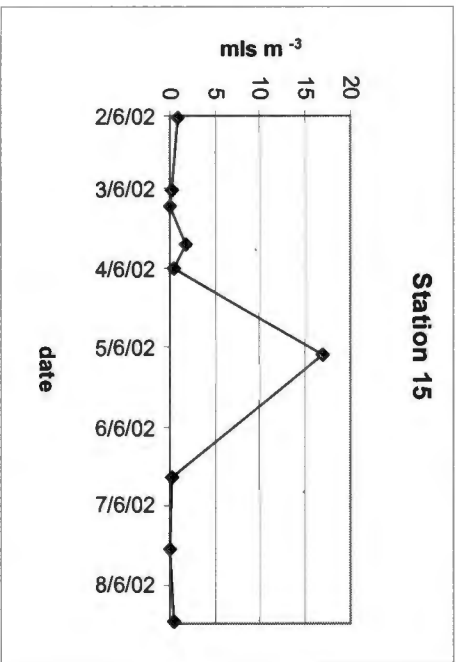
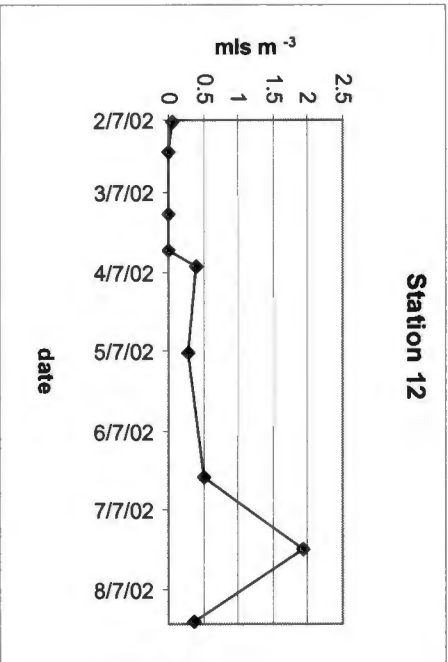
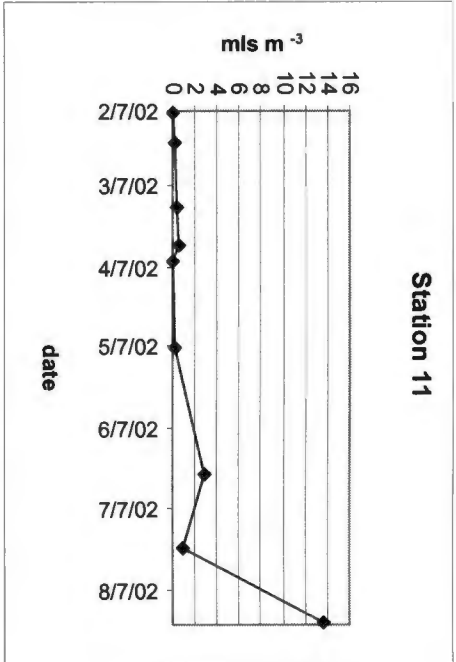


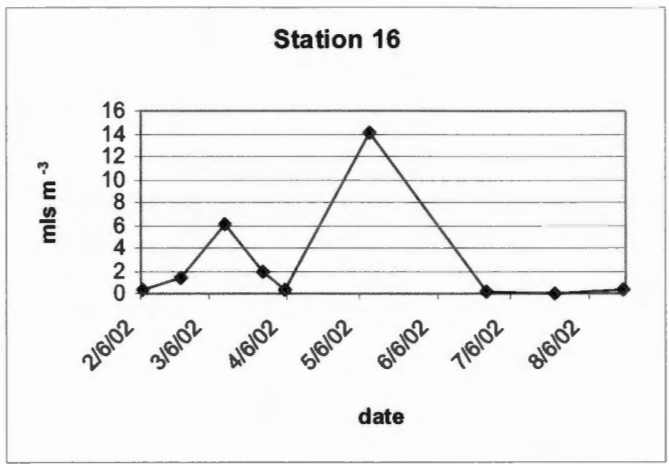
Figure A-1: Stations in Narragansett Bay where *M. leidy* biovolumes were recorded and b. Plots of the corresponding ctenophore data for each station from Klein-MacPhee (2002); where the x-axis is the date and the y-axis is mL of *M. leidy* per m^{-3} .







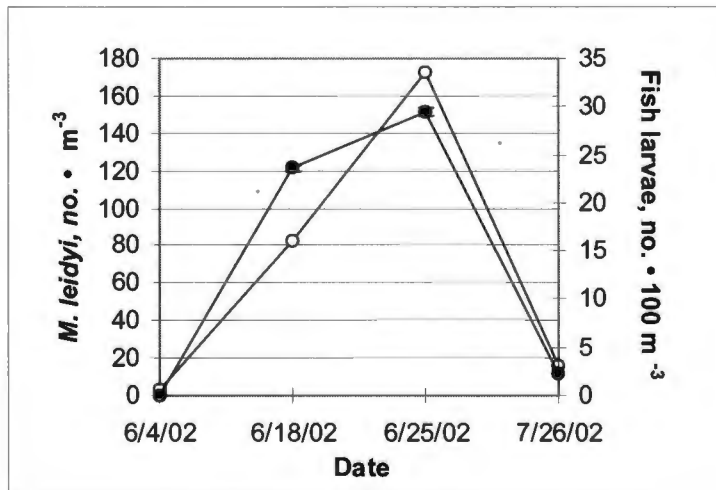
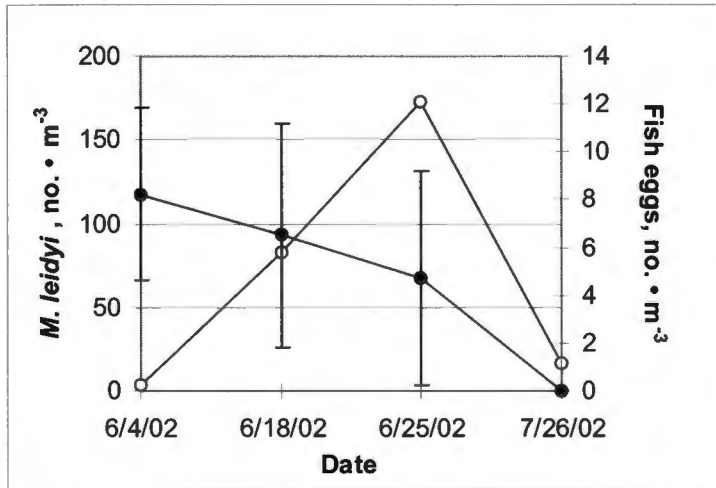




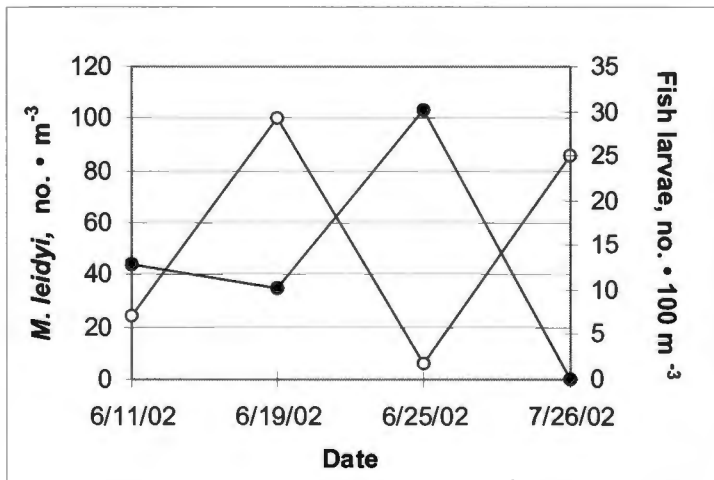
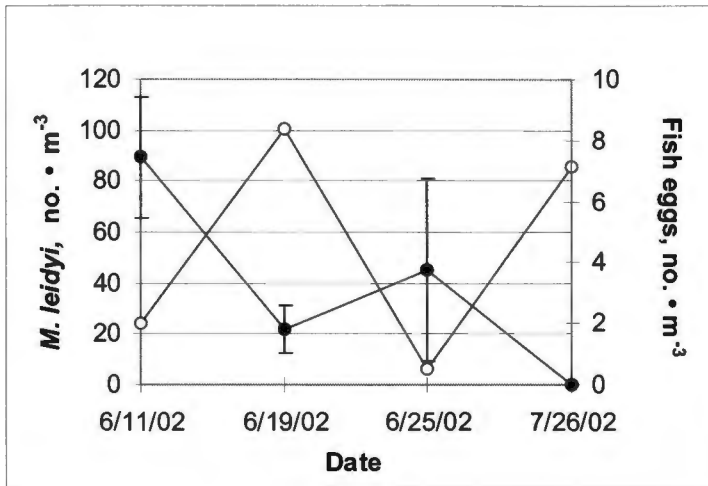
APPENDIX B

A. GRAPHS OF *M. LEIDYI* AND ICHTHYOPLANKTON ABUNDANCE FOR WARREN RIVER, GREENWICH BAY, AND PRUDENCE ISLAND (EAST) STATIONS. B. ICHTHYOPLANKTON COUNTS OF a. FISH EGGS AND b. FISH LARVAE IN ALL TOWS AT ALL STATIONS.

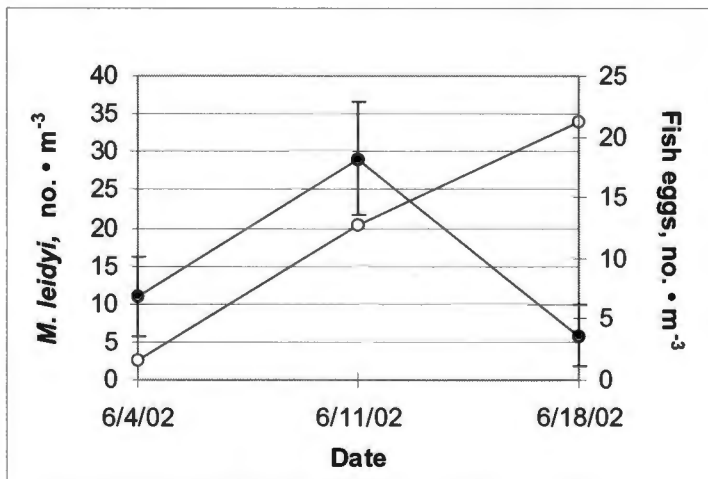
Warren River:

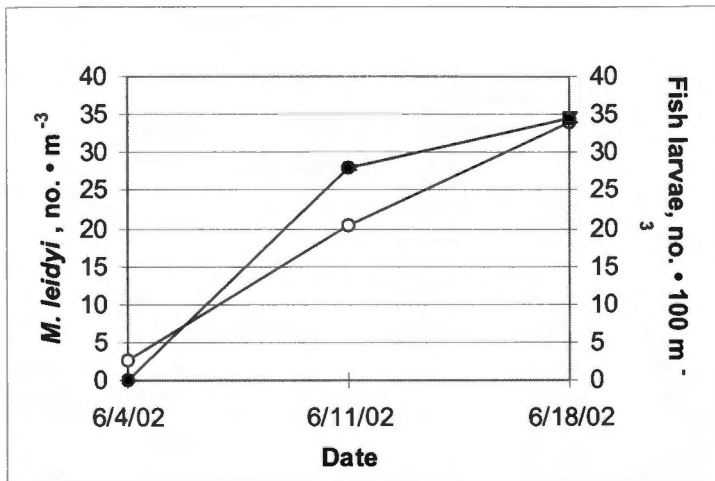


Greenwich Bay:



Prudence Island (East):





B.

a. Fish egg raw data from 20% subsample.

Date	Station	Net Mesh	Replicate #	Volume filtered, m ³	Cunner	Tautog	Butterfish
5/22/02	Dutch Island	133um	1	103.4	370	300	
5/29/02	Dutch Island	133um	1	168.5	480	450	1840
5/29/02	Dutch Island	133um	2	111.6	50	350	1120
6/12/02	Dutch Island	133um	1	104.8	380	155	195
6/12/02	Dutch Island	133um	2	69.7	153.7	58	69.6
6/12/02	Dutch Island	133um	3	76.4	25	4	37
6/19/02	Dutch Island	133um	1	69.9	4	44	4
6/19/02	Dutch Island	133um	2	66.7	20	60	40
6/19/02	Dutch Island	133um	3	72.4	46.2	128.7	23.1
6/26/02	Dutch Island	133um	1	47.2	46	12	6
6/26/02	Dutch Island	133um	2	64.8	37.8	8.4	12.6
6/26/02	Dutch Island	133um	3	98.3	56		24
7/1/02	Dutch Island	133um	1	65.4	150	55	15
7/1/02	Dutch Island	133um	2	40.2	40	12.5	10
7/1/02	Dutch Island	133um	3	61.3	4	92	14
7/10/02	Dutch Island	133um	1	82.9	29.4	12.6	2.1
7/10/02	Dutch Island	133um	2	61.2	13.2	3.3	13.2
7/10/02	Dutch Island	133um	3	65.9	5		1
7/17/02	Dutch Island	133um	1	83.0	9.9		3.3
7/17/02	Dutch Island	133um	2	52.6	17.5	2.5	
7/17/02	Dutch Island	133um	3	53.8	2		1
7/24/02	Dutch Island	133um	1	73.9			
7/24/02	Dutch Island	133um	2	67.7	10	5	
7/24/02	Dutch Island	133um	3	99.7	5		5
7/31/02	Dutch Island	133um	1	91.9	10		
7/31/02	Dutch Island	133um	2	92.6	10		
7/31/02	Dutch Island	133um	3	85.7	5	2	6
8/7/02	Dutch Island	133um	1	76.8			
8/7/02	Dutch Island	133um	2	71.5			
8/7/02	Dutch Island	133um	3	83.3			
8/14/02	Dutch Island	133um	1	45.6	6.6		
8/14/02	Dutch Island	133um	2	70.0		3.3	
8/14/02	Dutch Island	133um	3	59.9	2		
8/19/02	Dutch Island	133um	1	78.6	1.7		
8/19/02	Dutch Island	133um	2	73.4	2	3	
8/19/02	Dutch Island	133um	3	51.1	2		
5/22/02	Fox Island	133um	1	55.9	3	17	5
5/29/02	Fox Island	133um	1	44.3	20	70	50
6/12/02	Fox Island	133um	1	22.9	40	25	75
6/12/02	Fox Island	133um	2	28.8	40	5	35
6/12/02	Fox Island	133um	3	51.7	25	4	37
6/19/02	Fox Island	133um	1	39.5	17.5	27.5	40

6/19/02	Fox Island	133um	2	37.7	30	6	54
6/19/02	Fox Island	133um	3	34.6	6	15	32
6/26/02	Fox Island	133um	1	38.0	16.5	23.1	9.9
6/26/02	Fox Island	133um	2	37.8	33	16.5	9.9
6/26/02	Fox Island	133um	3	35.0	34	5	19
7/1/02	Fox Island	133um	1	57.9	49.5	36.3	33
7/1/02	Fox Island	133um	2	21.0	15	2.5	5
7/1/02	Fox Island	133um	3	23.4	2	10	9
7/10/02	Fox Island	133um	1	35.3	3		1
7/10/02	Fox Island	133um	2	55.5	9	6	
7/10/02	Fox Island	133um	3	32.2	16.5		
7/17/02	Fox Island	133um	1	23.0			
7/17/02	Fox Island	133um	2	28.2			
7/17/02	Fox Island	133um	3	37.4			
7/24/02	Fox Island	133um	1	75.3			
7/24/02	Fox Island	133um	2	60.6			
7/24/02	Fox Island	133um	3	67.5			
7/31/02	Fox Island	133um	1	80.4			
7/31/02	Fox Island	133um	2	42.4			
7/31/02	Fox Island	133um	3	93.1	3	1	1
8/7/02	Fox Island	133um	1	52.7			
8/7/02	Fox Island	133um	2	62.3			
8/14/02	Fox Island	133um	1	49.8		2.5	
8/14/02	Fox Island	133um	2	47.8		2.5	
8/14/02	Fox Island	133um	3	46.5	2		
8/19/02	Fox Island	133um	1	56.7			
8/19/02	Fox Island	133um	2	47.2			
8/19/02	Fox Island	133um	3	62.8			
6/4/02	Greenwich Bay	133um	1	6.5	52.8	3.3	72.6
6/4/02	Greenwich Bay	133um	2	5.9	45	15	67.5
6/11/02	Greenwich Bay	133um	1	47.5	35	1	89
6/11/02	Greenwich Bay	133um	2	108.2	194.4	194.4	180
6/11/02	Greenwich Bay	133um	3	58.7	70	85	145
6/19/02	Greenwich Bay	133um	1	63.4	20	20	37.5
6/19/02	Greenwich Bay	133um	2	65.0	20	12.5	65
6/19/02	Greenwich Bay	133um	3	56.3	2	12	10
6/25/02	Greenwich Bay	133um	1	29.8	50	20	
6/25/02	Greenwich Bay	133um	2	13.1	57.5	27.5	5
6/25/02	Greenwich Bay	133um	3	8.9	6		5
7/26/02	Greenwich	133um	1	57.8			

	Bay						
7/26/02	Greenwich Bay	133um	2	66.4	5		
6/4/02	Prudence East	133um	1	8.8	25	7.5	17.5
6/4/02	Prudence East	133um	2	9.7	59.4	29.7	6.6
6/4/02	Prudence East	133um	3	8.8	9	3	
6/11/02	Prudence East	133um	1	39.0	120	16	438
6/11/02	Prudence East	133um	2	34.8	97.5	71.25	37.5
6/11/02	Prudence East	133um	3	43.1	204.6	178.2	128.7
6/18/02	Prudence East	133um	1	28.3	2	10	7
6/18/02	Prudence East	133um	2	13.8	7.2	10.8	32.4
6/18/02	Prudence East	133um	3	28.9	80	20	45
6/4/02	Warren River	133um	1	7.2	16	34	28
6/4/02	Warren River	133um	2	7.9	75	40	60
6/4/02	Warren River	133um	3	6.8	8	14	4
6/18/02	Warren River	133um	1	53.1	1	69	11
6/18/02	Warren River	133um	2	38.8	105	120	25
6/18/02	Warren River	133um	3	44.1	69.3	354.2	30.8
6/25/02	Warren River	133um	1	50.9	185	155	
6/25/02	Warren River	133um	3	49.9	32	2	38
7/26/02	Warren River	133um	1	109.4			
7/26/02	Warren River	133um	2	79.3			
7/26/02	Warren River	133um	3	90.8			
Date	Station	Net Mesh	Repli-cate #	Volume filtered, m³	Searo bin	Bay Ancho vy	Silverh ake
5/22/02	Dutch Island	133um	1	103.4	110	20	840
5/29/02	Dutch Island	133um	1	168.5	140		
5/29/02	Dutch Island	133um	2	111.6	110		
6/12/02	Dutch Island	133um	1	104.8	75	20	
6/12/02	Dutch Island	133um	2	69.7	31.9	11.6	
6/12/02	Dutch Island	133um	3	76.4	7		
6/19/02	Dutch Island	133um	1	69.9	32		
6/19/02	Dutch Island	133um	2	66.7	50		
6/19/02	Dutch Island	133um	3	72.4	42.9		
6/26/02	Dutch Island	133um	1	47.2	2		
6/26/02	Dutch Island	133um	2	64.8			
6/26/02	Dutch Island	133um	3	98.3	10		
7/1/02	Dutch Island	133um	1	65.4	20		
7/1/02	Dutch Island	133um	2	40.2	10		
7/1/02	Dutch Island	133um	3	61.3	6		
7/10/02	Dutch Island	133um	1	82.9			

7/10/02	Dutch Island	133um	2	61.2			
7/10/02	Dutch Island	133um	3	65.9	3		
7/17/02	Dutch Island	133um	1	83.0	6.6		
7/17/02	Dutch Island	133um	2	52.6	5		
7/17/02	Dutch Island	133um	3	53.8	3		
7/24/02	Dutch Island	133um	1	73.9			
7/24/02	Dutch Island	133um	2	67.7			
7/24/02	Dutch Island	133um	3	99.7	1		
7/31/02	Dutch Island	133um	1	91.9			
7/31/02	Dutch Island	133um	2	92.6			
7/31/02	Dutch Island	133um	3	85.7			
8/7/02	Dutch Island	133um	1	76.8			
8/7/02	Dutch Island	133um	2	71.5			
8/7/02	Dutch Island	133um	3	83.3			
8/14/02	Dutch Island	133um	1	45.6			
8/14/02	Dutch Island	133um	2	70.0			
8/14/02	Dutch Island	133um	3	59.9			
8/19/02	Dutch Island	133um	1	78.6		5.1	
8/19/02	Dutch Island	133um	2	73.4		7	
8/19/02	Dutch Island	133um	3	51.1		1	
5/22/02	Fox Island	133um	1	55.9	13		
5/29/02	Fox Island	133um	1	44.3	60	10	190
6/12/02	Fox Island	133um	1	22.9	10	10	
6/12/02	Fox Island	133um	2	28.8	5		
6/12/02	Fox Island	133um	3	51.7	7		
6/19/02	Fox Island	133um	1	39.5	37.5	2.5	
6/19/02	Fox Island	133um	2	37.7	9		
6/19/02	Fox Island	133um	3	34.6	34		
6/26/02	Fox Island	133um	1	38.0	3.3		
6/26/02	Fox Island	133um	2	37.8	6.6	3.3	
6/26/02	Fox Island	133um	3	35.0	1		
7/1/02	Fox Island	133um	1	57.9	23.1	9.9	
7/1/02	Fox Island	133um	2	21.0	7.5		
7/1/02	Fox Island	133um	3	23.4	5	1	
7/10/02	Fox Island	133um	1	35.3	4		
7/10/02	Fox Island	133um	2	55.5	6		
7/10/02	Fox Island	133um	3	32.2		3.3	
7/17/02	Fox Island	133um	1	23.0			
7/17/02	Fox Island	133um	2	28.2			
7/17/02	Fox Island	133um	3	37.4			
7/24/02	Fox Island	133um	1	75.3			
7/24/02	Fox Island	133um	2	60.6			
7/24/02	Fox Island	133um	3	67.5			
7/31/02	Fox Island	133um	1	80.4			
7/31/02	Fox Island	133um	2	42.4			
7/31/02	Fox Island	133um	3	93.1		1	
8/7/02	Fox Island	133um	1	52.7			
8/7/02	Fox Island	133um	2	62.3			

8/14/02	Fox Island	133um	1	49.8		2.5
8/14/02	Fox Island	133um	2	47.8		2.5
8/14/02	Fox Island	133um	3	46.5		
8/19/02	Fox Island	133um	1	56.7		
8/19/02	Fox Island	133um	2	47.2		
8/19/02	Fox Island	133um	3	62.8		
6/4/02	Greenwich Bay	133um	1	6.5	13.2	3.3
6/4/02	Greenwich Bay	133um	2	5.9	25	2.5
6/11/02	Greenwich Bay	133um	1	47.5	27	
6/11/02	Greenwich Bay	133um	2	108.2	118.8	57.6
6/11/02	Greenwich Bay	133um	3	58.7	55	15
6/19/02	Greenwich Bay	133um	1	63.4	20	
6/19/02	Greenwich Bay	133um	2	65.0	10	5
6/19/02	Greenwich Bay	133um	3	56.3	7	
6/25/02	Greenwich Bay	133um	1	29.8	5	5
6/25/02	Greenwich Bay	133um	2	13.1		2.5
6/25/02	Greenwich Bay	133um	3	8.9	1	
7/26/02	Greenwich Bay	133um	1	57.8		
7/26/02	Greenwich Bay	133um	2	66.4		
6/4/02	Prudence East	133um	1	8.8		
6/4/02	Prudence East	133um	2	9.7	19.8	36.3
6/4/02	Prudence East	133um	3	8.8		
6/11/02	Prudence East	133um	1	39.0	23	
6/11/02	Prudence East	133um	2	34.8	7.5	
6/11/02	Prudence East	133um	3	43.1	3.3	
6/18/02	Prudence East	133um	1	28.3	4	
6/18/02	Prudence East	133um	2	13.8	3.6	
6/18/02	Prudence East	133um	3	28.9	20	
6/4/02	Warren River	133um	1	7.2	14	
6/4/02	Warren River	133um	2	7.9	10	10
6/4/02	Warren River	133um	3	6.8	1	

6/18/02	Warren River	133um		1	53.1		1			
6/18/02	Warren River	133um		2	38.8		20	5		
6/18/02	Warren River	133um		3	44.1		7.7	7.7		
6/25/02	Warren River	133um		1	50.9		20	40		
6/25/02	Warren River	133um		3	49.9		4	1		
7/26/02	Warren River	133um		1	109.4					
7/26/02	Warren River	133um		2	79.3					
7/26/02	Warren River	133um		3	90.8					
Date	Station	Net Mesh	Repl-icate #	Vol. filt., m ³	Sea Trout	4 spot floun-der	Men-hade n	Small mouth flound er	Four beard Rockli ng	
5/22/02	Dutch Island	133um	1	103.4						
5/29/02	Dutch Island	133um	1	168.5						
5/29/02	Dutch Island	133um	2	111.6				10		
6/12/02	Dutch Island	133um	1	104.8						
6/12/02	Dutch Island	133um	2	69.7				2.9		
6/12/02	Dutch Island	133um	3	76.4						
6/19/02	Dutch Island	133um	1	69.9						
6/19/02	Dutch Island	133um	2	66.7						
6/19/02	Dutch Island	133um	3	72.4				3.3		
6/26/02	Dutch Island	133um	1	47.2				2		
6/26/02	Dutch Island	133um	2	64.8				2	1	
6/26/02	Dutch Island	133um	3	98.3				4.2		
7/1/02	Dutch Island	133um	1	65.4				5		
7/1/02	Dutch Island	133um	2	40.2						
7/1/02	Dutch Island	133um	3	61.3						
7/10/02	Dutch Island	133um	1	82.9				8.4		
7/10/02	Dutch Island	133um	2	61.2						
7/10/02	Dutch Island	133um	3	65.9						
7/17/02	Dutch Island	133um	1	83.0						
7/17/02	Dutch Island	133um	2	52.6				5		
7/17/02	Dutch Island	133um	3	53.8						
7/24/02	Dutch Island	133um	1	73.9				10		
7/24/02	Dutch Island	133um	2	67.7						
7/24/02	Dutch Island	133um	3	99.7						
7/31/02	Dutch Island	133um	1	91.9				10		
7/31/02	Dutch Island	133um	2	92.6				5		
7/31/02	Dutch Island	133um	3	85.7						
8/7/02	Dutch Island	133um	1	76.8				1		
8/7/02	Dutch Island	133um	2	71.5						
8/7/02	Dutch Island	133um	3	83.3						
8/14/02	Dutch Island	133um	1	45.6						
8/14/02	Dutch Island	133um	2	70.0				9.9		
8/14/02	Dutch Island	133um	3	59.9				1		
8/19/02	Dutch Island	133um	1	78.6				6.8		
8/19/02	Dutch Island	133um	2	73.4				7		
8/19/02	Dutch Island	133um	3	51.1				1		

5/22/02	Fox Island	133um	1	55.9				
5/29/02	Fox Island	133um	1	44.3		20	10	
6/12/02	Fox Island	133um	1	22.9			10	
6/12/02	Fox Island	133um	2	28.8				
6/12/02	Fox Island	133um	3	51.7				
6/19/02	Fox Island	133um	1	39.5				7.5
6/19/02	Fox Island	133um	2	37.7				6
6/19/02	Fox Island	133um	3	34.6			1	
6/26/02	Fox Island	133um	1	38.0				6.6
6/26/02	Fox Island	133um	2	37.8				3.3
6/26/02	Fox Island	133um	3	35.0				
7/1/02	Fox Island	133um	1	57.9				23.1
7/1/02	Fox Island	133um	2	21.0				
7/1/02	Fox Island	133um	3	23.4				
7/10/02	Fox Island	133um	1	35.3				
7/10/02	Fox Island	133um	2	55.5				
7/10/02	Fox Island	133um	3	32.2				
7/17/02	Fox Island	133um	1	23.0				
7/17/02	Fox Island	133um	2	28.2				
7/17/02	Fox Island	133um	3	37.4				
7/24/02	Fox Island	133um	1	75.3				1
7/24/02	Fox Island	133um	2	60.6				1
7/24/02	Fox Island	133um	3	67.5				
7/31/02	Fox Island	133um	1	80.4				
7/31/02	Fox Island	133um	2	42.4				1
7/31/02	Fox Island	133um	3	93.1				1
8/7/02	Fox Island	133um	1	52.7				
8/7/02	Fox Island	133um	2	62.3				1
8/14/02	Fox Island	133um	1	49.8				4
8/14/02	Fox Island	133um	2	47.8				4
8/14/02	Fox Island	133um	3	46.5				
8/19/02	Fox Island	133um	1	56.7				
8/19/02	Fox Island	133um	2	47.2				
8/19/02	Fox Island	133um	3	62.8				
6/4/02	Greenwich Bay	133um	1	6.5			46.2	
6/4/02	Greenwich Bay	133um	2	5.9			30	2.5
6/11/02	Greenwich Bay	133um	1	47.5				
6/11/02	Greenwich Bay	133um	2	108.2			75.6	
6/11/02	Greenwich Bay	133um	3	58.7				
6/19/02	Greenwich Bay	133um	1	63.4				5
6/19/02	Greenwich Bay	133um	2	65.0			2.5	17.5
6/19/02	Greenwich Bay	133um	3	56.3				

6/25/02	Greenwich Bay	133um	1	29.8			5		
6/25/02	Greenwich Bay	133um	2	13.1					
6/25/02	Greenwich Bay	133um	3	8.9					
7/26/02	Greenwich Bay	133um	1	57.8					
7/26/02	Greenwich Bay	133um	2	66.4					
6/4/02	Prudence East	133um	1	8.8			17.5	2.5	2.5
6/4/02	Prudence East	133um	2	9.7			79.2		
6/4/02	Prudence East	133um	3	8.8					
6/11/02	Prudence East	133um	1	39.0					
6/11/02	Prudence East	133um	2	34.8			330	3.75	
6/11/02	Prudence East	133um	3	43.1			491.7		
6/18/02	Prudence East	133um	1	28.3					
6/18/02	Prudence East	133um	2	13.8			7.2		
6/18/02	Prudence East	133um	3	28.9					
6/4/02	Warren River	133um	1	7.2					
6/4/02	Warren River	133um	2	7.9					
6/4/02	Warren River	133um	3	6.8					
6/18/02	Warren River	133um	1	53.1					
6/18/02	Warren River	133um	2	38.8				5	
6/18/02	Warren River	133um	3	44.1			7.7		
6/25/02	Warren River	133um	1	50.9					
6/25/02	Warren River	133um	3	49.9					
7/26/02	Warren River	133um	1	109.4					
7/26/02	Warren River	133um	2	79.3					
7/26/02	Warren River	133um	3	90.8					

b. Fish larvae raw data

Date	Station	Net Mesh	Rep. #	Volume filtered, M ³	Cunner	Tautog	Butter fish	Sea Robin
5/22/2002	Dutch Island	133um	1	103.4				
5/29/2002	Dutch Island	133um	1	168.5				
5/29/2002	Dutch Island	133um	2	111.6				
6/12/2002	Dutch Island	133um	1	104.8			5	
6/12/2002	Dutch Island	133um	2	69.7	5.8	2.9		
6/12/2002	Dutch Island	133um	3	76.4				

6/19/2002	Dutch Island	133um	1	69.9			
6/19/2002	Dutch Island	133um	2	66.7	3.3		
6/19/2002	Dutch Island	133um	3	72.4			
6/26/2002	Dutch Island	133um	1	47.2			
6/26/2002	Dutch Island	133um	2	64.8			
6/26/2002	Dutch Island	133um	3	98.3			
7/1/2002	Dutch Island	133um	1	65.4			
7/1/2002	Dutch Island	133um	2	40.2			
7/1/2002	Dutch Island	133um	3	61.3			
7/10/2002	Dutch Island	133um	1	82.9	8.4		
7/10/2002	Dutch Island	133um	2	61.2	3.3		
7/10/2002	Dutch Island	133um	3	65.9	1		
7/17/2002	Dutch Island	133um	1	83.0	6.6	3.3	
7/17/2002	Dutch Island	133um	2	52.6			
7/17/2002	Dutch Island	133um	3	53.8	1		
7/24/2002	Dutch Island	133um	1	73.9		7.5	
7/24/2002	Dutch Island	133um	2	67.7		2.5	
7/24/2002	Dutch Island	133um	3	99.7	2	3	
7/31/2002	Dutch Island	133um	1	91.9			
7/31/2002	Dutch Island	133um	2	92.6			
7/31/2002	Dutch Island	133um	3	85.7			
8/7/2002	Dutch Island	133um	1	76.8			
8/7/2002	Dutch Island	133um	2	71.5			
8/7/2002	Dutch Island	133um	3	83.3	1		
8/14/2002	Dutch Island	133um	1	45.6			
8/14/2002	Dutch Island	133um	2	70.0			
8/14/2002	Dutch Island	133um	3	59.9	1	1	
8/19/2002	Dutch Island	133um	1	78.6	1.7		
8/19/2002	Dutch Island	133um	2	73.4			
8/19/2002	Dutch Island	133um	3	51.1			
5/22/2002	Fox Island	133um	1	55.9			
5/29/2002	Fox Island	133um	1	44.3	10		
6/12/2002	Fox Island	133um	1	22.9		5	
6/12/2002	Fox Island	133um	2	28.8			
6/12/2002	Fox Island	133um	3	51.7			
6/19/2002	Fox Island	133um	1	39.5	2.5	2.5	
6/19/2002	Fox Island	133um	2	37.7			
6/19/2002	Fox Island	133um	3	34.6			
6/26/2002	Fox Island	133um	1	38.0			
6/26/2002	Fox Island	133um	2	37.8	3.3		
6/26/2002	Fox Island	133um	3	35.0	1		
7/1/2002	Fox Island	133um	1	57.9			
7/1/2002	Fox Island	133um	2	21.0			
7/1/2002	Fox Island	133um	3	23.4	2.5		
7/10/2002	Fox Island	133um	1	35.3	3.3	3.3	
7/10/2002	Fox Island	133um	2	55.5		15	
7/10/2002	Fox Island	133um	3	32.2			
7/17/2002	Fox Island	133um	1	23.0			

7/17/2002	Fox Island	133um	2	28.2			
7/17/2002	Fox Island	133um	3	37.4	1		
7/24/2002	Fox Island	133um	1	75.3			
7/24/2002	Fox Island	133um	2	60.6			
7/24/2002	Fox Island	133um	3	67.5			
7/31/2002	Fox Island	133um	1	80.4	5		
7/31/2002	Fox Island	133um	2	42.4			
7/31/2002	Fox Island	133um	3	93.1	2		
8/7/2002	Fox Island	133um	1	52.7			
8/7/2002	Fox Island	133um	2	62.3	2	1	
8/14/2002	Fox Island	133um	1	49.8			
8/14/2002	Fox Island	133um	2	47.8			
8/14/2002	Fox Island	133um	3	46.5	1		
8/19/2002	Fox Island	133um	1	56.7			
8/19/2002	Fox Island	133um	2	47.2			
8/19/2002	Fox Island	133um	3	62.8			
6/4/2002	Greenwich Bay	133um	1	6.5			
6/4/2002	Greenwich Bay	133um	2	5.9			
6/11/2002	Greenwich Bay	133um	1	47.5			
6/11/2002	Greenwich Bay	133um	2	108.2			
6/11/2002	Greenwich Bay	133um	3	58.7		10	
6/19/2002	Greenwich Bay	133um	1	63.4	7.5	7.5	
6/19/2002	Greenwich Bay	133um	2	65.0	2.5		2.5
6/19/2002	Greenwich Bay	133um	3	56.3			
6/25/2002	Greenwich Bay	133um	1	29.8			
6/25/2002	Greenwich Bay	133um	2	13.1			
6/25/2002	Greenwich Bay	133um	3	8.9			
7/26/2002	Greenwich Bay	133um	1	57.8		5	
7/26/2002	Greenwich Bay	133um	2	66.4	11		1
6/4/2002	Prudence East	133um	1	8.8			
6/4/2002	Prudence East	133um	2	9.7		3.3	
6/4/2002	Prudence East	133um	3	8.8			
6/11/2002	Prudence East	133um	1	39.0	1	1	
6/11/2002	Prudence East	133um	2	34.8	7.5		

6/11/2002	Prudence East	133um	3	43.1	16.5			
6/18/2002	Prudence East	133um	1	28.3				
6/18/2002	Prudence East	133um	2	13.8	10.8	3.6		
6/18/2002	Prudence East	133um	3	28.9				
6/4/2002	Warren River	133um	1	7.2				
6/4/2002	Warren River	133um	2	7.9				
6/4/2002	Warren River	133um	3	6.8				
6/18/2002	Warren River	133um	1	53.1	1			
6/18/2002	Warren River	133um	2	38.8	5			
6/18/2002	Warren River	133um	3	44.1				
6/25/2002	Warren River	133um	1	50.9				
6/25/2002	Warren River	133um	2	49.9				
7/26/2002	Warren River	133um	1	109.4				
7/26/2002	Warren River	133um	2	79.3				
7/26/2002	Warren River	133um	3	90.8				2

Date	Station	Net Mesh	Rep. #	Vol. filt., m ³	Bay Anchovy	Silver hake	Sea Trout
5/22/02	Dutch Island	133um	1	103.4			
5/29/02	Dutch Island	133um	1	168.5			
5/29/02	Dutch Island	133um	2	111.6			
6/12/02	Dutch Island	133um	1	104.8			
6/12/02	Dutch Island	133um	2	69.7			
6/12/02	Dutch Island	133um	3	76.4			
6/19/02	Dutch Island	133um	1	69.9			
6/19/02	Dutch Island	133um	2	66.7			
6/19/02	Dutch Island	133um	3	72.4			
6/26/02	Dutch Island	133um	1	47.2			
6/26/02	Dutch Island	133um	2	64.8			
6/26/02	Dutch Island	133um	3	98.3			
7/1/02	Dutch Island	133um	1	65.4			
7/1/02	Dutch Island	133um	2	40.2			
7/1/02	Dutch Island	133um	3	61.3			
7/10/02	Dutch Island	133um	1	82.9			
7/10/02	Dutch Island	133um	2	61.2			
7/10/02	Dutch Island	133um	3	65.9			
7/17/02	Dutch Island	133um	1	83.0			
7/17/02	Dutch Island	133um	2	52.6			
7/17/02	Dutch Island	133um	3	53.8			
7/24/02	Dutch Island	133um	1	73.9			
7/24/02	Dutch Island	133um	2	67.7			
7/24/02	Dutch Island	133um	3	99.7			
7/31/02	Dutch Island	133um	1	91.9			
7/31/02	Dutch Island	133um	2	92.6			
7/31/02	Dutch Island	133um	3	85.7			

8/7/02	Dutch Island	133um	1	76.8		
8/7/02	Dutch Island	133um	2	71.5		
8/7/02	Dutch Island	133um	3	83.3		
8/14/02	Dutch Island	133um	1	45.6		
8/14/02	Dutch Island	133um	2	70.0		
8/14/02	Dutch Island	133um	3	59.9		
8/19/02	Dutch Island	133um	1	78.6		
8/19/02	Dutch Island	133um	2	73.4		
8/19/02	Dutch Island	133um	3	51.1		
5/22/02	Fox Island	133um	1	55.9		
5/29/02	Fox Island	133um	1	44.3		
6/12/02	Fox Island	133um	1	22.9		
6/12/02	Fox Island	133um	2	28.8		
6/12/02	Fox Island	133um	3	51.7		
6/19/02	Fox Island	133um	1	39.5		
6/19/02	Fox Island	133um	2	37.7		
6/19/02	Fox Island	133um	3	34.6		
6/26/02	Fox Island	133um	1	38.0		
6/26/02	Fox Island	133um	2	37.8		
6/26/02	Fox Island	133um	3	35.0		
7/1/02	Fox Island	133um	1	57.9		
7/1/02	Fox Island	133um	2	21.0		
7/1/02	Fox Island	133um	3	23.4		
7/10/02	Fox Island	133um	1	35.3		
7/10/02	Fox Island	133um	2	55.5		
7/10/02	Fox Island	133um	3	32.2		
7/17/02	Fox Island	133um	1	23.0		
7/17/02	Fox Island	133um	2	28.2		
7/17/02	Fox Island	133um	3	37.4		
7/24/02	Fox Island	133um	1	75.3		
7/24/02	Fox Island	133um	2	60.6		
7/24/02	Fox Island	133um	3	67.5		
7/31/02	Fox Island	133um	1	80.4		
7/31/02	Fox Island	133um	2	42.4		
7/31/02	Fox Island	133um	3	93.1		
8/7/02	Fox Island	133um	1	52.7		
8/7/02	Fox Island	133um	2	62.3		
8/14/02	Fox Island	133um	1	49.8		
8/14/02	Fox Island	133um	2	47.8		
8/14/02	Fox Island	133um	3	46.5		
8/19/02	Fox Island	133um	1	56.7		
8/19/02	Fox Island	133um	2	47.2		
8/19/02	Fox Island	133um	3	62.8		
6/4/02	Greenwich Bay	133um	1	6.5		
6/4/02	Greenwich Bay	133um	2	5.9		
6/11/02	Greenwich Bay	133um	1	47.5		

6/11/02	Greenwich Bay	133um	2	108.2				
6/11/02	Greenwich Bay	133um	3	58.7				
6/19/02	Greenwich Bay	133um	1	63.4				
6/19/02	Greenwich Bay	133um	2	65.0				
6/19/02	Greenwich Bay	133um	3	56.3				
6/25/02	Greenwich Bay	133um	1	29.8				
6/25/02	Greenwich Bay	133um	2	13.1				
6/25/02	Greenwich Bay	133um	3	8.9				
7/26/02	Greenwich Bay	133um	1	57.8				
7/26/02	Greenwich Bay	133um	2	66.4				
6/4/02	Prudence East	133um	1	8.8				
6/4/02	Prudence East	133um	2	9.7				
6/4/02	Prudence East	133um	3	8.8				
6/11/02	Prudence East	133um	1	39.0				
6/11/02	Prudence East	133um	2	34.8				
6/11/02	Prudence East	133um	3	43.1				
6/18/02	Prudence East	133um	1	28.3				
6/18/02	Prudence East	133um	2	13.8				
6/18/02	Prudence East	133um	3	28.9				
6/4/02	Warren River	133um	1	7.2				
6/4/02	Warren River	133um	2	7.9				
6/4/02	Warren River	133um	3	6.8				
6/18/02	Warren River	133um	1	53.1				
6/18/02	Warren River	133um	2	38.8				
6/18/02	Warren River	133um	3	44.1				
6/25/02	Warren River	133um	1	50.9				
6/25/02	Warren River	133um	2	49.9				
7/26/02	Warren River	133um	1	109.4				
7/26/02	Warren River	133um	2	79.3				
7/26/02	Warren River	133um	3	90.8				
Date	Station	Net Mesh	Rep. #	Vol. filt., m ³	4spot flounder	Men-haden	Small mouth flounder	Four beard Rockling
5/22/02	Dutch Island	133um	1	103.4				

5/29/02	Dutch Island	133um	1	168.5			
5/29/02	Dutch Island	133um	2	111.6			
6/12/02	Dutch Island	133um	1	104.8		5	
6/12/02	Dutch Island	133um	2	69.7			
6/12/02	Dutch Island	133um	3	76.4			
6/19/02	Dutch Island	133um	1	69.9			
6/19/02	Dutch Island	133um	2	66.7			
6/19/02	Dutch Island	133um	3	72.4			
6/26/02	Dutch Island	133um	1	47.2			
6/26/02	Dutch Island	133um	2	64.8			
6/26/02	Dutch Island	133um	3	98.3			
7/1/02	Dutch Island	133um	1	65.4			
7/1/02	Dutch Island	133um	2	40.2			
7/1/02	Dutch Island	133um	3	61.3			
7/10/02	Dutch Island	133um	1	82.9			
7/10/02	Dutch Island	133um	2	61.2			
7/10/02	Dutch Island	133um	3	65.9			
7/17/02	Dutch Island	133um	1	83.0			
7/17/02	Dutch Island	133um	2	52.6			
7/17/02	Dutch Island	133um	3	53.8			
7/24/02	Dutch Island	133um	1	73.9			
7/24/02	Dutch Island	133um	2	67.7			
7/24/02	Dutch Island	133um	3	99.7			
7/31/02	Dutch Island	133um	1	91.9			
7/31/02	Dutch Island	133um	2	92.6			
7/31/02	Dutch Island	133um	3	85.7			
8/7/02	Dutch Island	133um	1	76.8			
8/7/02	Dutch Island	133um	2	71.5			
8/7/02	Dutch Island	133um	3	83.3			
8/14/02	Dutch Island	133um	1	45.6			
8/14/02	Dutch Island	133um	2	70.0			
8/14/02	Dutch Island	133um	3	59.9			
8/19/02	Dutch Island	133um	1	78.6			
8/19/02	Dutch Island	133um	2	73.4			
8/19/02	Dutch Island	133um	3	51.1			
5/22/02	Fox Island	133um	1	55.9			
5/29/02	Fox Island	133um	1	44.3			
6/12/02	Fox Island	133um	1	22.9			
6/12/02	Fox Island	133um	2	28.8			
6/12/02	Fox Island	133um	3	51.7			
6/19/02	Fox Island	133um	1	39.5			
6/19/02	Fox Island	133um	2	37.7			
6/19/02	Fox Island	133um	3	34.6			
6/26/02	Fox Island	133um	1	38.0			
6/26/02	Fox Island	133um	2	37.8			
6/26/02	Fox Island	133um	3	35.0			
7/1/02	Fox Island	133um	1	57.9			
7/1/02	Fox Island	133um	2	21.0			

7/1/02	Fox Island	133um	3	23.4		5	
7/10/02	Fox Island	133um	1	35.3		3.3	
7/10/02	Fox Island	133um	2	55.5		6	
7/10/02	Fox Island	133um	3	32.2			
7/17/02	Fox Island	133um	1	23.0			
7/17/02	Fox Island	133um	2	28.2			
7/17/02	Fox Island	133um	3	37.4			
7/24/02	Fox Island	133um	1	75.3			
7/24/02	Fox Island	133um	2	60.6			
7/24/02	Fox Island	133um	3	67.5			
7/31/02	Fox Island	133um	1	80.4			
7/31/02	Fox Island	133um	2	42.4			
7/31/02	Fox Island	133um	3	93.1			
8/7/02	Fox Island	133um	1	52.7			
8/7/02	Fox Island	133um	2	62.3			
8/14/02	Fox Island	133um	1	49.8			
8/14/02	Fox Island	133um	2	47.8			
8/14/02	Fox Island	133um	3	46.5			
8/19/02	Fox Island	133um	1	56.7			
8/19/02	Fox Island	133um	2	47.2			
8/19/02	Fox Island	133um	3	62.8			
6/4/02	Greenwich Bay	133um	1	6.5		3.3	
6/4/02	Greenwich Bay	133um	2	5.9			
6/11/02	Greenwich Bay	133um	1	47.5			
6/11/02	Greenwich Bay	133um	2	108.2			
6/11/02	Greenwich Bay	133um	3	58.7		5	
6/19/02	Greenwich Bay	133um	1	63.4			
6/19/02	Greenwich Bay	133um	2	65.0			
6/19/02	Greenwich Bay	133um	3	56.3			
6/25/02	Greenwich Bay	133um	1	29.8			
6/25/02	Greenwich Bay	133um	2	13.1			
6/25/02	Greenwich Bay	133um	3	8.9			
7/26/02	Greenwich Bay	133um	1	57.8			
7/26/02	Greenwich Bay	133um	2	66.4			
6/4/02	Prudence East	133um	1	8.8			
6/4/02	Prudence East	133um	2	9.7			
6/4/02	Prudence East	133um	3	8.8			

	East							
6/11/02	Prudence East	133um	1	39.0				
6/11/02	Prudence East	133um	2	34.8		3.75		
6/11/02	Prudence East	133um	3	43.1				
6/18/02	Prudence East	133um	1	28.3				
6/18/02	Prudence East	133um	2	13.8				
6/18/02	Prudence East	133um	3	28.9				
6/4/02	Warren River	133um	1	7.2				
6/4/02	Warren River	133um	2	7.9				
6/4/02	Warren River	133um	3	6.8				
6/18/02	Warren River	133um	1	53.1				
6/18/02	Warren River	133um	2	38.8				
6/18/02	Warren River	133um	3	44.1				
6/25/02	Warren River	133um	1	50.9		2.5		
6/25/02	Warren River	133um	2	49.9				
7/26/02	Warren River	133um	1	109.4				
7/26/02	Warren River	133um	2	79.3				
7/26/02	Warren River	133um	3	90.8				
Date	Station	Net Mesh	Rep. #	Vol. filt., m³	Pipe fish	Sand Lance	Scup	Blenny
5/22/02	Dutch Island	133um	1	103.4				
5/29/02	Dutch Island	133um	1	168.5				
5/29/02	Dutch Island	133um	2	111.6				
6/12/02	Dutch Island	133um	1	104.8				
6/12/02	Dutch Island	133um	2	69.7	2.9	2.9	2.9	
6/12/02	Dutch Island	133um	3	76.4				
6/19/02	Dutch Island	133um	1	69.9				
6/19/02	Dutch Island	133um	2	66.7				
6/19/02	Dutch Island	133um	3	72.4				
6/26/02	Dutch Island	133um	1	47.2				
6/26/02	Dutch Island	133um	2	64.8				
6/26/02	Dutch Island	133um	3	98.3				
7/1/02	Dutch Island	133um	1	65.4				
7/1/02	Dutch Island	133um	2	40.2				
7/1/02	Dutch Island	133um	3	61.3				
7/10/02	Dutch Island	133um	1	82.9				
7/10/02	Dutch Island	133um	2	61.2				
7/10/02	Dutch Island	133um	3	65.9				
7/17/02	Dutch Island	133um	1	83.0	3.3			
7/17/02	Dutch Island	133um	2	52.6				
7/17/02	Dutch Island	133um	3	53.8	1			
7/24/02	Dutch Island	133um	1	73.9				
7/24/02	Dutch Island	133um	2	67.7	2.5			

7/24/02	Dutch Island	133um	3	99.7			
7/31/02	Dutch Island	133um	1	91.9			
7/31/02	Dutch Island	133um	2	92.6			
7/31/02	Dutch Island	133um	3	85.7			
8/7/02	Dutch Island	133um	1	76.8			
8/7/02	Dutch Island	133um	2	71.5			
8/7/02	Dutch Island	133um	3	83.3			
8/14/02	Dutch Island	133um	1	45.6			
8/14/02	Dutch Island	133um	2	70.0			
8/14/02	Dutch Island	133um	3	59.9			
8/19/02	Dutch Island	133um	1	78.6			
8/19/02	Dutch Island	133um	2	73.4			
8/19/02	Dutch Island	133um	3	51.1			
5/22/02	Fox Island	133um	1	55.9			
5/29/02	Fox Island	133um	1	44.3			
6/12/02	Fox Island	133um	1	22.9	5		
6/12/02	Fox Island	133um	2	28.8			
6/12/02	Fox Island	133um	3	51.7			
6/19/02	Fox Island	133um	1	39.5			
6/19/02	Fox Island	133um	2	37.7			
6/19/02	Fox Island	133um	3	34.6			
6/26/02	Fox Island	133um	1	38.0			
6/26/02	Fox Island	133um	2	37.8			
6/26/02	Fox Island	133um	3	35.0			
7/1/02	Fox Island	133um	1	57.9			
7/1/02	Fox Island	133um	2	21.0			
7/1/02	Fox Island	133um	3	23.4			
7/10/02	Fox Island	133um	1	35.3			
7/10/02	Fox Island	133um	2	55.5	12		
7/10/02	Fox Island	133um	3	32.2			
7/17/02	Fox Island	133um	1	23.0			
7/17/02	Fox Island	133um	2	28.2			
7/17/02	Fox Island	133um	3	37.4			
7/24/02	Fox Island	133um	1	75.3			
7/24/02	Fox Island	133um	2	60.6			
7/24/02	Fox Island	133um	3	67.5			
7/31/02	Fox Island	133um	1	80.4			
7/31/02	Fox Island	133um	2	42.4			
7/31/02	Fox Island	133um	3	93.1			
8/7/02	Fox Island	133um	1	52.7	5		
8/7/02	Fox Island	133um	2	62.3			
8/14/02	Fox Island	133um	1	49.8	2.5		
8/14/02	Fox Island	133um	2	47.8			
8/14/02	Fox Island	133um	3	46.5			
8/19/02	Fox Island	133um	1	56.7			
8/19/02	Fox Island	133um	2	47.2			
8/19/02	Fox Island	133um	3	62.8			
6/4/02	Greenwich Bay	133um	1	6.5			

6/4/02	Greenwich Bay	133um	2	5.9			
6/11/02	Greenwich Bay	133um	1	47.5			
6/11/02	Greenwich Bay	133um	2	108.2			
6/11/02	Greenwich Bay	133um	3	58.7			
6/19/02	Greenwich Bay	133um	1	63.4	2.5		
6/19/02	Greenwich Bay	133um	2	65.0	2.5		
6/19/02	Greenwich Bay	133um	3	56.3			
6/25/02	Greenwich Bay	133um	1	29.8			
6/25/02	Greenwich Bay	133um	2	13.1			
6/25/02	Greenwich Bay	133um	3	8.9			
7/26/02	Greenwich Bay	133um	1	57.8		16	
7/26/02	Greenwich Bay	133um	2	66.4			
6/4/02	Prudence East	133um	1	8.8		12.5	
6/4/02	Prudence East	133um	2	9.7			3.3
6/4/02	Prudence East	133um	3	8.8			
6/11/02	Prudence East	133um	1	39.0			
6/11/02	Prudence East	133um	2	34.8			
6/11/02	Prudence East	133um	3	43.1	3.3		
6/18/02	Prudence East	133um	1	28.3			
6/18/02	Prudence East	133um	2	13.8			
6/18/02	Prudence East	133um	3	28.9			
6/4/02	Warren River	133um	1	7.2			
6/4/02	Warren River	133um	2	7.9			
6/4/02	Warren River	133um	3	6.8			
6/18/02	Warren River	133um	1	53.1			
6/18/02	Warren River	133um	2	38.8		5	
6/18/02	Warren River	133um	3	44.1			7.7
6/25/02	Warren River	133um	1	50.9			12.5
6/25/02	Warren River	133um	2	49.9			
7/26/02	Warren River	133um	1	109.4			
7/26/02	Warren River	133um	2	79.3			
7/26/02	Warren River	133um	3	90.8			

Data for $I = G/D$ for 2 *M. leidyi* size classes: >4cm and 1-4cm. A digestion time of 1.1 hours was used in all the calculations.

Station/ Date	I, # of fish eggs or larvae ingested by >4cm h ⁻¹	G, # of eggs or larvae in >4 cm <i>M. leidyi</i> gut ⁻¹	I, # of fish eggs or larvae ingested by 1-4cm	G, # of eggs or larvae in 1-3.9 cm <i>M. leidyi</i> gut ⁻¹	I * # of cteno. >4cm m ⁻³	I * # of cteno. 1-4 cm m ⁻³	# of <i>M. leidyi</i> >4cm m ⁻³	# of <i>M. leidyi</i> 1-4cm m ⁻³	# of fish eggs m ⁻³
FI, 5/29/02	0.1	0.1	0	0	0	0	0	0	73
WR, 6/4/02	0.4	0.4	0	0.1	4.5	2.9	0.5	2.7	8.2
PI, 6/4/02	0.1	0.1	0	0	0	0	0	0	6.9
GB, 6/4/02	0.5	0.6	0	0	38.5	0	3	0	11.5
GB, 6/11/02	0.5	0.5	0	0	18.8	0	1.6	0	11.5
PI, 6/11/02	0.2	0.2	0	0	1.5	0	0.3	0	18.2
FI, 6/12/02	0.2	0.2	0	0	25.7	0	5.1	29.7	1.4
PI 6/18/02	0.1	0.1	0	0	0.6	0	0.2	1.4	3.6
WR, 6/18/02	0.1	0.1	0	0	1.1	2.5	0.7	2.4	6.5
DI, 6/19/02	0.3	0.3	0.1	0.2	1.8	11	0.3	13.9	1.8
FI, 6/19/02	0.1	0.1	0	0	0.8	143.3	0.4	41.6	3.2
GB, 6/19/02	0	0	0	0	0.7	0.2	2.4	0.2	1.4
WR, 6/25/02	0	0	0.1	0.1	0	0.1	1.2	0.1	4.1
FI, 6/26/02	0	0	0	0	0.4	57.4	0.7	26.3	2

APPENDIX D

TEMPERATURE AND SALINITY DATA FROM PI, GB, AND WR

Date	Station	Avg.Temp.	Avg. Salinity
6/4/2002	PI	15.65	28.45
6/11/2002	PI	15.675	28.68
6/18/2002	PI	16.9225	28.7175
6/4/2002	GB	18.32	26.61
6/11/2002	GB	16.8475	27.515
6/19/2002	GB	20.1	27.5975
6/25/2002	GB	21.83	27.745
7/26/2002	GB	21.8	28
6/4/2002	WR	15.6675	28.7525
6/18/2002	WR	16.9025	28.1125
6/25/2002	WR	20.7875	27.84
7/26/2002	WR	21.8325	30.24

APPENDIX E

CTENOPHORE DATA FROM ABUNDANCE TOWS

Date	Station	net mesh	replicate #	volume filtered (m3)	# of ctenophores <1cm	1-1.9cm
6/4/2002	PI	1mm	1	10.87336245	32	
6/4/2002	PI	1mm	2	10	22	
6/11/2002	PI	1mm	1	18.90829694	490	
6/11/2002	PI	1mm	2	24.19213974	360	
6/18/2002	PI	1mm	1	9.43231441	360	7
6/18/2002	PI	1mm	2	9.825327511	290	8
6/4/2002	GB	1mm	1	6.244541485	44	8
6/11/2002	GB	1mm	2	8.951965066	190	6
6/11/2002	GB	1mm	1	11.74672489		19
6/19/2002	GB	1mm	2	8.471615721	900	20
6/19/2002	GB	1mm	1	8.427947598	750	20
6/25/2002	GB	1mm	2	5.371179039	34	1
6/25/2002	GB	1mm	1	3.755458515	12	1
7/26/2002	GB	1mm	2	66.2591687	5120	560
6/4/2002	WR	1mm	1	8.515283843	3	16
6/4/2002	WR	1mm	2	10.08733624	7	14
6/18/2002	WR	1mm	1	6.812227074	85	11
6/18/2002	WR	1mm	2	7.379912664	62	22
6/25/2002	WR	1mm	1	7.379912664	290	4
6/25/2002	WR	1mm	2	5.76419214	260	10
7/26/2002	WR	1mm	1	194.9781659	2920	200

Date	Station	2-2.9cm	3-3.9cm	4-4.9cm	5-5.9cm	6-6.9cm
6/4/2002	PI					
6/4/2002	PI					
6/11/2002	PI	4	3	1		
6/11/2002	PI	3	2	1		
6/18/2002	PI	4	4		1	1
6/18/2002	PI	4		1	1	1
6/4/2002	GB	6	5	1		
6/11/2002	GB		1	1		
6/11/2002	GB	3			1	
6/19/2002	GB			2		
6/19/2002	GB			1	1	
6/25/2002	GB					
6/25/2002	GB	1				
7/26/2002	GB					
6/4/2002	WR	1	6	3	1	
6/4/2002	WR	5	8	3	1	1
6/18/2002	WR	1		1		
6/18/2002	WR					

6/25/2002WR		2		1		
6/25/2002WR						
7/26/2002WR						

APPENDIX F

RESULTS OF COEFFICIENT OF VARIATION ANALYSES OF REPLICATE TOWS TAKEN TO ESTIMATE CTENOPHORE ABUNDANCE.

Station	Date	Standard Deviation	Coefficient of Variation, %
DI	6/12/2002	36.7	84.4
DI	6/19/2002	61.3	21.1
DI	6/26/2002	16.5	2.2
DI	7/1/2002	237.7	28.1
DI	7/10/2002	60.4	9.2
DI	7/17/2002	26.4	3.4
DI	7/24/2002	39.9	17.3
DI	7/31/2002	22.6	12.3
DI	8/7/2002	155.2	70.5
DI	8/14/2002	35.4	71.4
WR	6/4/2002	0.0	0.0
WR	6/18/2002	13.2	16.0
WR	6/25/2002	43.3	25.0
GB	6/11/2002	3.1	12.8
GB	6/19/2002	12.2	12.2
GB	6/25/2002	4.6	76.2
PI	6/4/2002	0.4	13.6
PI	6/11/2002	7.8	38.2
PI	6/18/2002	6.1	17.8

APPENDIX G

RESULTS OF GUT CONTENT EXAMINATION FOR FISH EGGS.

Date	Station	Ctenophore total length (cm)	Egg Species and No. Ingested
5/22/2002	FI	8	
5/22/2002	FI	9	
5/22/2002	FI	8	
5/22/2002	FI	3.5	
5/22/2002	FI	8	1 Cunner
5/22/2002	FI	9.2	
5/22/2002	FI	6.5	
5/22/2002	FI	5.9	
5/22/2002	FI	7.2	
5/22/2002	FI	7.4	
5/22/2002	FI	8.5	
5/22/2002	FI	8	
5/22/2002	FI	8.4	
5/22/2002	FI	6.2	
5/22/2002	FI	5.9	
5/22/2002	FI	6.8	1 Tautog
5/22/2002	DI	6.2	
5/22/2002	DI	9	
5/22/2002	DI	8	
5/22/2002	DI	7	
5/22/2002	DI	1.3	
5/22/2002	DI	2.5	
5/22/2002	DI	2.2	
5/22/2002	DI	2.4	
5/22/2002	DI	2.8	
5/22/2002	DI	6	
5/22/2002	DI	8.5	
5/22/2002	DI	5	
5/22/2002	DI	2.5	
5/29/2002	FI	3.9	
5/29/2002	FI	3.2	
5/29/2002	FI	5.5	
5/29/2002	FI	2.5	
5/29/2002	FI	2	
5/29/2002	FI	6.6	
5/29/2002	FI	0.8	
5/29/2002	FI	8	
5/29/2002	FI	1.5	
5/29/2002	FI	9.2	
5/29/2002	FI	4.4	

5/29/2002	FI	1.5	
5/29/2002	FI	2	
5/29/2002	FI	1.7	
5/29/2002	FI	1.9	
5/29/2002	FI	2.5	
6/4/2002	WR	7.1	
6/4/2002	WR	6.6	
6/4/2002	WR	5.7	
6/4/2002	WR	1	
6/4/2002	WR	10.9	
6/4/2002	WR	5.1	
6/4/2002	WR	0.9	
6/4/2002	WR	6.6	
6/4/2002	WR	5.6	1 Cunner
6/4/2002	WR	3.9	
6/4/2002	WR	4.1	1 Searobin
6/4/2002	WR	4.8	
6/4/2002	WR	2.4	
6/4/2002	WR	4.9	1 Cunner, 1 Tautog
6/4/2002	WR	2.4	1 Butterfish
6/4/2002	WR	6.1	
6/4/2002	WR	4.9	
6/4/2002	WR	4.8	
6/4/2002	WR	4.1	1 Butterfish
6/4/2002	WR	2.4	
6/4/2002	WR	4	
6/4/2002	WR	4.1	
6/4/2002	WR	7.6	
6/4/2002	WR	7.5	1 Searobin
6/4/2002	WR	3.9	
6/4/2002	WR	4.4	
6/4/2002	WR	4.8	
6/4/2002	WR	6.3	
6/4/2002	WR	5.4	2 Butterfish, 1 Cunner, 2 Tautog
6/4/2002	WR	6.1	1 Butterfish
6/4/2002	WR	8.1	
6/4/2002	WR	3.4	1 Butterfish
6/4/2002	WR	5.1	1 Butterfish
6/4/2002	WR	6.6	
6/4/2002	WR	4.1	
6/4/2002	WR	6.4	1 Tautog
6/4/2002	WR	5.4	
6/4/2002	WR	7.1	1 Cunner, 1 Tautog
6/4/2002	WR	4.5	
6/4/2002	WR	5.8	1 Cunner
6/4/2002	WR	4.2	
6/4/2002	WR	4.6	

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6/4/2002	PI	6.9	
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6/4/2002	PI	4.9	
6/4/2002	PI	2.4	
6/4/2002	PI	7.1	
6/4/2002	PI	5.9	
6/4/2002	PI	0.7	
6/4/2002	PI	6.9	1 Tautog
6/4/2002	PI	4.1	
6/4/2002	PI	8.3	
6/4/2002	PI	8.4	
6/4/2002	PI	3.2	
6/4/2002	PI	2	
6/4/2002	PI	0.3	
6/4/2002	PI	0.4	
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6/4/2002	PI	5.1	
6/4/2002	PI	9.1	1 Tautog
6/4/2002	PI	5.6	
6/4/2002	PI	2.4	
6/4/2002	PI	7.9	
6/4/2002	PI	3.4	
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6/4/2002	PI	4.5	
6/4/2002	PI	4.6	
6/4/2002	PI	7.2	
6/4/2002	PI	3.4	
6/4/2002	PI	1.9	
6/4/2002	PI	5.4	
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6/4/2002	GB	4.1	1 Searobin
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6/4/2002	GB	1.9	
6/4/2002	GB	7.2	2 Butterfish
6/4/2002	GB	5.6	2 Butterfish
6/4/2002	GB	8.1	
6/4/2002	GB	6.9	
6/4/2002	GB	4.9	
6/4/2002	GB	3.9	1 Tautog
6/4/2002	GB	5.9	
6/4/2002	GB	3.9	1 Tautog
6/4/2002	GB	2.8	
6/4/2002	GB	4.4	

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6/11/2002	GB	2.9	
6/11/2002	GB	5.4	
6/11/2002	GB	6.9	1 Butterfish, 1 Cunner
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6/11/2002	GB	4	1 Butterfish
6/11/2002	GB	5.8	
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6/11/2002	GB	3.5	
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6/11/2002	PI	5.8	1 Tautog
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6/11/2002	PI	1.9	
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6/11/2002	PI	4	
6/11/2002	PI	4.4	
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6/12/2002	FI	5.2	1 Butterfish
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6/18/2002	PI	5.9	1 Tautog
6/18/2002	PI	2.4	
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6/18/2002	PI	7.2	
6/18/2002	PI	7.2	1 Cunner
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6/18/2002	WR	0.9	
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6/19/2002	DI	4.2	1 Searobin
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6/19/2002	GB	2.1	
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6/19/2002	GB	1.7	
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8/19/2002	DI	1.6	

APPENDIX H

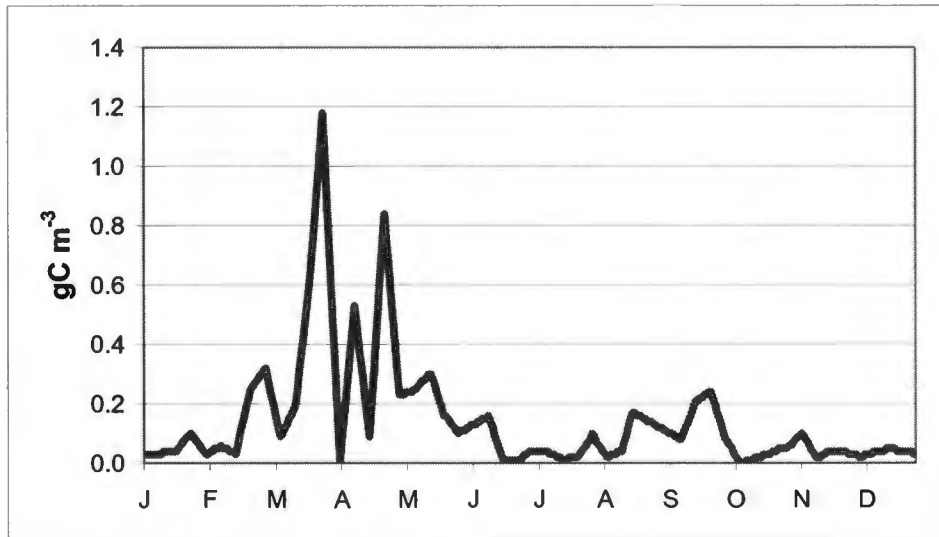
RESULTS OF DIGESTION RATE EXPERIMENTS WHERE THE EFFECT OF DYE WAS INVESTIGATED.

Date	Temp (degrees C)	Ctenophore Total length(cm)	Digestion Time(h)	Prey type	Prey number	Species type	Dye? Y/N
1/27/2003	7.5	2.5	1.1	larva	1	Winter flounder	Y
1/27/2003	7.5	1.6	1.0	larva	1	Winter flounder	N
1/28/2003	7.5	2.9	1.4	larva	2	Winter flounder	N
1/28/2003	7.5	3.4	1.4	larva	2	Winter flounder	Y
8/20/2003	21.5	ND	0.7	egg	1	S.Fl.	N
8/20/2003	21.5	1.8	1.2	egg	2	S.Fl.	Y
8/20/2003	21.5	5.3	1.5	egg	4	S.Fl.	N
8/20/2003	21.5	4.5	0.6	larva	1	S.Fl.	N
8/21/2003	24	5.2	0.4	larva	2	S.Fl.	Y
8/21/2003	24	3.1	0.3	larva	1	S.Fl.	N

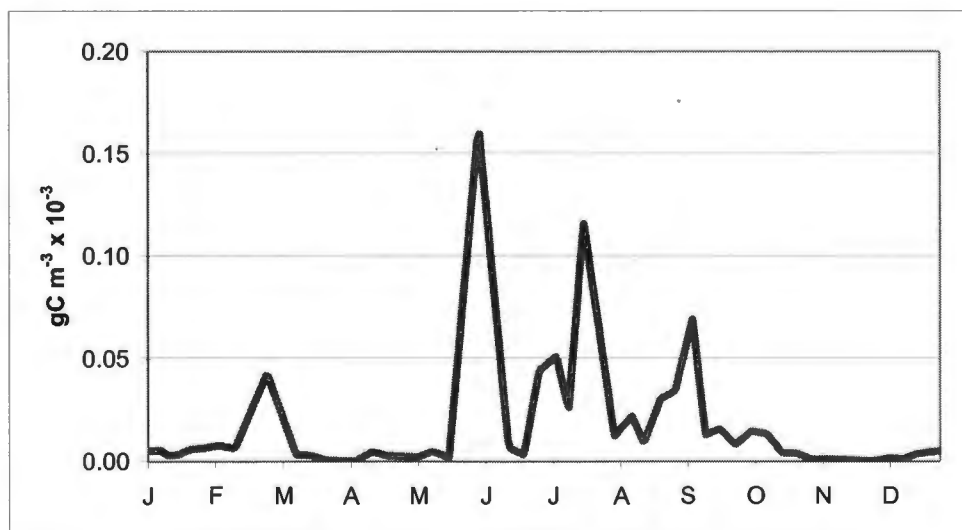
APPENDIX I

TIME SERIES DATA INPUT INTO DUTCH ISLAND MODEL OF *M. LEIDYI* BIOMASS; A. MESOZOOPLANKTON, B. MICROZOOPLANKTON, C. FISH EGGS, AND D. FISH LARVAE AND THE FOX ISLAND MODEL; E. MESOZOOPLANKTON, F. MICROZOOPLANKTON, G. FISH EGGS, AND H. FISH LARVAE

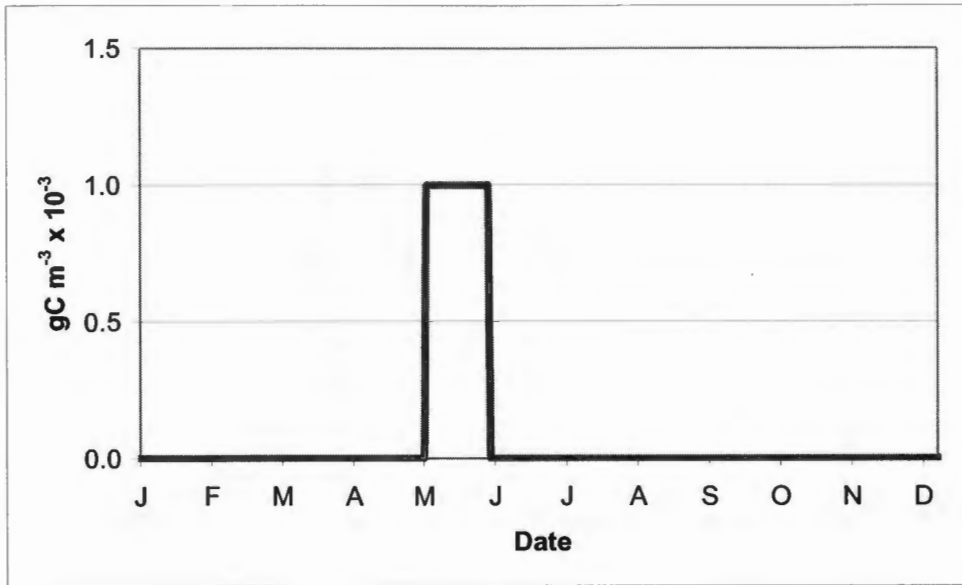
A.



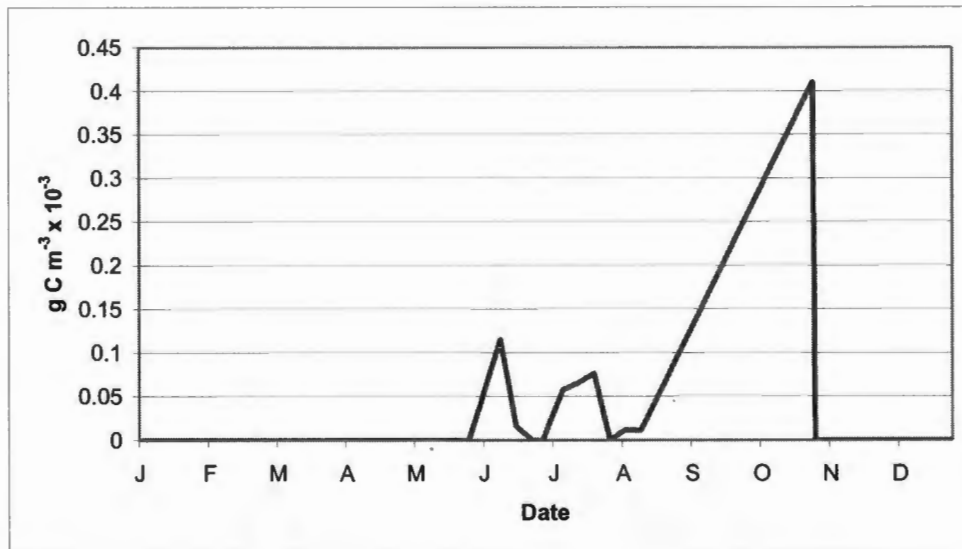
B.



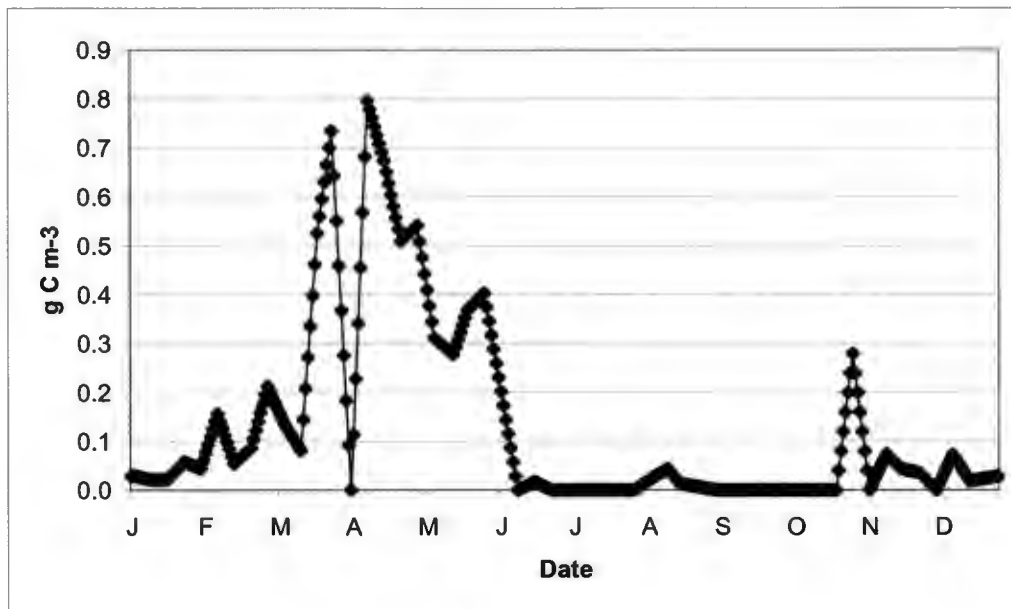
C.



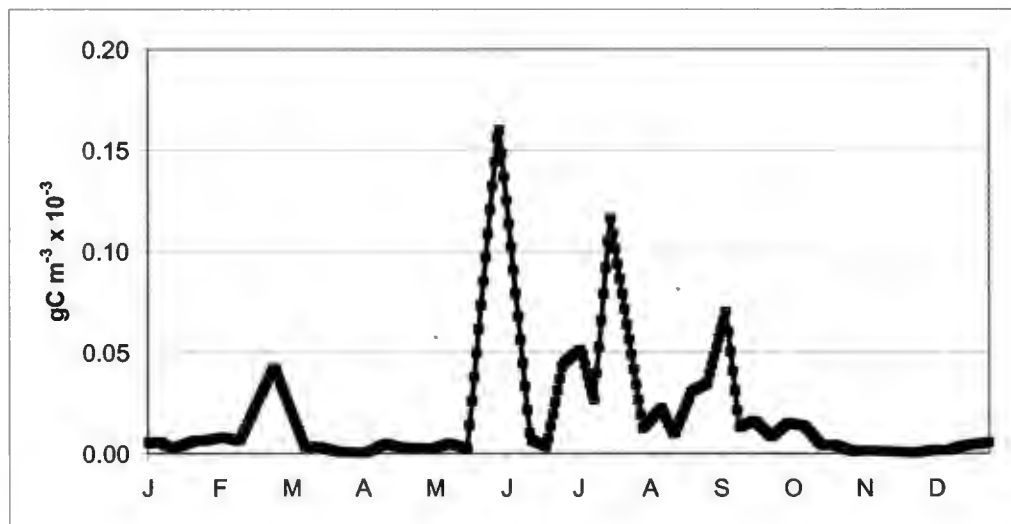
D.



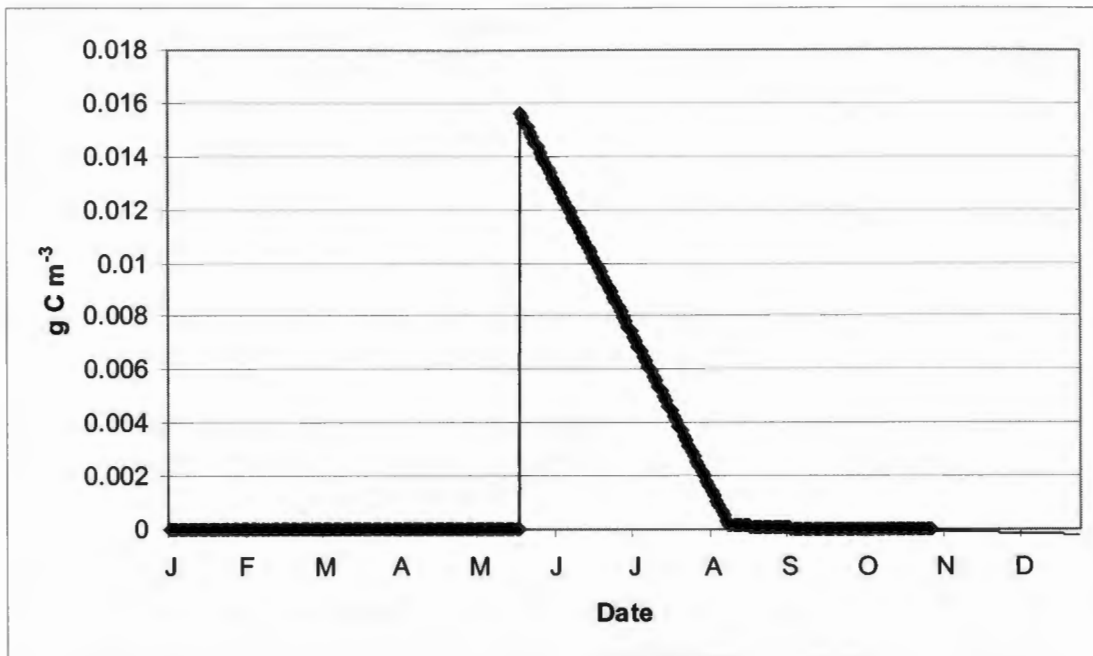
E.



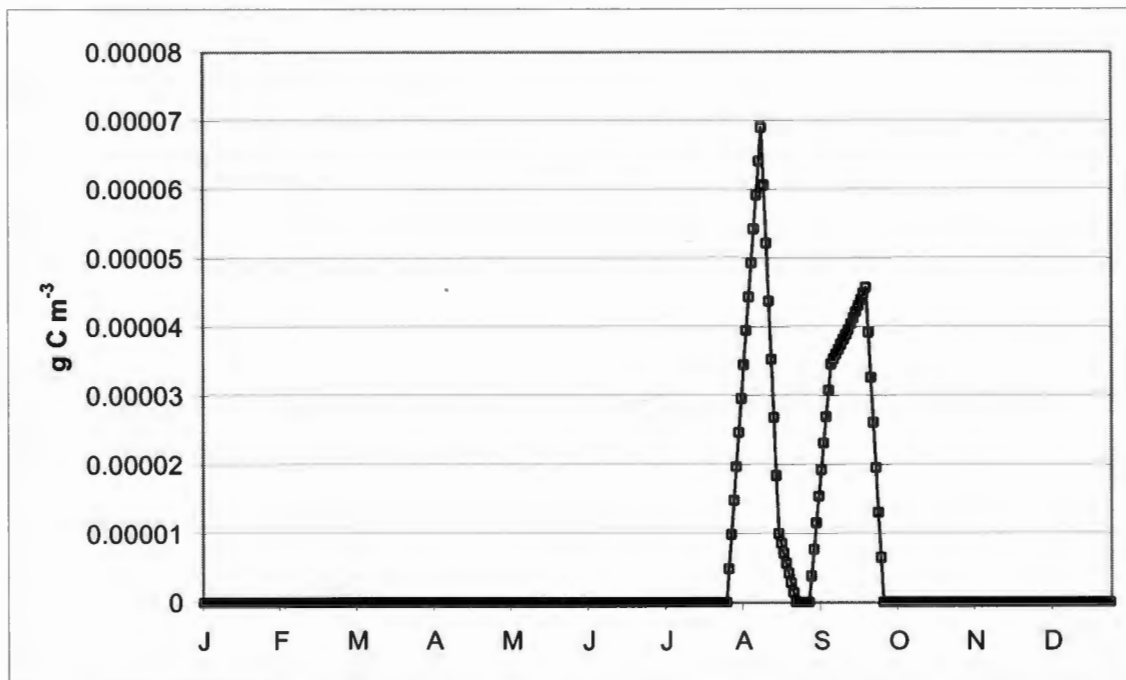
F.



G.



H.



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