ABSTRACT

Title of Dissertation:	FACTORS INFLUENCING APPEARANCE, DISAPPEARANCE, AND VARIABILITY OF ABUNDANCE OF THE SEA NETTLE, *CHRYSAORA QUINQUECIRRHA* IN CHESAPEAKE BAY
	Margaret A. Sexton, Doctor of Philosophy, 2012
Directed By:	Dr. Raleigh R. Hood Professor of Oceanography University of Maryland Center for Environmental Science

Some evidence suggests that jellyfish populations are increasing globally. Because of their nuisance to humans and trophic interactions, it is desirable to identify variables that control jellyfish blooms. *Chrysaora quinquecirrha* (Desor 1848) medusae are seasonally abundant in the mesohaline Chesapeake Bay. Efforts to predict medusa abundance have relied upon visual counts to estimate medusa abundance. A comparison of visual counts to vertical net hauls showed that visual counts underestimate abundance as compared to vertical net hauls, but the two measures captured the same trend 63% of the time. Smoothing improved agreement between estimates of abundance made by the two methods. The optimal moving average window size of 5 observations indicates that visual counting can be used to examine short term variability in abundance.

Previous efforts to identify variables that control the annual medusa bloom have traditionally focused on the magnitude of the peak in medusa abundance, but the timing of the bloom also varies from year to year. The timing of first appearance, peak abundance, and disappearance of medusae are examined for correlation with environmental conditions. Streamflow, which influences temperature and salinity, particularly in the first six months is an important driver of the timing of the medusa bloom; however, relationships between the timing of first appearance and both timing and magnitude of the peak indicate that the biology of the polyp stage needs to be considered in order to improve the predictability of the annual medusa bloom.

C. quinquecirrha medusae have a patchy distribution, even at times of high abundance and under optimal conditions. Two cyclic patterns in variability of abundance over short time scales were identified whose periods correspond to the lunar fortnightly constituent of the tidal force and the time between successive peaks in strobilation by the polyps. Apparent changes in abundance at the surface are caused by changes in depth distribution, which is influenced by water temperature and wind speed.

Finally, a laboratory experiment showed that low temperatures cause medusae to sink before cooling to the limit of their physiological tolerance and may have implications for deposition of organic matter associated with seasonal disappearance of medusae.

FACTORS INFLUENCING APPEARANCE, DISAPPEARANCE, AND
VARIABILITY OF ABUNDANCE OF THE SEA NETTLE, *CHRYSAORA
QUINQUECIRRHA* IN CHESAPEAKE BAY

By

Margaret A. Sexton

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2012

Advisory Committee:
Dr. Raleigh R. Hood, Chair
Dr. Denise L. Breitburg
Dr. Victoria J. Coles
Dr. Mary Beth Decker
Dr. David G. Kimmel
Dr. Patrick C. Kangas, Dean's Representative

Acknowledgements

Table of Contents

List of Tables

List of Figures

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Appendix 1

Chapter 1: Introduction and Synthesis

Introduction

Planktivorous jellyfishes are among the top predators in many different types of marine ecosystems (Mills 1995). Despite their obvious importance, long-term records of jellyfish abundance are scarce because the transparent and fragile nature of these organisms makes them difficult to sample (Purcell et al. 2007; Haddock 2004). Their painful sting, ability to reach high abundances, and competition with and predation on fish can cause negative impacts on recreation, aquaculture, and fisheries (Purcell et al. 2007). Climate change, cultural eutrophication, and over-fishing have all been hypothesized as factors that could cause jellyfish populations to increase globally. In recent years, increasingly negative effects of jellyfish on human activities have focused attention on jellyfish, but the lack of long-term observations make it difficult to determine whether jellyfish populations are in fact increasing (Purcell et al. 2007). As anthropogenic factors continue to affect coastal oceans, a better understanding of their relationship to jellyfish blooms will be important in the attempt to predict and mitigate the damage to recreation, aquaculture, and fisheries caused by jellyfish blooms.

Anthropogenic factors that are suspected to have the potential to increase jellyfish abundance include climate change, eutrophication, and overfishing (Purcell et al. 2007). In most cases, jellyfish not living near the upper limit of their temperature tolerance show increases in abundance as a direct or indirect result of climate warming (Lynam et al. 2004; Goy et al. 1989). Eutrophication can lead to increased jellyfish abundance in several different ways (Arai 2001). Some species are known to thrive under conditions of hypoxia that would be more detrimental to their

competitors (for example Rutherford and Thuessen 2005; Condon et al. 2001), and increased light attenuation due to increased primary production by phytoplankton can provide a competitive edge for jellyfish over visual predators (Eiane et al. 1999). Finally, there is evidence that overfishing of planktivorous fish can lead to increased jellyfish by releasing them from competitive pressure (Lynam et al. 2006; Daskalov 2002).

Economic losses due to damage of fishing nets, aquaculture efforts, nuclear power facilities, and tourism activities are all detrimental effects caused by high abundances of jellyfish (Purcell et al. 2007). Relatively large, heavy jellyfish clog fishing gear, sometimes making it impossible to retrieve (Kawahara et al. 2006), stings to the gills of penned animals can cause mass mortality in aquaculture facilities (Purcell et al. 1999a), high abundances can clog intake pumps used for cooling nuclear power facilities (Delano 2006), and the threat of painful stings can lead to beach closings (Ovitz 2007). For all of these reasons, it is important to understand the environmental factors that influence jellyfish populations. As anthropogenic alteration of ecosystems continues, there will be increasing potential for these influences to cause negative effects on human activities.

Jellyfish often appear in dense blooms, which can exert strong influences on nutrient cycling of the systems they inhabit (Pitt et al. 2009; Condon et al. 2011). These influences can include excretion of nitrogen and phosphorous, which can contribute to primary production. But perhaps more interesting is the fate of jellyfish biomass upon collapse of a bloom. Decomposition of gelatinous biomass can occur either in the water column or on the bottom. In deep systems where much of the

decomposition of a jellyfish may occur primarily in the water column as the jellyfish sinks slowly, the decaying gelatinous biomass leaches organic matter into the water column, providing a carbon source for bacterial production (Titelman et al. 2006). In the case of *Periphylla periphylla*, this dissolved organic matter leached from the decaying jellyfish stimulated the growth of certain groups of bacteria while inhibiting the growth of others. This suggests that the demise of a jellyfish bloom may act to structure the microbial community of a system. Several reports suggest that the remains of a jellyfish bloom can be deposited onto the sea floor, acting as a carbon source to the benthos (Billet et al. 2006; Yamamoto et al. 2008; Sexton et al. 2010). In an open ocean system where carbon sources may be scarce, this can represent an important food source to large benthic scavengers (Yamamoto et al., 2008). However, in coastal and estuarine systems that may be subject to periods of hypoxia, the increased microbial activity associated with the deposition of gelatinous biomass may have negative effects. West et al. (2009) showed that deposition of gelatinous biomass doubled sediment oxygen demand in a mesocosm experiment; therefore, it is possible that mass deposition of gelatinous biomass could contribute to hypoxia in coastal and estuarine systems.

In Chesapeake Bay, the dominant gelatinous species is the sea nettle *Chrysaora quinquecirrha,* a scyphozoan whose medusan stage is found in high concentrations in the mesohaline portion of Chesapeake Bay and in its tributaries during the summer and early fall. The typical scyphozoan life cycle consists of a sessile polyp stage, which undergoes two different asexual reproductive processes: budding to produce new polyps, and strobilation to produce free swimming larvae

called ephyrae (Arai 1997). The ephyrae develop into medusae, which reproduce sexually by broadcast spawning. The resulting larvae settle to the bottom to form new polyps. In *C. quinquecirrha*, strobilation is cued by the increase in temperature and salinity in spring (Cones and Haven 1969).

C. quinquecirrha has been shown to have an important influence on trophic dynamics in the Bay. Cowan and Houde (1993) showed that sea nettles may be the largest consumer of ichthyoplankton due to their spatial and temporal distribution, which coincides with the distribution of ichthyoplankton more frequently than other predators. Furthermore, Feigenbaum and Kelly (1984) suggest that *C. quinquecirrha* influences the trophic structure of the Bay through its predation on *Mnemiopsis leidyi*. By controlling the population of the voraciously feeding ctenophore, high abundances of sea nettles can positively affect secondary production.

Because of their trophic importance as well as their negative effects on recreation, it is desirable to be able to predict the abundance and distribution of sea nettles in Chesapeake Bay. Several studies have suggested that temperature and salinity are important variables in making such predictions. Cargo and Schultz (1966) showed that polyps, the source of ephyrae, are found within a salinity range of 5-20. The sessile polyps strobilate between temperatures of 18-27°C (Cargo and Schultz 1967). Cargo and King (1990) showed a relationship between January-June streamflow and average summer abundance of medusa. They showed that in years with below average streamflow in the first half of the year, sea nettle abundance tended to be high; whereas in years with high streamflow in the first half of the year, sea nettle abundance tended to be low. Breitburg and Fulford (2006) revisited this

model and showed that if a single anomalously high year was excluded from the analysis, or patterns were examined after a decline in sea nettle abundance in the mid-1980s, streamflow explained little of the variation in sea nettle abundance. On a smaller temporal scale, Decker et al. (2007) showed that high abundances of medusa are found within a narrow range of temperatures and salinities (26-30°C and 10-16 respectively) and that this relationship, along with modeled temperatures and salinities, can be used to predict the likelihood of encountering a high abundance of jellyfish at a specific location and time in Chesapeake Bay.

Objectives

The general goal of this dissertation is to improve the understanding of how environmental and biological factors impact the timing, intensity, and variability of the annual *C. quinquecirrha* medusa bloom in a tributary of Chesapeake Bay. Several previous efforts toward this end have relied to varying degrees on a time series of visual surface counts of medusae made at the Chesapeake Biological Laboratory in Solomons, Maryland, USA (Cargo and King 1990; Purcell and Decker 2005; Breitburg and Fulford 2006; Decker et al. 2007). Visual counting is an extremely useful tool for making frequent observations of the medusa population because it is simple and inexpensive. However, there are many factors, including water clarity, sea state, surface glare, and changes in vertical distribution of medusae that may affect the proportion of the water column sampled by visual counts or the proportion of the medusa population present in that section of the water column. The accuracy of visual counting as a measure of total medusa abundance has not previously been published;

therefore, the first objective of this work must be to assess how well visual counting measures the abundance of medusae in order to determine the most appropriate uses of this method.

Previous inquiries into the variability in the *C. quinquecirrha* medusa bloom have primarily focused on the magnitude of the bloom. Several different measures of medusa abundance have been used to characterize the magnitude of the bloom: Cargo and King (1990) used mean abundance in July and August to identify a relationship between abundance and streamflow; Purcell and Decker (2005) used total count over the entire season to illustrate the correlation between the North Atlantic Oscillation Index (NAOI) and medusa abundance; and Breitburg and Fulford (2006) examined both of these relationships more closely using the mean abundance over the four weeks surrounding the peak in medusa abundance. However, medusa abundance is not the only measurement that can be used to characterize the *C. quinquecirrha* bloom. The timing of the bloom, including the timing of the first appearance of medusae, the peak in abundance, and disappearance of medusae, can also vary widely from year to year. The second objective of this dissertation is to identify the variables that influence the inter-annual variability in the timing of the medusa bloom.

Over shorter time scales, temperature and salinity are generally understood to be the variables that identify habitat suitable for *C. quinquecirrha* medusae. Decker et al. (2007) showed that there is a very narrow range of temperature and salinity in which extremely high abundances of medusae occur and that knowledge of temperature and salinity for a given location and time can be used to predict the likelihood of medusae occurring there. However, when optimal conditions exist,

7

medusae are not always present. Like other types of zooplankton, *C. quinquecirrha* populations are characterized by patchy distributions that vary over shorter distances than the gradients in temperature and salinity. The third objective of this dissertation is to identify patterns in this patchy distribution that are related to biological, behavioral, or physical factors. Here, variability over short time scales will be considered analogous to variability over short spatial scales since patches of medusae moving through the counting area will cause variability in a time series of visual counts over the same area.

Finally, some attention has been paid to the supply of medusae to the Chesapeake Bay through strobilation by the polyp stage of *C. quinquecirrha*. Cargo and Schultz (1966), and Cargo and Rabenold (1980) describe the process and rates at which the polyp stage reproduces asexually, including the strobilation or budding of free-swimming ephyrae into the water column. Purcell et al. (1999b) examined the effects of temperature, salinity, and prey availability on rates of strobilation, and Condon et al. (2001) addressed the effect of low dissolved oxygen on asexual reproduction by polyps. Sources of mortality among medusae, on the other hand, have not been considered. Since the highly abundant medusae may represent a large pool of organic carbon, the annual decline of the medusa bloom may represent a pulse of carbon to the water column or benthos. In order to gain a better understanding of how this carbon may be released, the final objective of this work is to identify the factors that lead to the seasonal decline of the sea nettle population through examination of the multi-year time series and by experimentally testing the effects of

low temperature on the vertical position of sea nettles in the water column and starvation due to lack of available food.

Research Hypotheses

I. Chapter 2: Comparison of visual counting vs. net hauls as measures of sea nettle abundance

    1. There is a predictable relationship between medusa abundance as measured by a vertical net haul and visual count at the surface.

    2. The behavioral response of medusae to light (Schuyler and Sullivan 1997) cause differences in the proportion of the population that is available for visual count at different times of day.

    3. Since larger medusae are easier to see, the proportion available for visual count is greater than that of those in the smaller size class.

    4. Digital images of the water surface can be used to automate the counting process.

II. Chapter 3: Inter-annual variability: factors that influence the timing of appearance and disappearance, and timing and intensity of bloom

    5. Timing of first appearance, disappearance, and peak abundance of medusae as well as the magnitude of the peak are related to temperature, salinity, streamflow, and NAOI.

    6. These relationships are the same or similar at different locations on Chesapeake Bay.

7. Models of medusa abundance based on environmental conditions that have been previously developed using visual counts of medusae on the Patuxent River (Cargo and King 1990; Breitburg and Fulford 2006; Decker et al. 2007), will be similarly effective at predicting medusa abundance on the Choptank River.

III. Chapter 4: Identification and characterization of intra-annual variability in medusa abundance

8. Cyclic variables such as the lunar cycle and the spring-neap tidal cycle influence variability in sea nettle abundance.

9. Physical variables such as light, temperature, salinity, stratification, wind, and tides affect medusa abundance over short time scales.

10. Physical variables such as light, temperature, salinity, stratification, wind, and tides affect depth distribution over short time scales.

IV. Chapter 5: Response of *Chrysaora quinquecirrha* medusae to low temperature

11. Exposure to cold temperatures (< 15 °C) causes medusae to sink in the water column.

Summary of Results

This dissertation set out to contribute to a better understanding of how environmental and biological factors impact the timing, intensity, and variability of the annual *C. quinquecirrha* medusa bloom in Chesapeake Bay. First, it assesses the utility of visual counting as a measure of medusa abundance, which has been relied

upon for several previous efforts to understand inter-annual variability in medusa

abundance (Chapter 2). This assessment showed that while visual counts do tend to

underestimate the total abundance of medusae, time series of the two methods show

the same trends of increasing or decreasing abundance up to 72% of the time. In other

words, although visual counts may not offer an ideal measure of absolute abundance,

they do offer a measure of relative abundance, which can be used to identify trends.

Agreement between the two methods improved when the time series were smoothed

using a moving average, indicating that noise in the time series was partially

responsible for the difference between the two measures of abundance. Maximum

agreement between the time series of the two methods occurred at a moving average

window size of 5 observations (2.5 days when observations occur twice daily). This

means that visual counting can be used to identify changes in abundance that occurs

on a time scale of one week or more. Additionally, a preliminary attempt to use

digital images for the purpose of visual counting showed that jellyfish were visible in

the image, suggesting that it may be possible to automate the counting process in

order to make frequent, simultaneous counts at multiple locations.

In general, this work confirms the conventional understanding that

temperature and salinity are influence when and where *C. quinquecirrha* medusae

will be present, and it extends that understanding to apply not only to medusa

abundance, but also the timing of the arrival of medusae and the peak in medusa

abundance (Chapters 3 and 4). The relationship between medusa abundance on the

Choptank River and Chesapeake Bay streamflow is similar, but significantly different

from the relationship between abundance on the Patuxent River and Chesapeake Bay

streamflow, likely indicating that the exact nature of the relationship between medusa abundance and streamflow at any particular location depends on the degree to which that location is open to and influenced by the mainstem of the bay (Chapter 3). Comparison of the Choptank River time series to predicted probability of occurrence of medusa calculated using the model described by Decker et al. (2007) shows that agreement between observed abundance and the temperature and salinity-driven model predictions is different from year to year. I hypothesize that these differences are caused by factors other than salinity and temperature that affect asexual reproduction by polyps and mortality of medusae. Furthermore, several additional variables that affect medusa abundance were identified. Timing of the peak in medusa abundance depends on the timing of the initial appearance, and timing of disappearance of medusae depends on the timing of the peak. These results indicate that the seasonal presence of medusae in Chesapeake Bay follows a traditional bloom trajectory, in which the bloom runs its course in a predictable time frame.

In addition to temperature and salinity, several other variables that influence medusa abundance over intra-annual time scales were also identified using the time series of visual counts (Chapter 4). A Gaussian model was fit to the time series of abundance for each year from 2005-2010 in order to describe the pattern of the bloom. The period of the spring-neap tidal cycle and the time between successive peaks in strobilation, as reported by Cargo and Rabenold (1980), were both evident in the spectrum of the residuals from the Gaussian model, indicating that these factors are important sources of variability in abundance. A combined Gaussian and periodic model with sinusoidal terms that correspond to the spring-neap cycle and the period

between successive peaks in strobilation was created to describe the annual bloom cycle. In its current form, this model is only descriptive and not predictive of medusa abundance because it depends on the timing and magnitude of the annual peak in abundance. However, the relationships between timing and magnitude of the peak identified in Chapter 3 may provide insight into the factors that determine timing and magnitude of the peak in order to eventually develop a predictive model.

A variety of other environmental variables were examined for correlation with abundance as measured by visual counts over the course of a single season (Chapter 4). Four variables showed weak ($r2 < 0.05$), but significant ($p < 0.05$) relationships to medusa abundance. Not surprisingly, temperature and salinity had the strongest of these four relationships, but wind speed and the lunar phase also showed significant relationships with abundance. An examination of the depth distribution of medusae by comparing the visual count, which measures only surface abundance, with vertical net hauls, which measure abundance throughout the water column revealed that changes in depth distribution may explain the correlation between medusa abundance as measured by surface counts and temperature and wind speed. Under warm and calm conditions, the depth distributions varied. I hypothesize that under these optimal conditions, aggregation behaviors create variability in visual counts and net hauls as aggregations move into or out of the volumes sampled by the two different methods. When water temperature was colder, medusae were typically found deeper, indicating that low temperature caused medusae to sink, thereby impeding normal swimming and aggregation behavior. Similarly, under windy conditions, the medusae were found to have a more homogenous depth distribution, indicating that swimming and

aggregation behaviors were also impeded by water movement that occurs under high wind conditions.

Finally, in situ observations and results from a large tank experiment help to characterize the pattern of disappearance (Chapter 5). Field observations showed that at temperatures below 15 °C, medusae were no longer found near the surface, but remained abundant near the bottom. Medusae were subjected to low temperatures in a large tank experiment in order to confirm this observation experimentally. The experiment showed that medusae exposed to temperatures below 15 °C were found lower in the water column and pulsed slower than those in a control group held at a temperature of 18 °C. This result indicates that at the end of the season, carbon stored in medusa biomass may represent a pulse of organic matter delivered to the benthos as sinking medusae are deposited on the bottom. Calculations based on medusa abundance on the Choptank and Patuxent Rivers suggest that this pulse of carbon may be as much as one percent as large as the deposition from the spring bloom.

Conclusions

The results of this research contribute to the understanding of *C. quinquecirrha* blooms in Chesapeake Bay and jellyfish blooms more generally. The assessment of visual counting as a method of measuring medusa abundance clarifies the strengths and weaknesses of a simple, inexpensive method of making frequent measurements of a medusa population. As anthropogenic impacts continue to accumulate in coastal and estuarine systems and jellyfish blooms continue to interfere with human endeavors, monitoring of jellyfish populations will continue to be

necessary in order to understand how changing conditions will affect jellyfish populations. This method of visual counting is accessible both to researchers and to programs that utilize "citizen scientists" to collect large quantities of data at many locations because it does not require any specialized training or equipment. However, to maximize the utility of such a method, it is necessary to understand how it measures the variable in question as compared with more traditional methods. The assessment of visual counting as a measure of medusa abundance showed that it typically underestimates absolute abundance of medusae as compared with a vertical net haul, but that as a measure of relative abundance, visual counts show the same trends of growth or decline of the population. These results represent an assessment of visual counting in a shallow, turbid environment that is not necessarily applicable everywhere.

A second contribution of this dissertation is that it extends the understanding of how physical conditions, biology, and behavior influence the abundance of *C. quinquecirrha* medusae. Predicting the characteristics of the annual *C. quinquecirrha* bloom has been the objective of research efforts in Chesapeake Bay for decades (for example Cargo and King 1990; Decker et al. 2007) because of its impact on human activities and the trophic structure of the bay (Feigenbaum and Kelly 1984; Purcell 1992; Cowan and Houde 1993). In other locations, like the Barnegat Bay/Little Egg Harbor estuary, dense blooms of *C. quinquecirrha* medusae are a relatively new phenomenon (Kennish 2007). If the impacts of this and other species of medusae continue to grow in Chesapeake Bay and elsewhere, demand for accurate predictions of the blooms will only increase. In order to improve and expand existing models,

15

more information about how physical processes interact with the biology and behavior of these organisms is needed.

This research advances the understanding of how environmental variables impact the annual *C. quinquecirrha* bloom by addressing the variables that impact the timing of the bloom in addition to the magnitude of the bloom. Temperature and salinity, or other variables such as streamflow that affect temperature and salinity, have traditionally been thought of as the most important factors that influence medusa abundance. This work reinforces the importance of temperature and salinity to cue the annual bloom by identifying relationships between these two variables on both inter-annual and intra-annual time scales, but also suggests that the progression of the bloom is also important in determining the timing of peak medusa abundance and disappearance. Specifically, timing of first appearance explains only slightly less of the variability in the timing and magnitude of the peak in abundance than streamflow; therefore, future efforts to predict the timing and magnitude of peak abundance may be able to improve their accuracy by considering the timing of first appearance.

Several factors that influence variability in medusa abundance within a season are also identified here. A periodic pattern in abundance that has the same period as the time between successive peaks in strobilation as observed by Cargo and Rabenold (1980) suggests that pulses of asexual reproduction are reflected in medusa abundance. A second periodic pattern in abundance with the same time period as the spring-neap tidal cycle suggests that tidal currents are either physically transporting medusae or cuing horizontal swimming behavior.

Recent inquiry into the fate of jellyfish carbon has shown that jellyfish represent an important pool of organic matter whose release can be a significant source of carbon to the benthos, can structure microbial communities, and can increase sediment oxygen demand (reviewed in Pitt et al. 2009). Understanding the release of organic matter from this pool of gelatinous biomass requires an understanding of the sources of mortality among medusae. This dissertation describes one source of mortality, and describes the process by which the pulsation rate of medusae exposed to low temperature slows, and they are deposited onto the sediment before pulsation stops and the medusae eventually die. I also offer hypotheses for the mechanism of the decline of the bloom in years when it is terminated before water temperatures begin to decline.

Finally, this research suggests several directions for future efforts. First, the success of visual counting at measuring relative abundance of medusae and a preliminary attempt to identify medusae in digital images suggest that it may be possible to use cameras to automate the counting process in order to make frequent, simultaneous observations at multiple locations. This would offer the ability to examine variability in medusa abundance in time and space at the same time. The findings that the timing and magnitude of the peak in medusa abundance are related to the timing of the first appearance and that pulses of strobilation are reflected in the abundance of medusae highlight the importance of understanding the complete lifecycle of *C. quinquecirrha* in order to understand its annual bloom. More information regarding the distribution and abundance of the polyp stage, and the environmental variables that influence them, as well as information regarding

recruitment and mortality in the polyp population may advance understanding of the annual bloom of medusae. Similarly, more information is needed to identify sources of mortality. The annual decline of water temperature in the fall is one source, but it does not explain the disappearance in all years. The contribution of other sources of mortality in the annual disappearance of medusae needs to be explored in order to fully understand the release of organic matter from gelatinous biomass and its role in nutrient cycling as well as its role as a predator in the Chesapeake Bay.

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Chapter 2: Visual counting as a measure of medusa abundance

Abstract

Understanding changing populations of gelatinous zooplankton requires long-term records of abundance, but few such records exist because the delicate and patchily distributed organisms are difficult to sample. Many efforts to understand populations of *Chrysaora quinquecirrha,* a seasonally abundant medusa in the mesohaline Chesapeake Bay and its tributaries, have relied at least partially on daily visual surface counts. I use a comparison between the visual count and vertical net haul to determine how well the visual count represents the abundance of medusae in the water column and address the time scales over which the time series of visual counts is able to capture trends in abundance. Although visual counts do not provide a qualitative measure of medusa abundance, they do represent a measure of relative abundance that can be used to identify trends on intra-annual time scales. I also address differences in the relationship between visual counts and net hauls for different subsets of the time series including observations made at different times of day and observations of different sizes of medusae. These analyses reveal that although the relationship between abundance as measured by visual count and vertical net haul explains different amounts of the variability for different size classes and at different times of day, the slopes of those relationships were not different. Finally, I explore the use of cameras in order to allow for frequent sampling and simultaneous sampling at multiple locations.

Introduction

24

Jellyfish blooms have received increasing attention in recent years due to increasing interactions with humans; however, it remains unclear whether jellyfish abundance is increasing globally (Purcell et al. 2007; Condon et al. 2012). Jellyfish often act as top predators in a variety of marine ecosystems (Mills 1995). Although jellyfish have traditionally been regarded as a trophic dead end, as they have relatively few predators (Condon and Steinberg 2008; Hansson and Norrman 1995), they can act as a significant carbon source to the benthic environment (Yamamoto et al. 2008; Billet et al. 2006; Sexton et al. 2010). Both live jellyfish and decaying gelatinous biomass have been shown to impact nutrient cycling (Pitt et al. 2009), and decaying gelatinous biomass can influence the composition of the bacterial community by favoring certain members while inhibiting others (Condon et al. 2011; Tinta et al. 2010; Titelman et al. 2006). The painful sting delivered by some jellies presents a nuisance to recreational activities and commercial fishing, and their tendency to form intense blooms can clog fishing nets and nuclear power plant water intake pumps (Purcell et al. 2007). Because of their important trophic position and threat to human activities, it is desirable to understand and predict any changes that may be occurring in jellyfish populations.

The medusa stage of the scyphozoan *Chrysaora quinquecirrha* (Desor 1848) is seasonally abundant during the summer in the mesohaline Chesapeake Bay and its tributaries. Like other jellyfish worldwide, *C. quinquecirrha* is important to the trophic structure and a nuisance to human activity in the bay. This voracious predator has been shown to impact the abundance of other planktonic species including

copepods, fish larvae, and the ctenophore *Mnemiopsis leidyi* (A. Agassiz 1865) (Feigenbaum and Kelly 1984; Purcell 1992; Cowan and Houde 1993).

Several studies have addressed the relationship between medusa abundance and environmental variables in Chesapeake Bay. Cargo and King (1990) linked mid-summer medusa abundance to streamflow in the first six months of the year. Purcell and Decker (2005) showed an inverse correlation between medusa abundance and the North Atlantic Oscillation (NAO), but Breitburg and Fulford (2006) indicate that these trends break down after a decrease in medusa abundance that occurred in the late 1980s and coincided with the decline of the Chesapeake Bay oyster population. Changes in *C. quinquecirrha* populations are not limited to Chesapeake Bay. In the nearby Barnegat Bay-Little Egg Harbor Estuary, medusae were present, but not in high abundance before 2000 (Kennish 2007). Since then, intense blooms have occurred annually (S. Hales, personal communication).

Understanding of how changing climate and other anthropogenic forcing, including eutrophication, overfishing, and construction projects affect changing *C. quinquecirrha* and other jellyfish populations requires long term observations of abundance, but very few such data sets exist (Mills 2001). The long term, high frequency data needed to address small scale variability in medusa abundance makes it necessary to use a method for evaluating abundance that is inexpensive and simple. Collection with nets can require expensive boat time, may damage fragile organisms like jellyfish making them difficult to identify and quantify, and can exclude large, strong-swimming individuals. Visual counting performed from a dock or shore, on the other hand, is inexpensive, does not require specialized equipment, and allows the

observer to easily identify individuals. Cargo and King (1990) used a 30-year time series of visual counts of *C. quinquecirrha* to estimate seasonal abundance for the development of a model to predict average summer abundance. While there are many sources of error involved in visual counts, including differences between observers, sea state, and weather conditions, they provide a manageable method for gathering long term, high frequency observations of jellyfish abundance. Observation by visual counting assumes that individuals visible at the surface represent some constant or predictable proportion of the total number of individuals present in a given volume. However, this assumption has never been tested for *C. quinquecirrha* in Chesapeake Bay or, to my knowledge, for any other gelinatinous species or marine environment.

Here, I address the utility of visual counting as a measure of *C. quinquecirrha* medusa abundance in Chesapeake Bay by comparing measures of abundance provided by two different methods: visual counting and vertical net hauls. I also examine the viability of digital video cameras for automating the counting process in order to allow for high frequency, simultaneous sampling at multiple locations. Specifically, I address the following hypotheses:

1. There is a predictable relationship between medusa abundance as measured by a vertical net haul and visual count at the surface.

2. The behavioral vertical swimming response of medusae to light (Schuyler and Sullivan 1997) causes differences in the proportion of the population that is available for visual count at different times of day.

3. Since larger medusae are easier to see, the proportion available for visual count is greater than that of those in the smaller size class.

27

4. Digital images of the water surface can be used to automate the counting process.

I show that although visual counts do not provide a qualitative measure of medusa abundance, they do represent a measure of relative abundance that can be used to identify trends on intra-annual time scales, and digital cameras present a promising option for automating the process of collecting count data.

Methods

Abundance of *Chrysaora quinquecirrha* medusae was measured in two different ways: visual counts and vertical net hauls. The visual counts were made over a 9 m^2 area on the right side of the pier at the Horn Point Laboratory, Cambridge, Maryland, USA on the south east side of the Choptank River (38° 35.610' N, 76° 7.725' W). Net hauls were made using a 9 m^2 net, which was raised from the bottom to collect all medusae in the water column over the same area as the visual counts. Each medusa counted visually in the visual count area or captured in the net was placed into a size category based on a visual estimate of the diameter of its bell. The categories were <4 cm, 4-8 cm, and >8 cm. Visual counts and net hauls began on 17 July 2005. Both measures of abundance were made twice daily at 7 AM and 7 PM until 16 September 2005, when decreasing day length made it impossible to make visual counts at 7 PM due to lack of daylight. At that time, observations were rescheduled in an attempt to better control for changing light conditions. Morning observations were made at sunrise, and evening observations were made 20 minutes before sunset in order to allow sufficient time to make counts and net hauls before it

became too dark. Calculated sunrise and sunset times for Cambridge, Maryland, USA were downloaded from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Observations continued on this schedule until no medusae had been observed by visual count, net haul, or visual observation of the surrounding area for ten consecutive days. In subsequent years, 2006-2010, observations followed the sunrise and sunset schedule, beginning on June 1 and continuing until ten days after the last medusa was observed.

In addition to the visual count and net haul, Secchi depth and water depth were measured at the time of each observation. Secchi depth was measured inside the visual counting transect and was used to estimate the depth to which medusae could be seen in order to calculate the water volume sampled by visual counting. Water depth over the net was measured in order to calculate the volume sampled by the net. These two volumes were then used to calculate the density of medusae measured by each method in individuals per cubic meter.

A paired comparisons t-test was used to determine whether the estimates of abundance from the two sampling methods differed significantly from each other (Sokal and Rohlf 1995). Least squares linear regression was used to describe the relationship between the estimates of abundance provided by the two different methods. Additionally, the first difference of the time series for each method, or its slope, was calculated for the time of each observation in order to compare the trends in abundance captured by the two different sampling methods. The slopes were compared using the paired comparisons t-test and least squares regression as above.

The time series of the two methods were smoothed using moving averages with window sizes of 3, 5, 10, and 20 observations, and the first differences of the smoothed data sets were also calculated. Each smoothed dataset and its first difference were analyzed using the paired comparisons t-test and linear regression as above to determine whether and what level of smoothing would improve the agreement between estimates of abundance based on the two different methods. Additionally, the first differences were examined for their sign, and the percentage of time when the signs were the same for the two different measures of abundance was calculated.

Finally, analysis of covariance (ANCOVA; Sokal and Rohlf 1995) was used to determine whether the relationship between abundance as measured by the two different methods was the same for different subsamples of the data. ANCOVA determines whether the slopes and intercepts of two different linear regression lines are significantly different from one another. Subsamples to be compared were counts and net hauls of large individuals versus small individuals and morning counts versus evening counts. Using the five-point moving averages calculated for the time series, least squares linear regression lines were calculated for each of the subsamples. The regression line for the subsample containing only large individuals was compared to the regression line for the subsample containing only small individuals, and the regression line for the subsample containing only observations made in the morning was compared to the regression line for the subsample containing only observations made in the evening in order to determine whether the relationship between

30

abundance as measured by visual counts and net hauls differs at different times of the day or among different size classes of medusae.

In 2010, a video surveillance camera was installed above the visual counting area in order to determine whether automated visual sampling is possible. The camera (Vivotek IP7330 outdoor surveillance camera with 640 X480 pixel resolution) was mounted perpendicular to the water surface, approximately 2.5 m above the water level at high tide in order to view the same 9 m^2 area described above for visual counts. Late arrival and low abundances of medusae during the 2010 season necessitated the use of simulated jellyfish for this trial. A weighted line with a float attached was deployed within the camera's view. At 20 cm intervals below the float, translucent, white disks with 10 cm diameter, made of high-density polyethylene were attached to the line to simulate medusae at different depths. Still images of the water surface were captured at two-hour intervals during daylight hours, Monday-Friday from 13 July 2010 to 3 August 2010. These images were processed using ImageJ (http://rsbweb.nih.gov/ij/) to determine the number of disks that were observable in each image. A series of test images were processed using various combinations of features available in the ImageJ software package to maximize the ability to distinguish the disks in the images. It was determined that the most effective processing technique was to first convert the color image to a 32 bit, black and white image. Next, a Fast Fourier Transform (FFT) band pass filter (large structures filtered to 40 pixels, small structures filtered to 3 pixels, and 5% tolerance of direction) was applied to the black and white image. Finally, the contrast was enhanced by 1%. Once each image was processed using this technique, the number of simulation jellyfish

disks visible in the image was counted. At the time that each image was captured, an individual standing on the dock counted the number of disks that were visible below the float. The number of disks visible in the processed image was compared to the number of disks visible to the observer using Fisher's Exact test to determine whether there was a relationship between the two counts and the Wilcoxon sign-rank test to determine whether the observer on the dock was consistently able to see more disks than were visible in the camera images (Sokal and Rohlf 1995).

Results

The time series of medusa abundances calculated from visual counts and net hauls (Fig. 2.1) showed that the first appearance of medusae in the visual counts and net hauls occurred within one week of each other in all years and that peaks in abundance were frequently observed at the same time using both measures. However, the densities measured by net hauls were frequently higher than those measured by visual counts. Also, abundance as measured by net hauls often remained high after abundance as measured by visual counts decreased and reached zero at the end of the season (for example, 2005 and 2006; Fig. 2.1a and b).

The time series exhibited a large amount of apparently stochastic high frequency variability (noise). Moving averages were calculated for each year with window sizes of 3, 5, 10, and 20 points in order to determine what level of smoothing best removed the noise (Fig. 2.2). Visual inspection of the smoothed time series indicates that the lower frequency peaks and troughs in the data become clearer with

32

the three-point moving average (for example Fig. 2.2a), but as the window size

increases to twenty points, information about these features is lost to the smoothing.

The first differences of abundance, or change in abundance over time, of the

time series showed a similar pattern to the raw time series. In general, when density

as measured by net hauls showed a positive first difference, which indicates

increasing medusa abundance, the density as measured by visual counts also showed

a positive first difference, (Fig. 2.3). The largest deviation from this pattern occurred

near the end of some seasons when the first differences of the time series of visual

counts approached zero before those of the time series of net hauls. Also similar to

the raw time series, smoothing the time series of first differences of abundance using

a moving average removes noise so that pulses in changing abundance can be

identified more easily (Fig. 2.3).

Densities measured by net hauls were consistently of greater magnitude than

those measured by visual counts for all levels of smoothing based on a paired

comparisons t-test ($p < 0.01$); however the mean difference between the density

measured by the two different methods decreased slightly with smoothing and did not

change with increasing moving average window size (Fig. 2.4b). First differences of

abundance from the two different measures of abundance were not significantly

different from one another at any level of smoothing, but variability shows a marked

decrease with increasing moving average window size (Fig. 2.4a).

Least squares linear regression showed that there is a significant relationship

between the abundances and the first differences of abundance, or change in

abundance over time, as measured by the two methods at all window sizes ($p < 0.01$;

Table 2.1). The relationship with abundance also had a y-intercept that was significantly different from zero at all moving average window sizes. The first difference, on the other hand, had y-intercepts that were not significantly different from zero at any window size. The r^2 values ranged from 0.1588 to 0.2453 and reached their maximum at a moving average window size of 5 observations for medusa abundance. For the first difference of abundance, r^2 values ranged from 0.1596 to 0.2592 and reached their maximum at a moving average window size of 10 observations. The r^2 values for both medusa abundance and the first difference of medusa abundance initially increased, and then began to decline with increasing moving average window size (Fig. 2.5). The percentage of observations at which the signs of the first differences were the same showed a similar pattern. In the unsmoothed time series (moving average window size = 1), the sign of the first difference of the time series of visual counts agreed with the sign of the first difference of the time series of net hauls at 63% of the observations (Table 2.1). As with the r^2 values, the agreement initially increased, and then began to decrease with increasing moving average window size (Fig. 2.6).

Least squares linear regression indicated that variability in abundance as measured by visual counts explained 32% of variability as measured by net haul for morning counts ($r^2 = 0.3233$, p <0.01) but only 26% of variability in evening counts ($r^2 = 0.2584$, p<0.01). However, slopes of the regression lines for these two subsets of the time series did not differ significantly from each other (ANCOVA, p = 0.0613). Similarly, variability in abundance as measured by visual counts explained much more of the variability measured by net haul in the subset of the time series that

includes only medusae with bell diameter greater than 8 cm ($r^2 = 0.4053$, p <0.01) than in the subset of the time series that includes only medusae with bell diameter less than 4 cm ($r^2 = 0.1024$, p <0.01), but the slopes of these two regression lines do not differ significantly from each other (ANCOVA, p = 0.3150).

An observer viewing the simulated jellyfish from the dock was consistently able to see more disks than were visible from still images captured using the digital video camera (Wilcoxon sign-rank test, p <0.01). However, Fisher's exact test indicates that the two are not independent (p = 0.0037; Table 2), which means that although an observer viewing the surface of the water samples a larger volume of water than the camera images, the camera samples the simulated medusa abundance, and likely actual medusa, abundance in a similar way.

Discussion

Prior to this study, daily visual counts have been used to identify characteristics of the annual bloom of *Chrysaora quinquecirrha* medusae, such as peak abundance, in order to identify patterns in inter-annual variability. Cargo and King (1990) related summer medusa abundance as measured by daily visual counts to streamflow in the first half of the year in order to predict the intensity of the annual bloom. A re-examination of the same daily visual counts along with continued counts through 2005 by Breitburg and Fulford (2006) showed a similar trend between streamflow and the July-August medusa abundance as well as a relationship between the NAO and peak medusa abundance. However, they also illustrated that both trends broke down after 1990 and point out that although the relationship is significant, only

a small percentage of the variability in abundance is explained by streamflow when

the longer time series is considered and when the four week mean peak in abundance

is considered rather than the July-August abundance of medusae. Finally, Sexton et

al. (2010) used the date of annual disappearance, calculated from the same visual

counts made by D. Cargo from 1960-1995, to identify the occurrence of early

disappearances. In each of these cases, a single piece of information was extracted

from the annual time series of visual counts in order to compare it with the same

characteristic in other years. The results of this study indicate that such high-

frequency visual counts can also be used to examine intra-annual variability in order

to better understand and perhaps predict the progression of the annual bloom of *C.*

quinquecirrha medusae.

The time series of net hauls from 2005-2010 (Fig. 2.1) indicate that although

measurements of abundance based on net hauls are typically higher than those made

by visual counts, there is a significant relationship between the two methods. The

time series of the first difference of abundance (Fig. 2.3) indicates that the two show

the same trends up to 72% of the time (Table 2.1) with peaks and troughs occurring at

the same times. At all moving average window sizes, the mean difference between

abundance as measured by net haul and visual count was greater than zero, but the

difference between first differences of the two methods was never significantly

different from zero (Fig. 2.4). This indicates that although visual counts

underestimate abundance compared with net hauls regardless of moving average

window size, both measures of abundance show the same trends as measured by their

first differences or change in abundance over time. Although the linear relationship

between the two methods of measuring medusa abundance only explains 16% of the variability in abundance and 18% of the variability in the first difference of abundance, the significant relationships (Table 2.1) indicate that the abundance as measured by visual count is related to the total population size as measured here by vertical net hauls. The low r^2 values indicate that while there is a relationship, visual counts do not represent a quantitative measure of medusa abundance, but the agreement between the trends in visual count and vertical net haul measurements indicates that visual counts do represent a relative measure of medusa abundance. Thus, visual counts are not a strong tool for estimating the total size of the medusa population or biomass and will generally underestimate population size if used in this way. However, the frequent agreement between the trends of the two measures indicates that visual counts do provide a useful measure of population change. Previous studies have used visual counts primarily as relative measures of abundance. Cargo and King (1990) identified a trend of relative high abundance during dry years, and Breitburg and Fulford (2006) used visual counts in a similar way to show that the relationship between this trend broke down over time. Our results indicate that the use of visual counts should not be extended beyond use as a relative measure to a quantitative one.

Smoothing the time series by moving average increased the amount of variability explained by the linear relationship between abundance as measured by visual count and vertical net haul and the first difference of abundance measured by the two methods by as much as 10% (Fig. 2.2, Table 2.1). As moving average window size increased, the r^2 values initially increased for both abundance and the

37

first difference of abundance, but eventually began to decrease (Fig. 2.5). This indicates that at the lower moving average window sizes, the smoothing removed noise from the time series, allowing the trends to be seen more clearly. This noise is likely introduced by behavioral factors that cause aggregations of medusae to form either inside or outside of the visual counting area. As a patch moves, it may enter the count area and then exit the area in a matter of hours or even minutes, which can result in two successive observations with extremely different measures of abundance. By using a moving average to smooth the effects of patch formation and movement that occurs over very small time scales, we are better able to visualize the effects of processes that work at longer time scales such as population growth or changes in physical variables that may cause larger scale movement of the population, such as changes in current velocity. At higher window sizes, the smoothing began to dampen the signal of the time series. Maximum r^2 values were observed at a window size of 5 observations (2.5 days) for abundance and 10 observations (5 days) for the derivative of abundance, indicating that the minimum scale on which to examine intra-annual variability in abundance using twice daily visual counts is in the range of 1-2 weeks. This time scale allows for the removal of noise related to the patchy distribution of medusae without removing the effects of relatively short term processes such as pulses in strobilation or physical movement of the population.

The non-zero y-intercept of the linear regression model for abundance as measured by the visual count versus that measured by vertical net haul (Table 2.1) indicates that the proportion of the population near the surface and available for

38

visual count is not constant and depends on the value of the total abundance. Since the y-intercept is positive at all moving average window sizes, the proportion of the population that is available for visual count increases as abundance increases. A possible explanation for this is that vertical swimming behavior of medusae may be related to abundance. *C. quinquecirrha* medusae are known to exhibit diel vertical migration and to spend the daylight hours at deeper depths (Schuyler and Sullivan 1997). This means that during the day, more medusae are expected to be nearer to the bottom and unavailable for visual counting. However, at high abundances, space near the bottom may become limited, forcing more medusae to move toward the surface, thus increasing the proportion available for visual counting. Although swimming behaviors that avoid physical contact between individual medusae have not been identified in *C. quinquecirrha*, a switch from horizontal swimming to vertical swimming behavior observed after *Aurelia aurita* medusae were recruited to an aggregation (reviewed in Albert 2011) suggest that it is a potential hypothesis. Field observations from this study occasionally included masses of between two and thirty medusae with tentacles and oral arms tangled together when abundance was very high. Based on this observation, it would likely be beneficial for medusae to avoid contact with one another in order to avoid damage.

At all moving average window sizes, the visual count underestimated abundance of medusae as compared to the abundance measured by a vertical net haul (Fig. 2.4). One explanation for this difference is that the use of Secchi depth overestimates the depth to which medusae can be identified and counted by an observer. Depth to which medusae can be seen can be influenced by the concentration

of suspended particles and colored dissolved material, light intensity and angle, and surface glare. Conveniently, Secchi depth provides a measure of water clarity that depends on all of these variables, and so it provides a measure of the depth to which objects can be seen. However, not all types of objects can be seen equally well in the water. While the color of the disk corresponds well to the color of medusae, it is both larger and more opaque than the medusae, therefore it is likely to be visible at deeper depths. At this time, it is not known how Secchi depth is related to the depth to which a medusa can be seen, but understanding this relationship might allow for an improved measure of water volume sampled and medusa density. Alternatively, it might be advisable to measure the depth to which medusae can be seen using simulated medusae like those used in the camera versus visual count comparison.

Although densities as measured by visual counts may underestimate the total abundance of medusae, examination of the derivative of abundance as measured by the two different methods show that 63% of the time, the same trend is captured by both of the methods. In other words, most of the time, when one measure indicates that the population is increasing, the other measure agrees. This is especially important because it indicates that while visual counts may not be a particularly accurate measure of absolute abundance, they are a good measure of relative abundance; therefore, they can be used to identify intra-annual increases and decreases in abundance that may be related to environmental conditions. The increase in agreement as moving average window size increases to a maximum of 72% agreement at a window size of 10 observations further supports the conclusion that

this is the appropriate window size to maximize the removal of noise from the time series.

The lack of significant difference between the relationship of net hauls to visual counts in the large size class (<8 cm bell diameter) versus the small size class (<4 cm bell diameter) indicates that visual counts made at different times of year when the size distribution of the medusa population may be different can be compared with one another in order to identify changes in relative abundance over time. Although there was no difference between the relationships at sunrise versus sunset, comparison with regression equations for counts made at other times of day would be necessary to make a similar statement about time of day. Schuyler and Sullivan (1997) showed that medusae exhibit diel vertical migration cued by rapid changes in light, and they can be found nearer to the surface during the night. Both sunrise and sunset represent times of rapidly changing light and fall within the time period in which migration was occurring in their experiment, therefore it is not surprising that the proportion of the population available for visual counting is the same at sunrise and sunset since both represent a transitional phase in the medusa's diel vertical migration. At other times of day, however, the relationship between abundance as measured by visual counts and net hauls may not be the same as at sunrise and sunset, and comparisons between counts should be limited to those made at a standardized time.

Finally, a preliminary attempt to use a digital video camera to make observations shows promise. Although medusae were not available for this trial, simulated medusae were visible in images produced by the camera. The simulated

medusae were visible to a greater depth when viewed by an observer present on the dock than in the camera images; however the number of disks visible to the observer on the dock was related to the number visible in the camera image. This result suggests that while the camera may not be as good as visual counts made by an observer, they are likely to have some utility in capturing trends in relative abundance. Use of cameras for visual counting could allow for more frequent counts made simultaneously at many locations without significant increase in effort. It may also be possible to automate these counts using computerized image analysis techniques. The current study focuses on changes in medusa abundance over time at a single location. The use of camera images for obtaining counts could facilitate the consideration of changes in medusa abundance over both time and space.

In conclusion, visual counting provides a simple and inexpensive method for addressing medusa abundance over a variety of time scales. Previous studies have shown the utility of visual counts for identifying indices that describe a season for inter-annual comparisons. Here I show that frequent visual counts capture the trends of medusa abundance on shorter time scales that will allow for intra-annual comparison. Identifying patterns of intra-annual variability may provide insight into the environmental factors that cue changes in the medusa population within a single season. This analysis considers only one species of medusa in one location. Although the environmental and behavioral factors that affect the relationship between visual counts and the absolute abundance will vary between locations and species, I suggest that visual counting may be a useful tool for monitoring trends in relative abundance of any medusa species that is routinely observable near the water surface.

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Tables

	Window size	Slope	Intercept	r^2	% agreement of sign
Medusa abundance	1	1.0439	0.4454	0.1588	
	3	1.3642	0.3002	0.2305	
	5	1.4255	0.2915	0.2453	
	10	1.4035	0.2983	0.2281	
	20	1.2972	0.3227	0.201	
First difference of abundance	1	0.9146	NS	0.1841	63
	3	1.0484	NS	0.1733	68
	5	1.1376	NS	0.2081	71
	10	1.3538	NS	0.2592	72
	20	1.0766	NS	0.1596	71

Table 2.1: Slope, intercept, and r^2 values for least squares regression between *C. quinquecirrha* medusa abuncance and first difference of abuncance as measured by visual counts and vertical net hauls, and the percentage of observations at which the first difference of the time serise of visual counts and the first difference of the time series of vertical net hauls have the same sign. NS indicates that the value was not significantly different from zero ($p > 0.05$).

Camera Counts

		0	1	2	3
Visual Counts	**0**	0	0	0	0
	1	8	22	2	0
	2	13	28	20	0
	3	0	0	2	0

Table 2.2: Contingency table for Fisher's exact test to determine whether the number of simulated jellyfish disks counted by an observer is related to the number of disks visible in a camera image. The entries in the diagonal box represent instances where the camera count and the observer's count were equal to each other. Those above the box represent instances where the camera count was greater than the observer's count, and those below the box represent instances where the camera count was less than the observer's count.

48
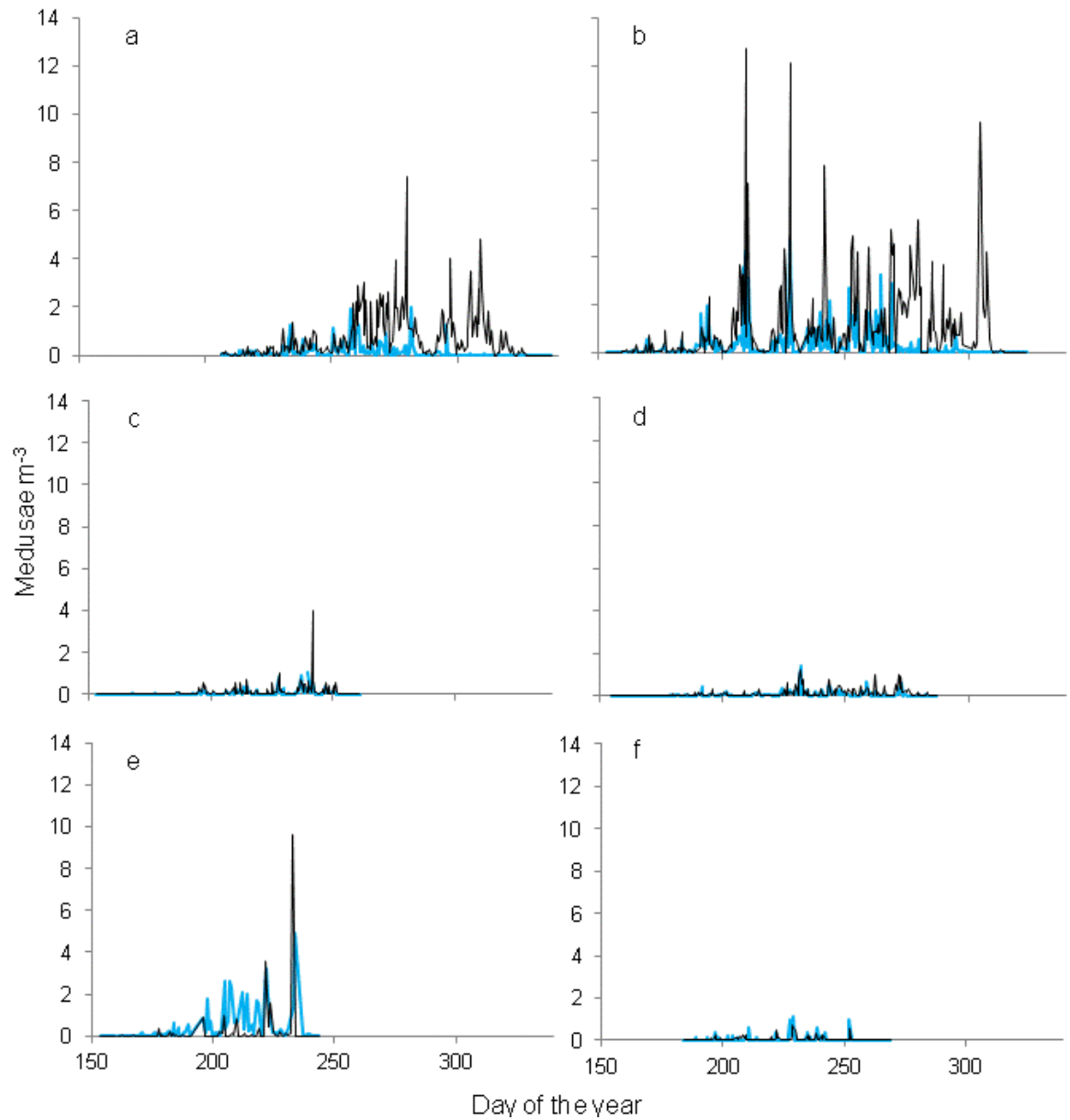
Figures

Figure 2.1: Time series of *C. quinquecirrha* medusa abundance as measured by visual counts (blue) and vertical net haul (black) in 2005 (a), 2006 (b), 2007 (c), 2008 (d), 2009 (e), and 2010 (f).
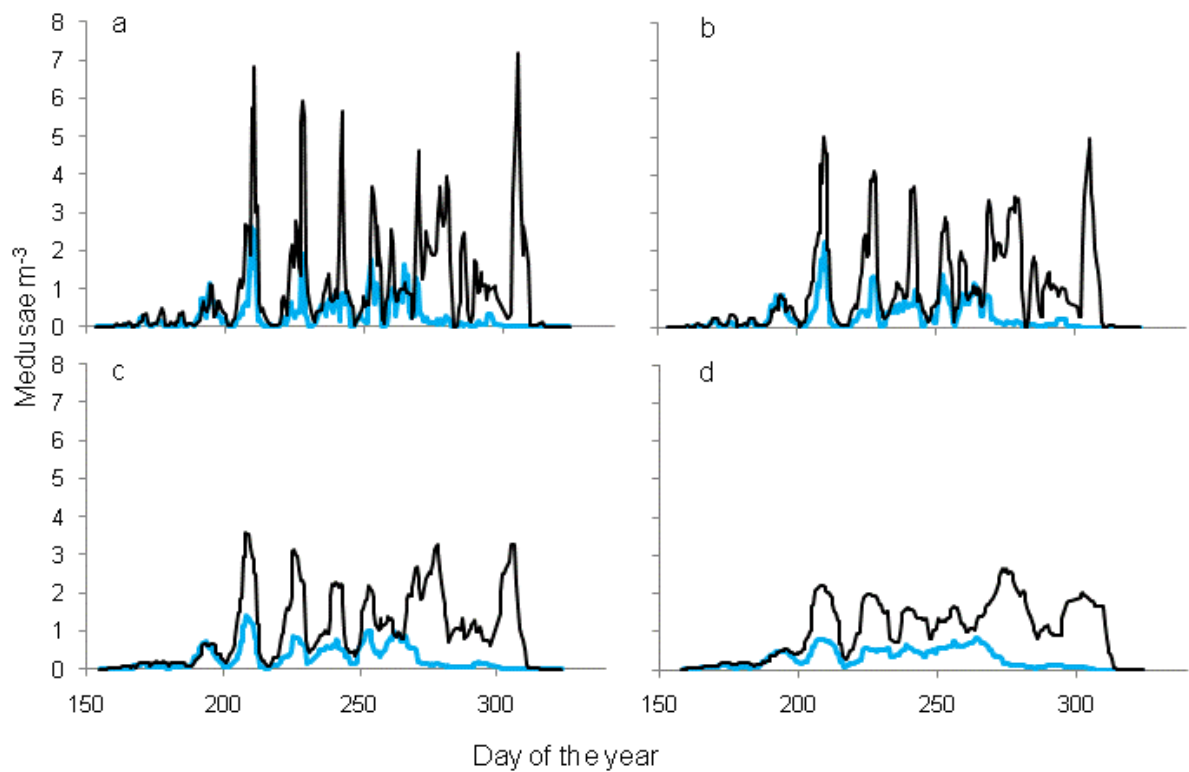
Figure 2.2: Three-point (a), five-point (b), ten-point (c), and twenty-point (d) moving averages of the *C. quinquecirrha* abundance in 2006 as measured by visual count (blue) and vertical net haul (black).
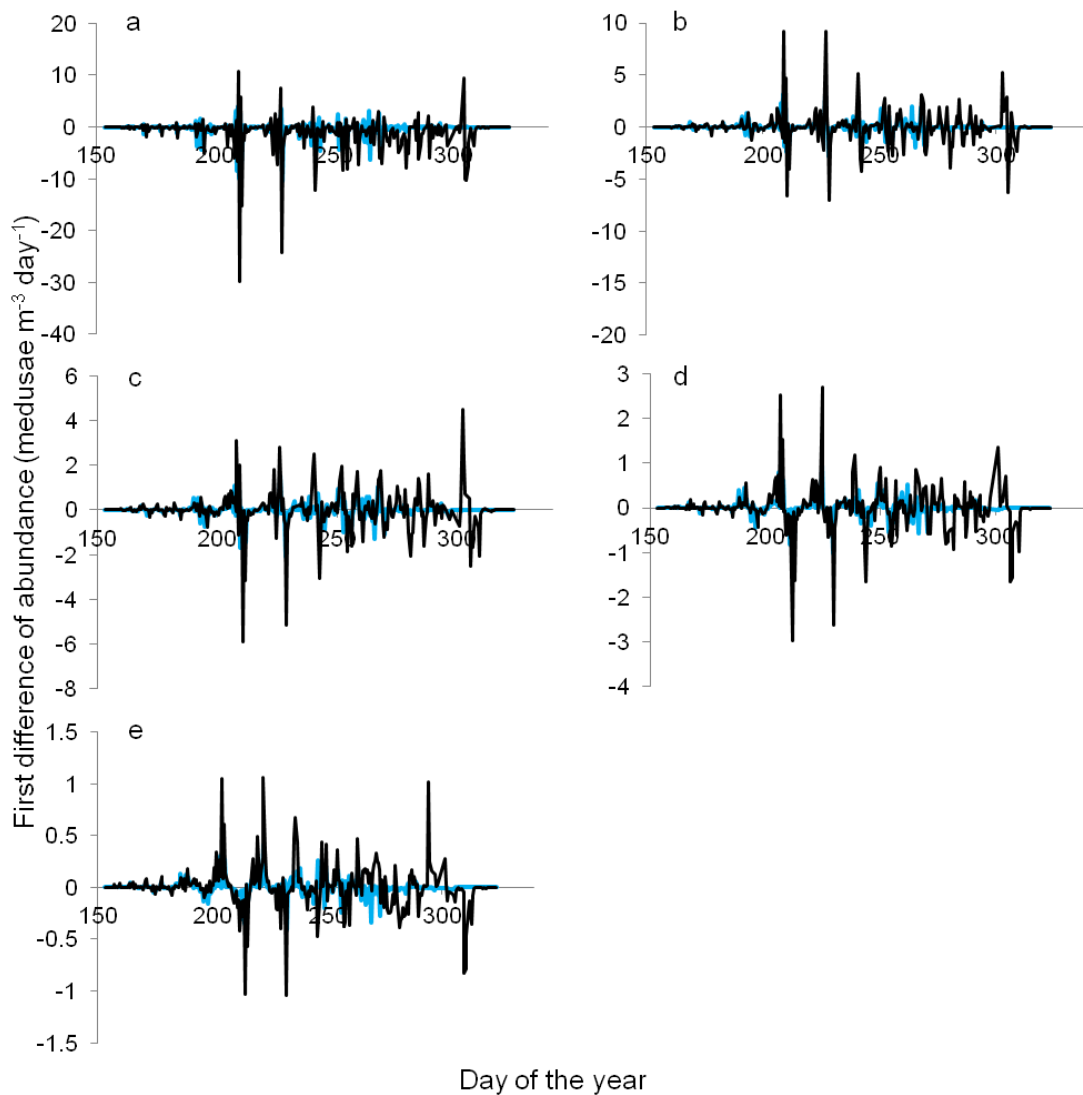
Figure 2.3: First difference of *C. quinquecirrha* abundance in 2006 as measured by visual counts (blue) and vertical net haul (black) with no smoothing (a), and as 3-point (b), 5-point (c), 10-point (d), and 20-point (e) moving averages.
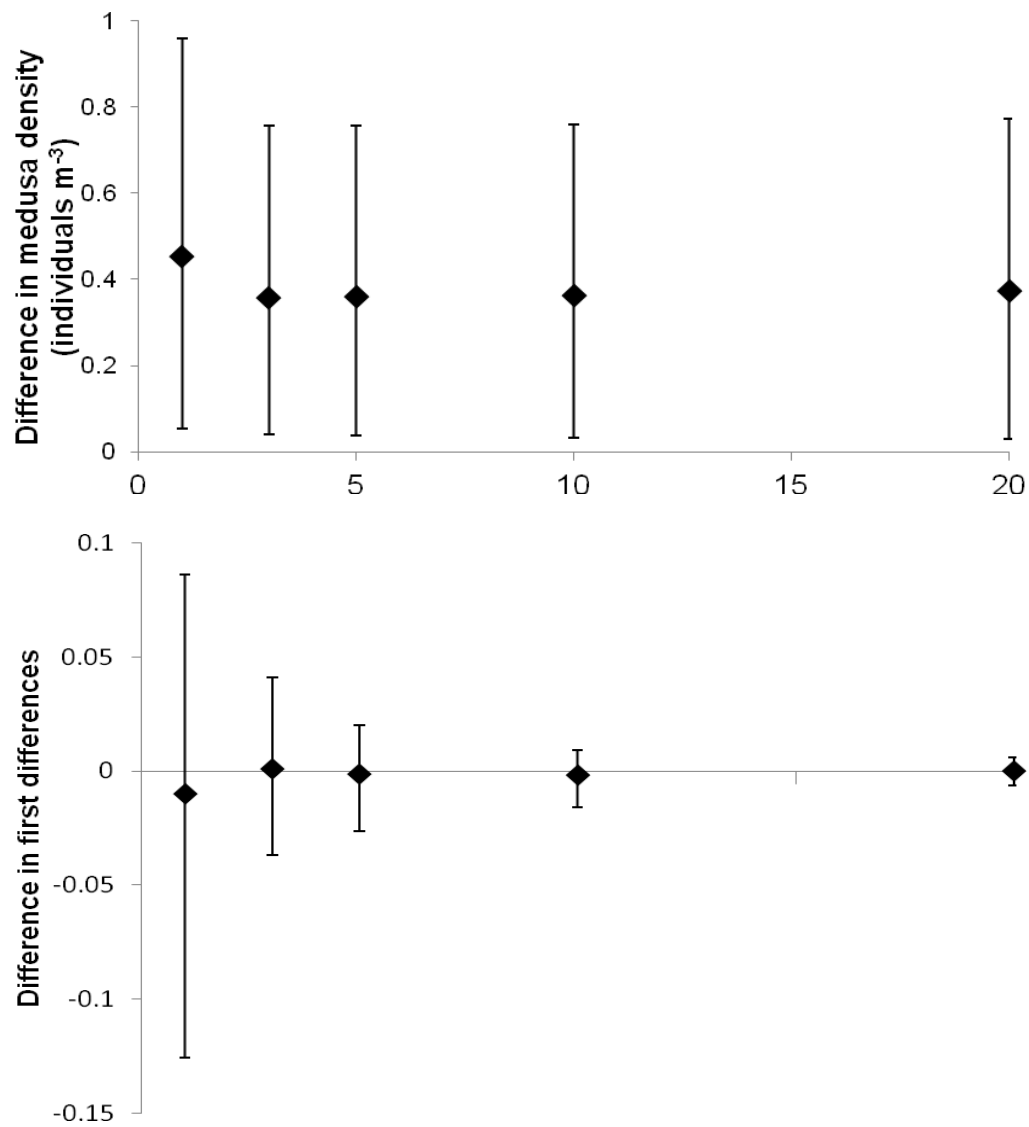
Figure 2.4: Mean difference in first difference of *C. quinquecirrha* medusa abundance as measured by visual count and vertical net haul (a), and mean difference in *C. quinquecirrha* medusa abundance as measured by visual count and vertical net haul (b). Error bars represent 95% confidence interval of the mean.
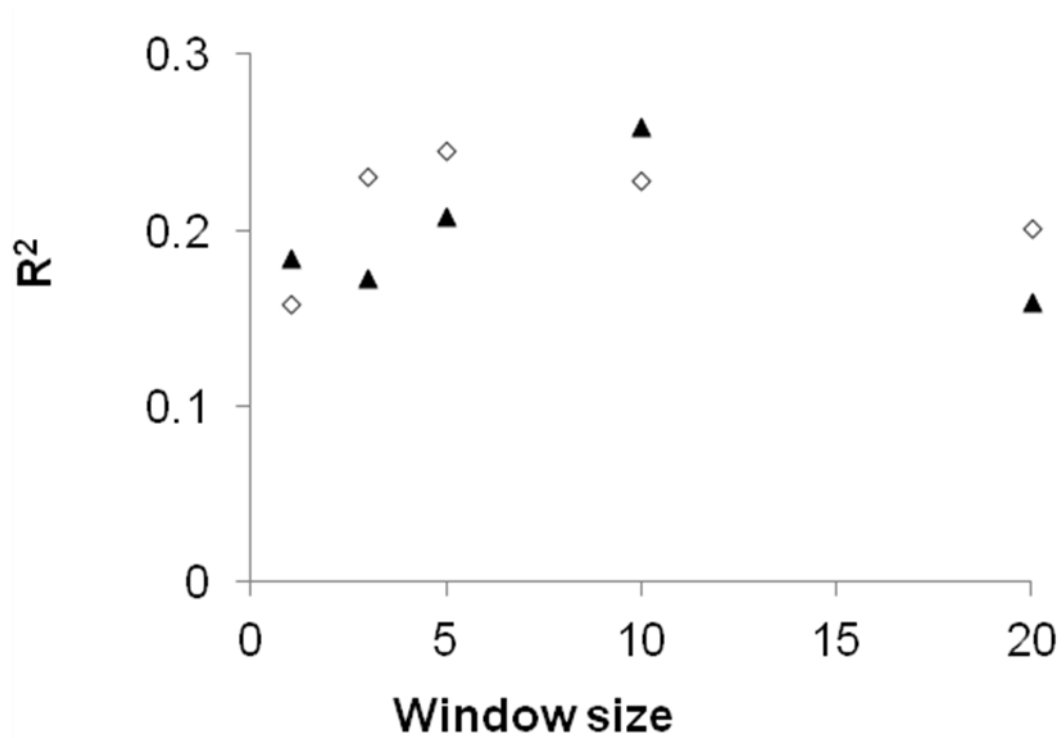
Figure 2.5: r^2 values for least squares linear regression calculated for the relationship between *C. quinquecirrha* abundance as measured by visual counts and vertical net hauls (◊) and the relationship between the first differences of abundance as measured by the same two methods (▲) at varying moving average window sizes.
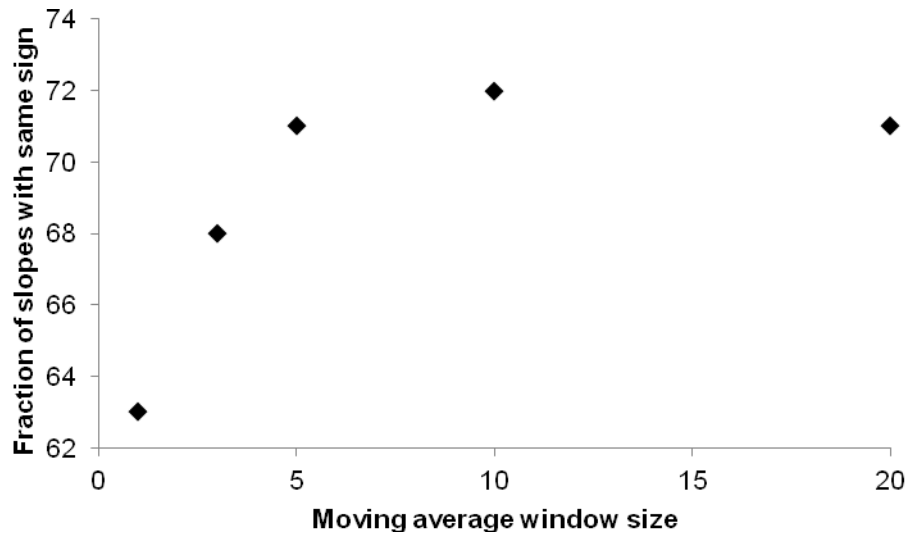
Figure 2.6: Percentage of observations at which the first difference of the time series of visual counts and the first difference of the time series of vertical net hauls have the same sign at varying moving average window size.

Chapter 3: Inter-annual variability: factors that influence the timing of appearance and disappearance, and timing and intensity of bloom

Abstract

With the increasing attention on climate change and other types of anthropogenic alteration of estuarine systems, it is important to understand the factors that determine the timing and intensity of gelatinous zooplankton blooms in order to understand how ecosystem changes may affect these populations. Because *Chyrsaora quinquecirrha* is a dominant predator and considered a nuisance in Chesapeake Bay, it is desirable to be able to make predictions about the characteristics of the annual bloom. Cargo and King (1990) used streamflow during the first six months of the year to predict July-August abundance, which is treated as an index of the size of the population for the entire season; however, they only address one characteristic of the annual bloom. Here, several indices are used to describe the annual jellyfish bloom using the Patuxent River time series described by Cargo and King (1990) as well as a new time series of visual counts on the Choptank River, Cambridge, Maryland, USA from 2005-2010. Indices include the day of first appearance, day of peak abundance, day last observed, and magnitude of the peak abundance of *C. quinquecirrha*. Each index is examined for relationships with environmental conditions including temperature, salinity, streamflow, and NAOI as well as with each other to determine which variables affect each characteristic of the annual bloom. Existing models from Cargo and King (1990), Breitburg and Fulford (2006), and Decker et al. (2007) that predict medusa abundance based on environmental factors are applied to the Choptank River time series.

56

Introduction

An apparent increase in the frequency with which jellyfish blooms impact

human activities in recent decades has fueled efforts to understand how

environmental conditions influence jellyfish populations (reviewed in Purcell et al.

2007). As a result of these efforts, several examples of fluctuations in jellyfish

abundance have been attributed to environmental conditions, particularly temperature

and salinity or the climatic patters that affect them (reviewed by Purcell 2005). For

example, Lynam et al. (2005a) identified an inverse relationship between abundance

of three species of medusa in the North Sea and the North Atlantic Oscillation.

Similarly, Brodeur et al. (1999) showed that high abundance of several species of

medusae in the Bering Sea coincided with periods of high values of the North Pacific

Index, higher summer sea surface temperature, and greater area of sea ice. Both

studies suggested that these fluctuations in medusa abundance may have been caused

by the effects of temperature on strobilation, differences in prey availability under

different climatic conditions, or both. Lynam et al. (2005a) propose that a late spring

phytoplankton bloom and the associated increase in zooplankton abundance that

occur under low North Atlantic Oscillation Index (NAOI) in the North Sea coincide

with strobilation and growth of ephyrae, resulting in greater medusa abundance under

these conditions. Brodeur et al. (1999) hypothesized that an earlier spring bloom

associated with a greater area of sea ice may represent an important resource for

ephyra prey in this region. Further studies of the medusae in both of these locations

indicate that the medusae may also exert top-down effects on the trophic structure of

their communities. Lynam et al. (2005b) proposes several mechanisms to explain the

decrease in abundance of herring associated with high medusa abundance. These mechanisms include competition for zooplankton prey as well as predation on larval herring. Brodeur et al., (2002) showed that grazing by the dominant medusa species in the Bering Sea, *Chrysaora melanaster*, reduced zooplankton abundance.

With the increasing attention on climate change and other types of anthropogenic alterations of ecosystems, phenology of a variety of organisms from commercially fished species to song birds have also received increasing attention (Cushing 1990, Stenseth and Mysterud 2002). Cushing's match-mismatch hypothesis suggests that the reproductive success of a population may depend on synchronizing important events in its life history with those of its prey (1990). While the match-mismatch hypothesis has been shown to be a small part of the story of cod recruitment, it is still part of that story and has been applied to many other organisms (Houde 2008; Stenseth et al. 2002), and it follows that changes in synchrony between important developmental events of a population, such as the onset of a bloom, and those of its prey populations may have significant effects on trophic dynamics of a system.

Jellyfish frequently appear in high densities that can affect the composition of their communities through predation and competition (Purcell 1997). *C. quinquecirrha* medusae are in a position to be involved in such trophic changes because they are voracious predators that impact the populations of their prey (Feigenbaum and Kelly 1984; Purcell 1992; Cowan and Houde 1993). Because *Chyrsaora quinquecirrha* is a voracious predator and considered a nuisance to recreational and fishing activities in the mesohaline portion of Chesapeake Bay and

its tributaries, it is desirable to be able to make predictions about their population size and distribution. There is considerable variability in both the timing and intensity of the seasonal *C. quinquecirrha* medusa bloom. There have been several efforts to understand the sources of this variability in order to predict when and where high abundances of medusae are likely to be present. First, Cargo and King (1990) used streamflow during the first six months of the year to predict July-August abundance, which is treated as an index of the size of the population for the entire season. However, since the timing of the bloom varies from year to year, it may be more useful to consider the magnitude at maximum abundance. Breitburg and Fulford (2006) showed that when a four-week mean around the peak in medusa abundance was used as the measure of abundance in the Cargo and King (1990) model, streamflow explained less of the variability in medusa abundance. Decker et al. (2007), on the other hand, used modeled temperature and salinity values to make daily nowcasts of the likelihood of occurrence of medusae at any location in the bay by determining where optimal conditions are occurring.

In order to understand how jellyfish blooms may affect the trophic structure of their community, it is necessary to understand how environmental factors influence the timing of their blooms. *C. quinquecirrha* has a seasonal life cycle that is strongly dependent on environmental cues (Cargo and Rabenold 1980) and is often found in highly impacted estuarine environments. Understanding their phenology will be an important step in understanding how climate and other environmental changes may affect the trophic structure of estuarine environments as well as enhancing the ability

59

to make predictions about the characteristics of the seasonal bloom in order to mitigate the negative effects on human activities.

This study attempts to address variability in several characteristics of the sea nettle bloom focusing on phenology, or the timing of biological events and their environmental cues. Specifically, it addresses the following hypotheses:

1. Timing of first appearance, disappearance, and peak abundance of medusae as well as the magnitude of the peak are related to temperature, salinity, streamflow, and NAOI.

2. These relationships are the same or similar at different locations on Chesapeake Bay.

3. Models of medusa abundance based on environmental conditions that have been previously developed using visual counts of medusae on the Patuxent River (Cargo and King 1990; Breitburg and Fulford 2006; Decker et al. 2007), will be similarly effective at predicting medusa abundance on the Choptank River.

Methods

Indices of the annual medusa bloom, including timing of first appearance, timing of the annual peak, magnitude of the peak, and timing of disappearance were identified from a time series of weekly mean visual counts of medusa made at the Chesapeake Biological Laboratory in Solomons, Maryland, USA from 1960 to 1995. Average July-August counts from 1960 to 1986 from this series and mean monthly streamflow for Chesapeake Bay over the first six months of each year are published in Cargo & King (1990). Counts were made by D. G. Cargo with assistance from M.

Wiley and H. Millsap until 1991. Wiley continued the counts in 1992 and 1993, and Millsap continued them in 1994 and 1995. Water temperature and salinity were also measured at the time of each count.

A second time series of visual counts consists of observations made twice daily over a 183 m^2 area on the south east side of the pier at the Horn Point Laboratory, Cambridge, Maryland, USA on the south side of the Choptank River (38° 35.610' N, 76° 7.725' W) from 2005 to 2010. Water temperature and salinity were also measured at the time of each of these observations. Counts were suspended at the end of each season when no medusae had been seen in the transect or the surrounding area for ten consecutive days. A five point moving average of this time series (as described in Chapter 2) was used to identify the timing of first appearance, timing of the annual peak, magnitude of the peak, and timing of disappearance. Mean monthly streamflow for the first six months of each year in this time series was downloaded from the United States Geological Survey website (http://md.water.usgs.gov/waterdata/chesinflow/data/monthly). Average North Atlantic Oscillation Index (NAOI) for December to March for each year of both time series was downloaded from the National Oceanic and Atmospheric Administration Climate Prediction Center website (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml).

Temperatures and salinities measured as part of the two time series were averaged over one, three, and six month periods. These averaged temperatures and salinities, as well as the average temperature and salinity measured in the first week of May, the average streamflow for January to June for the entire Chesapeake Bay,

and the average NAOI for December to March for each year were examined using least squares linear regression (Sokal and Rohlf 1995) in order to identify relationships between these environmental variables and the indices that describe the annual medusa bloom on the Patuxent River. The indices were also examined for relationships with one another in order to determine, for example, how time of medusa disappearance is related to the time of the peak and the time of first appearance. The regression analysis was repeated for the indices on the Choptank River in order to compare the relationships between the timing and magnitude of the bloom and the environmental variables in two different locations.

Finally, patterns in the Choptank River time series were compared to the patterns described by existing models that predict medusa abundance based on environmental conditions in order to determine how these models apply at this location. Average July-August abundance and the four-week mean around the peak in medusa abundance were calculated from the time series of visual counts to correspond to the measures of medusa abundance used by Cargo and King (1990) and Breitburg and Fulford (2006) respectively. Least squares regression models were calculated to describe the relationship between the log of average July-August abundance and January-June streamflow. Similarly, a regression model was also calculated to describe the relationship between four-week mean peak abundance and December-March NAOI. Where statistically significant relationships existed, analysis of covariance (ANCOVA; Sokal and Rohlf 1995) was used to compare the slopes and intercepts to those reported for existing models. The five-point moving averages of temperature and salinity measured at the time of medusa counts were used to

calculated the probability of occurrence of medusa as described by Decker et al. (2007). Temperature and salinity measurements made by the Horn Point Oyster Hatchery were used to extend the predicted probability of occurrence beyond the date when medusa counts and concurrent temperature and salinity measurements stopped each season. Probability of occurrence was then compared to the five-point moving average of medusa abundance using least squares linear regression, and ANCOVA was used to identify significant differences between the relationships for each year.

Results

Based on the time series of visual counts made on the Patuxent River, Maryland, USA, timing of first appearance, peak abundance, and disappearance varied widely from year to year (Fig. 3.1 and 3.2). The date of first appearance ranged from day 136 to day 226, with median of day 163 (June 12), date of peak abundance ranged from day 193 to day 295, with median of day 234 (August 22), and date of disappearance ranged from day 230 to day 341, with median of day 311 (November 7). Similarly, the magnitude of the peak medusae abundance ranged from only 5 medusae per 1000 m^2 to 2227 medusa per 1000 m^2 (Fig. 3.2).

Several significant relationships were identified between the indices of the annual medusa bloom and the environmental variables considered (Table 3.1, Fig. 3.3). The timing of the first medusae appearance was most strongly related to January to June streamflow ($r^2 = 0.5693$, $p < 0.05$), but had significant relationships with salinity and temperature in the early part of the year and the NAOI in December to March. Timing of peak medusa abundance was also most strongly related to January

63

to June streamflow ($r^2 = 0.3189$, $p < 0.05$), but had significant relationships with salinity and temperature in the spring. Salinity showed a significant relationship with streamflow (r2 = 0.5400, $p < 0.05$). Magnitude of the peak was most strongly related to December to March NAOI ($r^2 = 0.2408$, $p < 0.05$), January to June streamflow ($r^2 = 0.2367$, $p < 0.05$), and date of first appearance ($r^2 = 0.2023$, $p < 0.05$). The magnitude of the peak in medusa abundance also showed weaker, but significant relationships with temperature and salinity in January. Finally, the date of disappearance of medusa was most strongly related to the timing of the peak in medusa abundance ($r^2 = 0.2729$, $p < 0.05$), but was also related to temperature in spring and salinity in November.

None of the indices from the Choptank River time series showed any significant relationships with any of the environmental variables ($p = 0.1421$-0.9002). This is likely due to the small sample size of only six years. Although the relationships were not significant, the slopes of the regression lines had the same signs as those for the regression lines of significant relationships between the indices and environmental factors on the Patuxent River (Table 3.1).

When compared with the relationship between July-August abundance and January to June streamflow on the Patuxent River from 1960 to 1986 reported by Cargo and King (1990), the July-August medusa abundance on the Choptank River from 2005 to 2010 showed a similar relationship (Figure 3.4). Both data sets have a strong negative relationshop with streamflow for the entire Chesapeake Bay; however, the slopes to the two regression lines are significantly different from one

another (ANCOVA, $p < 0.0001$), and the relationship explains 17% more of the variability in medusa abundance on the Choptank River than on the Patuxent.

The relationship between the four-Week mean peak of medusa abundance and the December to March NAOI of the Choptank River time series is not statistically significant (Fig. 3.5). The slope of the regression line is positive, like that of the Patuxent River time series over the time period of 1990 to 2005 as reported by Breitburg and Fulford (2006), but because the relationship is not significant, a direct comparison cannot be made.

In general, the probability of occurrence of medusae as calculated using the model from Decker et al. (2007) and the five-point moving average of medusa abundance both show a pattern of increase during the late spring and early summer, peak in midsummer, and decline in fall (Fig. 3.6). However, in years with early disappearances (2007-2010; Fig. 3.6 c-f), defined as years when medusae disappeared before temperatures began to approach 15°C and most of the medusae were observed with no oral arms shortly before the medusae disappeared from the river (see Appendix 1), probability of occurrence remained high at the time of medusa disappearance. Least squares linear regression showed that there was a significant relationship between probability of occurrence and observed abundance ($p < 0.05$; Fig. 3.7), but that the slope of that relationship for each year was significantly different from all other years (ANCOVA, $p < 0.001$). Years with the highest total abundance of medusae (2005, 2006, and 2009; Fig. 3.6 a,b, and e) also have the highest r^2 values and lowest slopes of the relationship between probability of occurrence and medusa abundance.

Discussion

The significant relationships between temperature, salinity, and streamflow and the timing and magnitude of the *C. quinquecirrha* medusa bloom are generally in agreement with the conventional wisdom that higher temperature, relatively higher salinity within the mesohaline range, and low streamflow provide the optimal conditions for medusae. Despite a strong relationship between streamflow and salinity, variability in streamflow during the first half of the year explains more of the variability in timing of first appearance, timing of the peak, and magnitude of the peak than salinity averaged over any time period. This is likely because the measure of streamflow used here is the total Chesapeake Bay streamflow, which is a spatially integrated measure that reflects conditions through the entire range of the *C. quinquecirrha* population rather than the local conditions measured at one location and experienced by only a small part of the population.

Although temperature and salinity in all time periods explain relatively little of the total variability in medusa abundance, examination of these relationships still offers some insight into the progression of the annual bloom. When temperatures and salinities are higher, especially between January and June, the three benchmarks of the medusa bloom, appearance, peak, and disappearance, tend to happen earlier as indicated by a negative slope of the regression model, and the magnitude of the peak tends to be higher as indicated by a positive slope of the regression model (Table 3.1). However, there are some exceptions. For example, date of first appearance shows a weak positive relationship with temperature in January but a weak negative

66

relationship with salinity at the same time. Similarly, the magnitude of the peak has a negative relationship with temperature in January while also exhibiting a positive relationship with salinity during that month. Finally, timing of the peak showed a positive relationship with salinity in April and May, but a stronger relationship with salinity in the first Week of May. These differences from the expected direction of the slope of the regression models are likely due to the fact that excystment of the polyps and strobilation are cued by both temperature and salinity (Cargo and Schultz 1967; Purcell et al. 1999).

Among the strongest influences on the timing of the peak in medusa abundance and the timing of disappearance is the timing of the previous benchmark of the season. Timing of first appearance explains 28% of the variability in the timing of the peak, while timing of the peak explains 27% of the variability in the timing of disappearance. Additionally, all of the indices of the timing of the bloom have similar ranges (Fig. 3.1). This suggests that although environmental variables are responsible for providing the cue for the first strobilation, the progression of the bloom depends strongly on the lifecycle of *C. quinquecirrha*. The current conceptual model of the annual *C. quinquecirrha* bloom suggested by Decker et al. (2007) relies entirely on the relationship between medusa abundance and temperature and salinity. These results indicate that the conceptual model of the bloom could be improved by incorporating environmental factors and the important aspects of the organism's lifecycle, such as rates of strobilation or ephyra growth. This information may allow for prediction of the timing of the peak or disappearance of medusae for a season based on the date of first appearance.

The negative relationship between the magnitude of the peak and the date of first appearance indicates that when strobilation starts later in the year, the magnitude of the peak is lower (Fig. 3.3). A laboratory experiment by Purcell et al. (1999) shows that low temperature delays strobilation, but does not reduce total production, but that ephyra production does depend on food availability. According to Roman et al. (2005), maximum zooplankton biomass in Chesapeake Bay occurs in the spring and decreases by mid-summer. Therefore, it is possible that when strobilation begins later in the year, the polyps miss the peak in zooplankton abundance, which limits ephyra production and leads to a lower magnitude of the peak. This pattern would constitute a mismatch under Cushing's (1990) match/mismatch hypothesis where changes in the phenology of a species due to environmental conditions may cause it to fail to coincide in time with its prey. Furthermore, such a mismatch may have greater implications for the community. According to Feigenbaum and Kelly (1984), high medusa populations are linked to increased secondary production by copepods because medusae control ctenophore populations. Low abundances of medusae caused by this type of mismatch may lead to increased competition for mesozooplankton by ctenophores.

Cargo and King (1990) show that streamflow in the first six months of the year had a strong influence on July-August medusa abundance ($r^2 = 0.57$, $p < 0.01$), but Breitburg and Fulford (2006) showed that streamflow had a much weaker influence on the mean four-week peak of medusa abundance ($r^2 = 0.18$, $p = 0.03$). Since the median day of the peak in abundance is on August 22 (day 234), abundance in July and August is not a good measure of the peak abundance, but may be a better

indicator of the progress of the bloom. In other words, if July-August abundance is particularly high, it is likely that the date of first appearance and date of the peak in medusa abundance is also quite early. Taken together, the two studies indicate that streamflow influences the timing of the bloom more than its magnitude. The results of this study using the same Patuxent River time series are in agreement, with a stronger relationship between the timing of first appearance and timing of the peak in medusa abundance than on the magnitude of the peak (Table 3.1). The Choptank River time series shows a similar, but stronger relationship between July-August medusa abundance and streamflow in the first six months of the year ($r^2 = 0.74$, $p = 0.03$). The total streamflow of Chesapeake Bay explains 17% more of the variability in medusa abundance on the Choptank River than on the Patuxent River, likely because of the different characteristics of the two tributaries. The Choptank River is relatively more open to the mainstem of Chesapeake Bay and has lower flow than the Patuxent River (Fisher et al. 2006); therefore it is likely that total Chesapeake Bay flow influences conditions at the Choptank River study site more strongly than the Patuxent River location, and it is not surprising that the Choptank River medusa bloom is also more strongly influenced by Chesapeake Bay streamflow.

In addition to the impact of streamflow, Breitburg and Fulford (2006) address the relationship between medusa abundance and the NAOI. They suggest that the relationship between the NAOI from December to March had a negative relationship with four-week mean peak in medusa abundance before 1986, but a positive relationship with medusa abundance after 1990. Examination of the Choptank River time series for a similar pattern is inconclusive. While the relationship has a positive

69

slope like that of the 1990-2005 time period on the Patuxent River, the relationship is not statistically significant ($r^2 = 0.1387$, $p = 0.4833$; Fig. 3.4), likely due to the small sample size (n = 6). This distribution appears to contain an outlier that drives the regression. While the removal of this outlier would dramatically change the trend and increase the amount of variability explained by the relationship, I have chosen not to remove it on the grounds that neither the NAOI nor the observed medusa abundance was outside of the range observed by Breitburg and Fulford (2006). More data is needed to determine whether this point truly represents an unusual occurrence on the Choptank River. A more conclusive result may be obtained if the Choptank River time series is continued for several more years.

The comparison between the probability of occurrence of medusae based on the Decker et al. (2007) model and observed medusa abundance on the Choptank River lend some insight into when this model is most effective and when factors other than temperature and salinity are more important. The modeled probabilities of occurrence explained between 10% and 37% of the variability in observed abundance. It should be noted that the Decker et al. (2007) model was developed using medusa abundance data from the mainstem of Chesapeake Bay, but the observations reported here come from one tributary. This difference in location may be responsible for the low proportion of the variability that is explained. However, the differences in explained variability between years suggests that factors other than temperature and salinity may be more important in some years than others. Years when the modeled probability of occurrence explains the most variability in medusa abundance are characterized by high abundances sustained over long periods of time

70

while years when the modeled probability explains less of the variability in medusa abundance are characterized by lower abundance sustained over shorter time periods (Figs. 3.6 and 3.7). This suggests that in those years with lower abundance and shorter duration, some factor other than the temperature and salinity conditions considered by the model are responsible for the low abundance. As with the negative relationship between the magnitude of the peak in medusa abundance and the timing of the first appearance, it seems likely that the factor involved here is related to *C. quinquecirrha's* polyp stage, since reduced ephyra production by the polyps would result in lower abundance of medusae. A reduction in ephyra production would occur if delayed onset of strobilation shortens the window of time in which ephyra production occurs, or if conditions at the time of a late strobilation are not as advantageous for ephyra production or survival as an early strobilation. One possible cause of decreased ephyra production by the polyps is low food availability as suggested by Purcell et al. (1999). Their experiment showed that under low food conditions, the number of ephyrae produced per polyp was reduced. A later onset of strobilation is more likely to miss the high zooplankton abundance that follows the spring phytoplankton bloom (Roman et al., 2005), and therefore result in lower medusa abundance, as discussed above. A second possibility is low dissolved oxygen. Condon et al. (2001) illustrated that while polyps are able to survive and even strobilate at extremely low dissolved oxygen concentrations, the proportion of the polyp population strobilating decreases with decreasing dissolved oxygen, which would imply a lower total supply of medusae. For example, if strobilation is delayed, it is more likely to coincide with the low oxygen conditions that can occur, even in

shallow coastal areas, during the summer months (Breitburg 1990). Under these conditions, fewer polyps are likely to strobilate, resulting in a lower abundance of medusae. Finally, later strobilation may represent a better match with a predator population. For example, a later strobilation may coincide with higher ctenophore abundance, which may lead to significant predation on ephyrae.

Another time when the discrepancy between the modeled probability of occurrence of medusae based on the Decker et al. (2007) model and the observed abundance suggests that other factors are influencing abundance is at the end of the season. Decker et al. (2007) observed that in 2002, model predictions remained high after observed medusa abundance decreased in both the Choptank and Patuxent Rivers. Agreement between the model predictions and observations of medusa abundance varied for the years addressed in this study. In 2005 and 2006, the decrease in probability of occurrence at the end of the season coincides well with the timing of the decrease in medusae abundance. In each of these years, disappearance coincided with the decrease in temperature to 10 °C, which is the lower limit of the medusae's temperature tolerance (Gatz et al. 1973). In 2006-2010, on the other hand, predicted probability of occurrence remains high at the time of medusa disappearance. In each of these four years, the majority of the medusa population was observed to have lost their oral arms approximately two weeks before they disappeared. Several mechanisms of this oral arm loss and early disappearance have been hypothesized in Sexton et al. (2010). These include starvation, senescence, predation, and disease as sources of mortality. Since these sources of mortality are not

dependent on temperature, they would not be reflected in the predictions made by the Decker et al. (2007) model.

Previous work by Decker et al (2007) identified temperature and salinity as factors that contribute to the probability of occurrence of *C. quinquecirrha* medusae, and Cargo and King (1990) linked summer abundance of medusae to streamflow in the first half of the year. Together, those studies suggest a conceptual model of the annual bloom in which timing of the annual bloom is primarily influenced by temperature, and magnitude and location of the bloom is primarily influenced by salinity. The results presented here confirm these relationships between environmental conditions and magnitude of the bloom, elaborate on the relationships between environmental conditions and the timing of the bloom, and suggest that timing of first appearance, peak abundance, and disappearance of medusae are also related to strobilation and mortality. Therefore, understanding and improving predictability of the annual bloom requires further examination of the variables that control supply of medusae through strobilation and those that contribute to mortality of medusae. A new conceptual model should include population dynamics in addition to environmental factors.

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Tables

Table 3.1: r^2 values and sign of the slope from regression analysis of the timing of first appearance, disappearance, and peak abundance of medusae from visual counts made at the Chesapeake Biological Laboratory on the Patuxent River from 1960 to 1995 versus environmental variables. In cases where no value is present, the relationship was not significant ($p > .10$). Bold values represent relationships with $p < 0.05$. Relationships that are not aplicable are labeled n/a.

Environmental variable		Appearance	Peak	Magnitude	Disappearance
Salinity	**Jan**	0.1063(-)		0.0849(+)	
	Feb	**0.1391(-)**			
	Mar				
	Apr		**0.1248(+)**		
	May	0.0947(-)	**0.1115(+)**		
	Jun	0.0939(-)			
	Jul	n/a			
	Aug	n/a			
	Sept	n/a			
	Oct	n/a	n/a	n/a	
	Nov	n/a	n/a	n/a	**0.1275(-)**
	Dec	n/a	n/a	n/a	
	Jan-Mar	**0.1432(-)**		0.09633(+)	
	Apr-Jun	0.0637(-)	0.0989(+)		
	Jan-Jun	**0.1978(-)**			
	First Week in May	**0.2022(-)**	**0.1921(-)**		0.1043(-)
Temperature	**Jan**	0.0907(+)		0.1057(-)	
	Feb				
	Mar				
	Apr	0.116(-)			**0.1281(-)**
	May				**0.1512(-)**
	Jun				**0.1417(-)**
	Jul	n/a			
	Aug	n/a			
	Sept	n/a			
	Oct	n/a	n/a	n/a	
	Nov	n/a	n/a	n/a	
	Dec	n/a	n/a	n/a	
	Jan-Mar			0.09605(-)	
	Apr-Jun				**0.1758(-)**
	July-Sept	n/a			
	First Week in May		**0.1769(-)**		0.107(-)
Date of	**First appearance**	n/a	**0.2784(+)**	**0.2003(-)**	
	Peak abundance		n/a		**0.2729(+)**
Streamflow		**0.5693(+)**	**0.3189(+)**	**0.2367(-)**	
Dec-Mar NAOI		**0.1896(+)**		**0.2408(-)**	

Figures
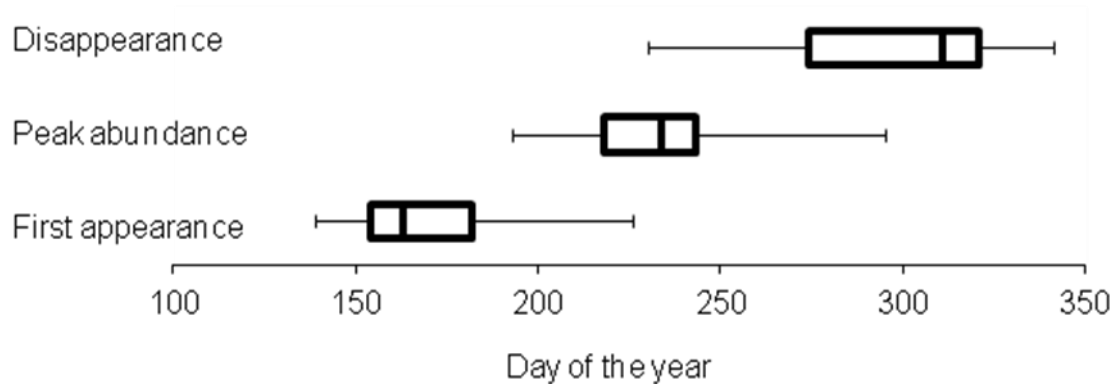
Figure 3.1: Box plots representing first quartile, median, and third quartile of the timing of medusa appearance, peak abundance and disappearance based on data collected by D. Cargo, M. Wiley, and H. Millsap at the Chesapeak Biological Laboratory pier in on the Patuxent River, Solomons, Maryland from 1960-1995. Whiskers represent minimum and maximum values.
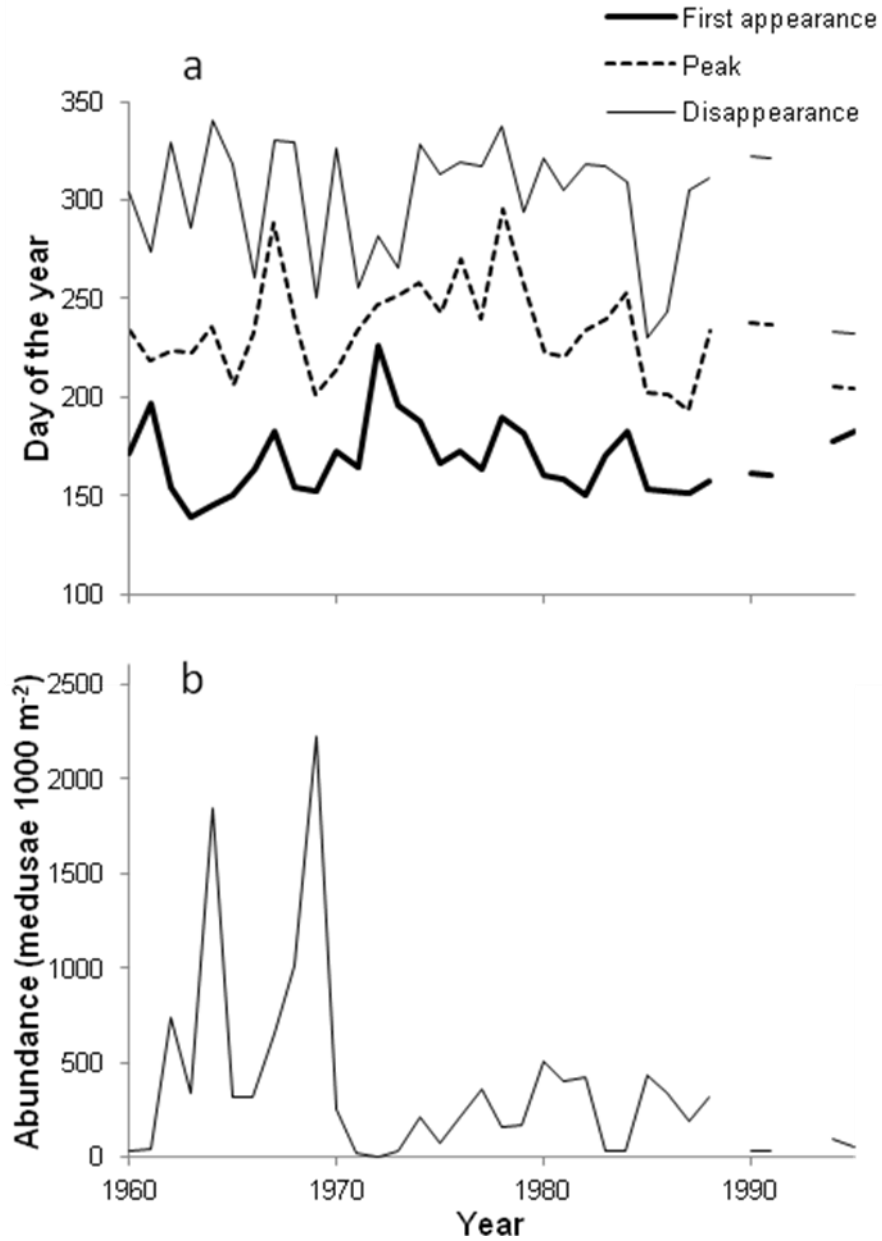
Figure 3.2: Time series of the timing of annual first appearance, peak abundance,

disappearance (a), and magnitude of peak abundance (b) based on data collected by

D. Cargo, M. Wiley, and H. Millsap at the Chesapeak Biological Laboratory pier in

on the Patuxent River, Solomons, Maryland from 1960-1995.
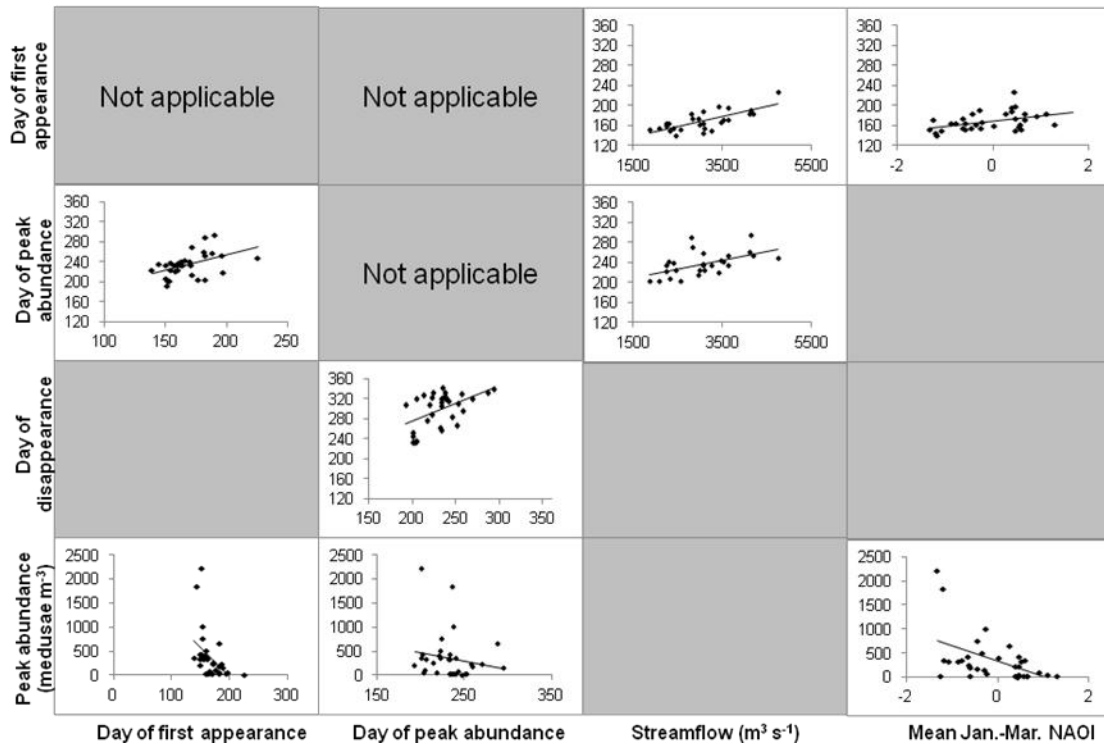
Figure 3.3: Significant relationships among the descriptive indices of the *C. quinquecirrha* medusa season and between the indices and environmental conditions on the Patuxent River from 1960-1995 ($p < 0.05$). Where no plot is present (grey boxes), the relation was not significant. Streamflow indicates total Chesapeake Bay streamflow from January through June of each year.
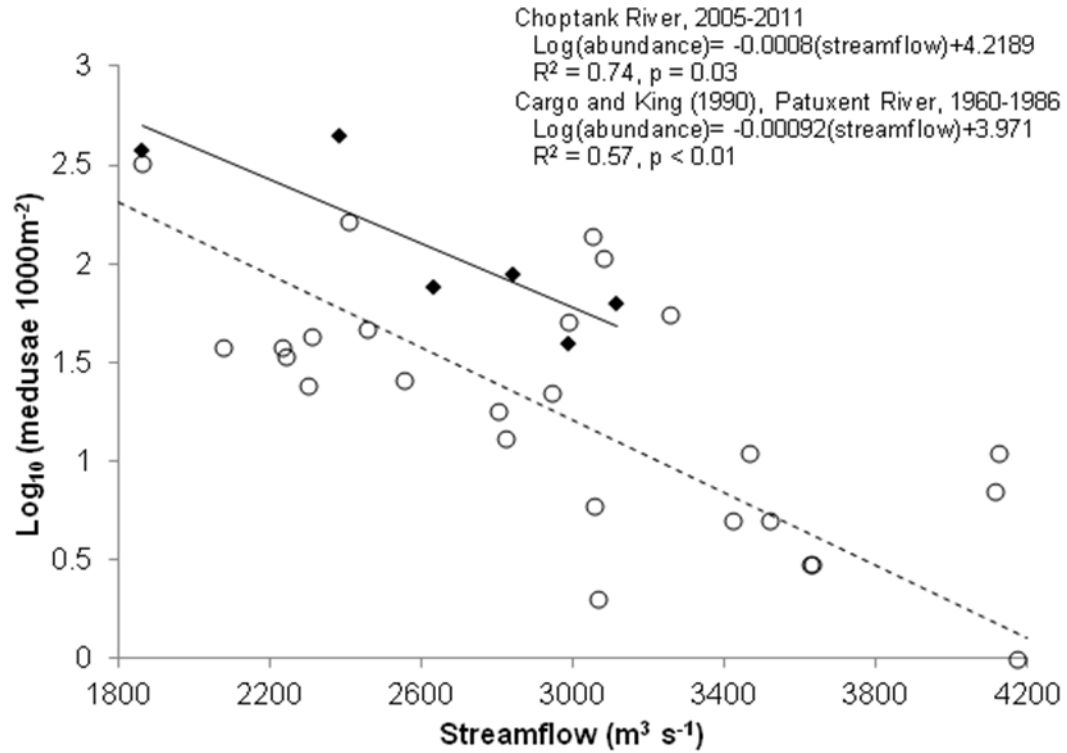
Figure 3.4: Log of mean July-August medusa abundance on the Choptank River from 2005 to 2010 (■) and Patuxent River from 1980-1986 (○) plotted with respect to mean of monthly streamflow for Chesapeake Bay in the first six months of the year and least squares regression lines of the relationship between medusa abundance and stream flow in this study (solid) and Cargo and King (1990).
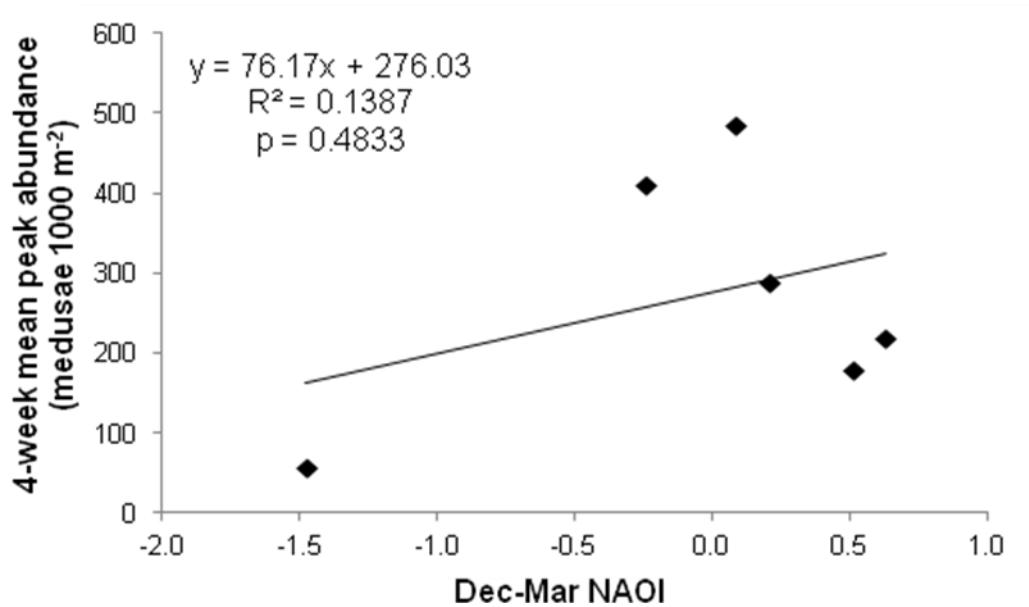
Figure 3.5: The annual four-week mean of the peak in medusa abundance on the

Choptank River, Cambridge, Maryland from 2005-2010 plotted with respect to the

NAOI for the preceding December through March.
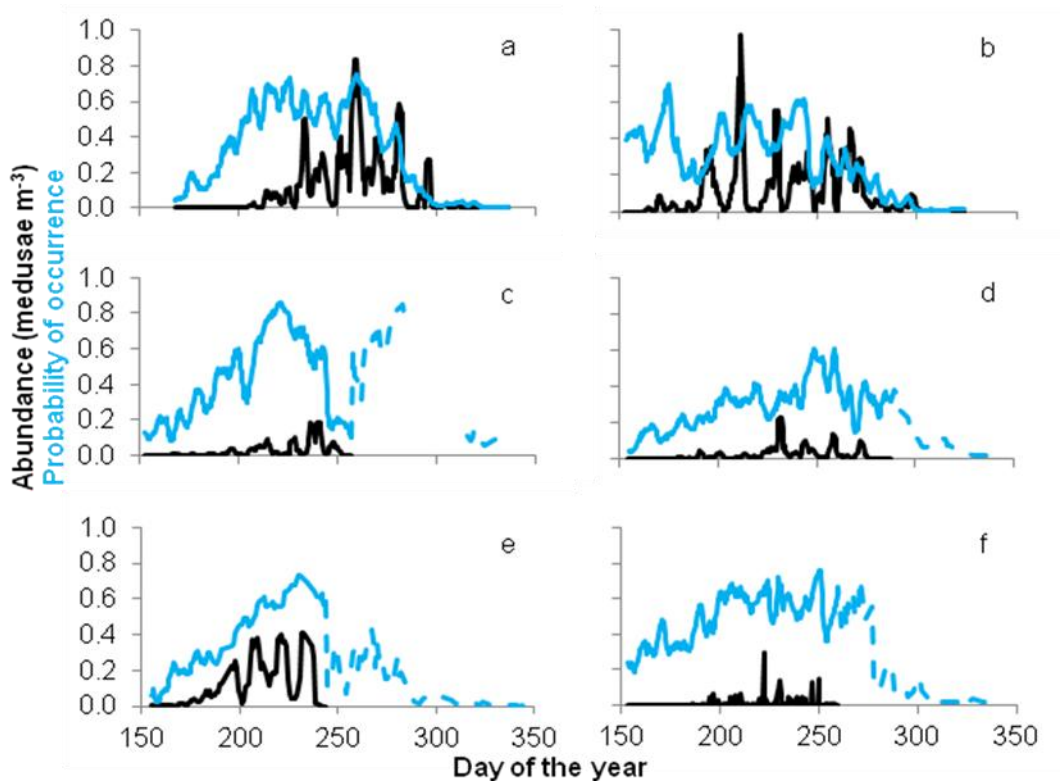
Figure 3.6: Time series of the five point moving average of medusa abundance as measured by visual counts on the Choptank River, Cambridge, Maryland (black) and the probability of occurrence of medusae calculated as described in Decker et al. (2007) using temperature and salinity measurements made at the same time as each visual observation (blue) for 2005 (a), 2006 (b), 2007 (c), 2008 (d), 2009 (e), and 2010 (f). Where available, temperature and salinity measured by the Horn Point Laboratory Oyster Hatchery is used to calculate probability of occurrence of medusae after medusae disappeared (dashed).
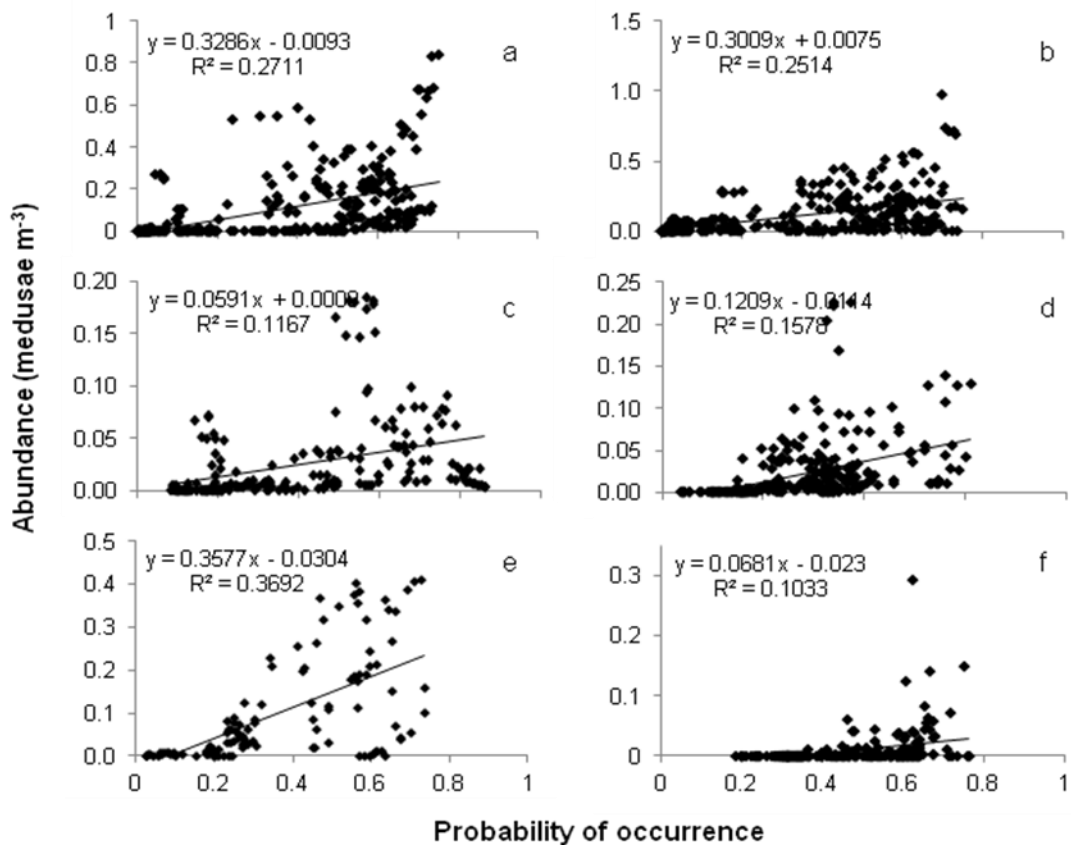
Figure 3.7: Medusa abundance as measured by visual counts on the Choptank River, Cambridge, Maryland versus the probability of occurrence of medusae calculated as described in Decker et al. (2007) using temperature and salinity measurements made at the same time as each visual observation in 2005 (a), 2006 (b), 2007 (c), 2008 (d), 2009 (e), and 2010 (f). All regression equations are statistically significant with $p <$ 0.01.

Chapter 4: Identification and characterization of intra-annual variability in medusa abundance

Abstract

Medusae of the scyphozoan *Chrysaora quinquecirrha* in the Chesapeake Bay and its tributaries are known to appear in highest abundance within a narrow range of temperature and salinity, and this relationship has been used to predict the likelihood of occurrence of medusae at a specific time and location. However, they are also known to have an extremely patchy distribution which varies over much smaller spatial and temporal scales than temperature and salinity. This study seeks to identify patterns of change in abundance as measured by visual counting in a single location on the Choptank River, Cambridge, Maryland, USA over intra-annual time scales in order to determine what biological and physical processes are responsible for the variability. Two cyclic patterns in abundance were identified whose periods correspond to that of the lunar fortnightly constituent of the tidal force and the time between successive strobilations by *C. quinquecirrha* polyps. In addition to the expected relationships between medusa abundance and temperature and salinity, wind speed is also related to medusa abundance. Finally, apparent changes in abundance in the visual count can be caused by changes in depth distribution, which is influenced by water temperature and wind speed.

Introduction

Sudden appearances of high densities of jellyfish have been observed in many different locations (reviewed by Graham et al. 2001). These high abundances can be attributed to both the complex life cycle of cnidarian jellyfish that allows them to build large populations over short time periods and the formation of aggregations,

87

which cause patchiness in space. Both of these mechanisms of short term changes in jellyfish abundance are related to environmental conditions. Environmental conditions that can affect the rates of strobilation, or the asexual budding of polyps to produce the free-swimming ephyrae, include temperature, salinity, light, and food availability (for example Loeb 1973; Purcell et al. 1999; Purcell et al. 2009). Aggregations have been shown to form by a combination of physical factors and swimming behaviors. These include vertical or horizontal migration in response to light and aggregation near physical boundaries, including the surface, bottom, shoreline, pycnoclines, or convergence zones (reviewed by Graham et al. 2001).

The medusae of the scyphozoan *Chrysaora quinquecirrha* (Desor 1848) appear annually in high abundance in the mesohaline region of the Chesapeake Bay and its tributaries. Several studies have explored the environmental factors that influence the distribution and abundance of medusa with the goal of explaining and predicting the location and intensity of the summer bloom (for example Cargo and King 1990; Decker et al. 2007). This type of prediction is useful for mitigating the nuisance caused by *C. quinquecirrha* medusae to fishing, tourism, and nuclear power generation (reviewed by Purcell et al. 2007). Decker et al. (2007) shows that very high sea nettle abundances are most likely within a well defined range of temperature and salinity, and that this information can be used to identify areas where high abundances of sea nettles are likely to occur. This provides a basis for beginning to understand and predict jellyfish abundance in Chesapeake Bay. However, field observations indicate that medusa abundance varies on smaller temporal and spatial scales than the temperature and salinity gradients. More information regarding ephyra

production and behavior of medusae is needed to improve understanding of the patchy distribution of *C. quinquecirrha*.

The complex life cycle of *C. quinquecirrha* determines the total number of medusae in the bay and tributaries over the course of the year. The appearance of medusae produced by the sessile polyp stage can be described as a cycle of bloom and bust (Cargo and Schultz 1967). As strobilation begins in late spring, the first medusae have been reported as early as May. Abundance typically reaches its peak in mid to late summer, followed by a decline in the population.

A second source of intra-annual variability in localized abundance of medusae is patchiness, which can be influenced by physical or behavioral factors. Zooplankton communities are characterized by their patchiness, and this patchy distribution has often been attributed to physical processes that cause the weakly swimming organisms to form aggregations (Folt and Burns 1999; Graham et al. 2001). For example, several species of medusa have been observed in high abundance near areas of wind-driven convergence (Hamner and Schneider 1986; Larson 1992). However, biological factors are also important drivers in zooplankton patchiness. Common biological drivers include diel vertical migration, avoidance of predators, patchiness in food distributions, and location of mates (Folt and Burns 1999). High frequency variability in the abundance of the sea nettle *C. quinquecirrha* indicates that like other zooplankton, its distribution is patchy. Here I use variability over time in one location to estimate patchiness in space as patches move into and out of the visual counting transect and/or net haul area over time to create that variability. Biological drivers are likely important in creating this patchiness. Schuyler and Sullivan (1997) showed that

C. quinquecirrha moves toward the surface in response to decreased light, suggesting diel vertical migration. Matanoski et al. (2001) identified behaviors in *C. quinquecirrha* medusae that would allow an individual to maximize time spent in a patch of food once it has located the prey.

This study uses visual counts and vertical net hauls of medusae conducted at the Horn Point Laboratory, Cambridge, Maryland, USA on the Choptank River, a tributary of the Chesapeake Bay in an attempt to identify patterns of short term variability in medusa abundance that can be attributed to biology, behavior, and environmental conditions and to identify cues of behavioral patch formation. Specifically, it addresses the following hypotheses:

1. Cyclic variables such as the lunar cycle and the spring-neap tidal cycle influence variability in sea nettle abundance.

2. Physical variables such as light, temperature, salinity, stratification, wind, and tides affect medusa abundance over short time scales.

3. Physical variables such as light, temperature, salinity, stratification, wind, and tides affect depth distribution over short time scales.

Methods

Abundance of *Chrysaora quinquecirrha* medusae was measured in three different ways: visual counts over a 3 m by 61 m transect, visual counts over a 3 m by 3 m area, and vertical net hauls over the same 3 m by 3 m area. The visual counts were made over a 183 m^2 area on the south east side of the pier at the Horn Point Laboratory, Cambridge, Maryland, USA on the south side of the Choptank River (38°

90

35.610' N, 76° 7.725' W). A second visual count was made over a 9 m^2 area above the net, and then the 9 m^2 net was raised from the bottom in order to collect all medusae in the water column over that same area. Visual counts and net hauls began on 17 July 2005. Both measures of abundance were made twice daily at 7 AM and 7 PM until 16 September 2005, when decreasing day length made it impossible to make visual counts at 7 PM due to lack of daylight. At that time, observations were rescheduled in an attempt to better control for changing light conditions. Morning observations were made at sunrise, and evening observations were made 20 minutes before sunset in order to allow sufficient time to make counts and net hauls before it became too dark. Calculated sunrise and sunset times for Cambridge, Maryland, USA were downloaded from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Observations continued on this schedule until no medusae had been observed by visual count, net haul, or visual observation of the surrounding area for ten consecutive days. In subsequent years, 2006-2010, observations followed the sunrise and sunset schedule, beginning on June 1 and continuing until ten days after the last medusa was observed. All medusa observed in visual counts and net hauls were classified as <4 cm, 4-8 cm, or >8 cm in diameter by visual estimation.

Secchi depth and water depth were measured at the time of each observation. Secchi depth was measured inside the visual counting transect and was used to estimate the depth to which medusae could be seen in order to calculate the water volume sampled by visual counting. Water depth over the net was measured in order to calculate the volume sampled by the net. These two volumes were then used to

calculate the density of medusae measured by each method in individuals per cubic meter.

Additionally, surface water temperature and salinity were measured at the time of each observation using the YSI Model 30 handheld conductivity meter. In 2006, measurements of temperature and salinity at 1 m depth were added and continued through the remainder of the time series. Also in 2006, light measurements using the Fisher Scientific Traceable Dual-Range Light Meter began and continued at every observation thereafter. Wind speed and wind direction at the Horn Point weather Station, averaged over a half hour, was downloaded from the Chesapeake Bay Observing System (http://www.cbos.org) for the time of each observation. Moon illumination, or the fraction of the moon's surface that is illuminated by the sun as a measure of the lunar cycle, was downloaded from the United States Naval Observatory (http://www.usno.navy.mil/USNO/astronomical-applications/data-services/frac-moon-ill). Finally, expected and observed tidal height at Cambridge, MD (station identification number 8571892) at the time of each observation was downloaded from the National Oceanic and Atmospheric Administration (http://www.tidesandcurrents.noaa.gov/).

The time series of visual counts over the 183 m^2 transect for each year was examined for periodic patterns using the method described by Rust and Kirk (1978). First, a simple Gaussian model was fitted by least squares regression:

eq. 4.1

$$count = Amplitude * e^{-0.05*\left(\frac{day-mean}{stdev}\right)^2}$$

where *day* is the day of the year, *mean* and *stdev* are the mean and standard deviation of the days on which counts took place, and *Amplitude* is the coefficient calculated by least squares regression. Next, the residuals from those models were examined for periodic patterns by calculating a smoothed periodogram using the autoregressive Yule-Walker method (TIBCO, 2010; Kedem and Fokianos, 2002). The periodograms were examined for frequencies that occur every year. Frequencies that appeared in all years were examined for physical or biological meaning, and those that were found to have meaning were added to the regression equation in the form of periodic terms:

$$count = Amplitude * e^{-0.05 * \left(\frac{day - mean}{stdev} \right)^2} + \sum A_i \sin\left(\frac{2\pi}{T_i} (day + \phi_i) \right) \qquad eq.\ 4.2$$

where T_i is the period and A_i and ϕ_i are coefficients calculated by least squares regression. The result of this process is a descriptive model for each year from 2005-2010. The r^2 values of these models were examined in order to determine whether the inclusion of the periodic terms increased the fit.

The time series of visual counts of medusae over the 183 m^2 transect was also used to examine the relationship between medusa abundance and environmental variables. A five-point moving average of the time series was calculated (see Chapter 2), and cross correlation functions were calculated using Matlab software version 7.12.0.635 in order to identify correlations between medusa abundance environmental conditions in each year (Chatfield, 2009). Conditions considered included light, surface temperature, surface salinity, difference in temperature between the surface and 1 m depth, difference in salinity between the surface and 1 m depth, wind speed, wind direction, moon illumination, observed tidal height, and expected tidal height.

93

Additionally, least squares regression using a time lag of zero was performed using linear, quadratic, exponential and Gaussian models (Sokal and Rohlf, 1995) to better describe the relationships between medusa abundance and these environmental variables.

Where significant relationships existed between medusa abundance and an environmental variable, the time series was further examined to determine whether depth distribution varied with respect to that variable. In order to do this, a linear regression equation was calculated to describe the relationship between the five point moving averages of the net haul and visual count over the same 9 m^2 area (see Chapter 2). The regression equation uses the medusa abundance observed by the visual count to predict the medusa abundance measured by the net haul:

$$net\ haul = 1.43*visual\ count +0.29 \qquad\qquad eq.\ 4.3$$

Therefore residuals from this equation represent the difference between the observed abundance as measured by the net haul and the expected abundance based on the visual count. Positive residuals represent instances in which the observed net haul was higher than expected, indicating that the medusae were deeper than average at the time of the count and net haul. Negative residuals represent instances in which the observed net haul was lower than expected, indicating that the medusae were shallower than average at the time of the count and net haul. These residuals were plotted with respect to the each of the environmental variables that exhibited a significant relationship with medusa abundance in order to examine the plots for patterns.

94

Results

Medusae with bell diameters greater than 8 cm dominated the population in all years (Figure 4.1); however, in most years, specifically 2006, 2008, 2009, and 2010, smaller size classes were more prevalent in the early part of the year. Notably in 2009, a second peak in the relative abundance of smaller individuals appeared near the end of the season, and in 2010, larger medusae dominated the population in the very early part of the season.

The Gaussian curve fit to the time series of visual counts of *C. quinquecirrha* medusae described a significant relationship in all years ($p<0.05$) with r^2 values ranging from 0.21 to 0.49 (Table 4.1, Fig. 4.2). On average, theses curves explained 34% of variability in abundance over time. Examination of the periodogram of the residuals from the Gaussian model for each year showed that the periodogram varied from year to year, but that all years shared two features (Fig. 4.3). First, in all years, there was a peak near a frequency of 0.46 days^{-1} (range = 0.45-0.47 days^{-1}, median = 0.46 days^{-1}), which corresponds to a period of 13.66 days (range = 13.36-13.96 days, median = 13.66 days). This period exactly matches the lunar fortnightly tidal constituent (M_f), which has a period of 13.66 days (Wahr 1995). The second feature shared by the periodogram from each year is the wide peak centered at a frequency of 0.3 day^{-1}. This corresponds to a period of 21 days. Cargo and Rabenold (1980) reported a period of 21 days between successive peaks in strobilation by *C. quinquecirrha* polyps. When sinusoidal functions as described by equation 4.2, with periods of 13.66 days and 21 days were added to the Gaussian models, the amount of variability in medusa abundance increased for every year with r^2 values ranging from

0.32 to 0.53 (Table 4.1, Fig. 4.2). On average, the new models that include both Gaussian and periodic terms explained 42% of the variability in medusa abundance over time.

For all variables, and all years, the cross correlation functions showed a wide peak in correlation that included a time lag of zero days (results not shown); however, the lag at which maximum correlation occurred varied widely from year to year for most variables. Because of this wide peak in correlation near a time lag of zero days, it was reasonable to conduct regression analysis with no time lag in order to identify the relationships between medusa abundance and the environmental variables. The only notable exceptions to this wide variation in time lag at maximum correlation were expected and observed tidal height. Both of these variables did exhibit the pattern of relatively wide peaks near zero, but also showed maximum correlation at lags between 1 and 5 days in all but one year.

Regression analysis of the relationship between medusa abundance and environmental factors showed no significant relationship between abundance and light, difference in temperature between the surface and 1 m depth, difference in salinity between the surface and 1 m depth, wind direction, observed tidal height, or expected tidal height (Table 4.2). Temperature, salinity, and moon illumination showed a positive linear relationships with medusa abundance while wind speed had a significant negative linear relationship with abundance ($p<0.05$). None of the non-linear regression equations were significant ($p > 0.1$). Although the relationships between medusa abundance and temperature, salinity, and moon illumination are

statistically significant, they all explained very low proportions of the variability in the observed abundance ($r^2 = 0.011\text{-}0.038$).

Residuals calculated from the regression equation for the relationship between abundance as measured by visual count and abundance as measured by vertical net haul (see Chapter 2) represent deviations from the expected vertical distribution of medusae. Plotted with respect to wind speed (Fig. 4.4a), the residuals show greater variability, both positive and negative at lower wind speeds. There is no discernible pattern in the distribution of residuals plotted with respect to the fraction of the moon illuminated at the time of each observation (Fig. 4.4b). Two different patterns are evident in the distribution of residuals plotted with respect to water temperature (Fig. 4.4c). At temperatures below 18 °C, high positive residuals indicate that medusae are found closer to the bottom than average. At higher temperatures, there is high variability in the distribution of residuals. Finally, negative residuals are present across the entire range of salinity, but positive residuals (more medusae near the bottom) are present only within a very narrow range of relatively high salinity from 12 to 14 (Fig. 4.4d). When separated by year, it becomes evident that all of the positive residuals in the narrow range of salinity represent observations made in 2005 (Fig. 4.5). The majority of the high negative residuals represent observations made in 2006, while the residuals from all other years are found near the axis at all values of salinity.

Discussion

      Several patterns in the intra-annual variability of *C. quinquecirrha* medusae can be clearly identified from these analyses. First, a higher relative abundances of smaller medusae near the beginning of the season followed by a shift to larger individuals later in the year (Fig. 4.1) indicate growth of the majority of individuals from ephyrae to medusae with bell diameters greater than 8 cm. Later in the season, larger individuals tend to predominate. However, there are notable deviations from this pattern. In 2010, larger individuals tended to dominate the population at the time of first appearance, and smaller individuals appeared later. This may indicate that in at least some years, medusae arrive at this location from a remote source before strobilation occurs more locally. Finally, in some years, especially 2009, a second period of high abundance of smaller individuals occurs near the end of the season. This may represent a second cohort of newly strobilated individuals entering the population, or it may indicate the degrowth of older individuals that has been observed in years with early disappearance (see Chapter 5).

      A Gaussian regression model (eq. 4.1) describes the annual cycle of bloom and bust exhibited by medusae. Examination of the spectrum of the residuals from that model identifies two periodic patterns. The first has the same period as the lunar fortnightly tidal constituent of the tidal force, which controls the spring-neap cycle of the tides. The cross correlations function for medusa abundance and expected and observed tidal height showed maximum correlation between medusa abundance and tides at lags of 1 to 5 days in most years. This indicates that maximum medusa

98

abundances tended to occur shortly after the maximum tidal heights that occur at spring tide. Based on this pattern, it is reasonable to hypothesize that the medusae are being physically transported toward and away from the counting transect as a result of the M_f tidal force, or they are exhibiting a behavioral response to it, or both. Another physical force, the currents created by Langmuir circulation have been observed to transport several species of hydromedusae and scyphomedusae to form aggregations at convergence zones (Hamner and Schneider 1986; Larson 1992). In the case of the M_f tidal force, it is possible that the higher tidal current velocity that occurs during spring tides may transport the medusae differently than the lower velocity currents that occur at neap tide with respect to distance from shore or along the axis of the estuary. In other cases, medusae have been observed using horizontal, directional swimming behaviors to form aggregations. *Mastigias sp.* and *Aurelia aurita* have both been shown to use the sun to navigate during daily horizontal migrations that result in the formation of dense aggregations (Hamner and Hauri 1981; Hamner et al. 1994). It is unlikely that the light from the moon cues a swimming behavior in *C. quinquecirrha* in the same way that light from the sun cues *Mastigias sp.* and *Aurelia aurita*. Since the period of the cyclic pattern in medusa abundance is half of the lunar period, the cycle is at the same phase during both full and new moon in the same way that the spring tide occurs near the time of both full and new moon. However, other tidal signals may provide the behavioral cue. Synchronized spawning related to the lunar cycle has been established in a variety of coral species (reviewed by Richmond and Hunter 1990). Babcock et al. (1986) hypothesizes that tidal amplitude may be one of the factors linked to the lunar cycle

99

that cues synchronized spawning by corals on the Great Barrier Reef. Hamner and Dawson (2009) illustrate that aggregation behavior is an evolved characteristic that increases reproductive success among scyphomedusae. If corals, which also belong to the phylum Cnidaria, are able to behave in response to tidal amplitude, it is reasonable to suggest that the scyphomedusa *C. quinquecirrha* may use the tidal amplitude, which is influenced by the M_f force, as a behavioral cue to form aggregations for spawning.

The second periodic pattern evident from the spectrum of the residuals from the Gaussian models has a period of 21 days. A possible explanation of this pattern is that it may represent pulses of strobilation that periodically increase the population of *C. quinquecirrha* medusae. Cargo and Rabenold (1980) showed that the number of individuals strobilating among *C. quinquecirrha* polyps collected from the Chesapeake Bay and maintained in a flow-through system changed over time with 21 days between successive peaks in strobilation, which coincides with the period of the cyclic pattern in medusa abundance observed here.

The combined Gaussian and periodic model (eq. 2) provides a descriptive model of a single season that explains 42% of the variability in medusa abundance for a given year, 8% more than the Gaussian model alone (eq. 1). However, this model does not provide a predictive understanding of the variability in medusa abundance. An attempt to divide the time series into a multiyear training set to calculate a predictive model and a multiyear validation set to test the model was unsuccessful because of the large amount of inter-annual variability in the timing, duration, and magnitude of the peak in medusa abundance (see Chapter 3). Since the Gaussian

model depends on these characteristics of the bloom to calculate amplitude, mean day of the year, and the standard deviation of the time, a useful Gaussian model can only be calculated after those characteristics of the season have been measured. Several attempts have been made to identify relationships between seasonal medusa abundance and environmental conditions (Cargo and King 1990; Purcell and Decker 2005; Breitburg and Fulford 2006), and Chapter 3 of this dissertation attempts to identify relationships between the timing and duration of the annual bloom. In most cases, the regression models that describe these relationships describe less than half of the variability in the medusa population; however, it may be possible to use information about the relationships between the timing, duration, and magnitude of the medusa bloom and environmental conditions to predict the coefficients of the Gaussian term of equation 4.2.

In addition to the cyclic patterns, the medusa abundance was also examined for relationships with non-cyclic environmental variables. Cross correlation indicated that although the time lag at which maximum correlation between each of the environmental variables and medusa abundance occurred was variable from year to year, all variables showed wide peaks in correlation that included a time lag of zero days. Thus regression analysis was conducted with no time lag included. Unsurprisingly, the strongest relationships were with temperature and salinity. It has been established that the highest abundances of *C. quinquecirrha* medusae in Chesapeake Bay occur within a narrow range of temperature and salinity (Decker et al. 2007). Statistically significant linear relationships also existed between medusa abundance and wind speed and moon illumination. Although all of these relationships

were statistically significant, they explain only 1%-4% of the total variability in medusa abundance. Despite the weak relationships, I examined these variables further in an attempt to understand the mechanisms by which they may influence intra-annual variability in medusae abundance.

One mechanism by which environmental conditions can affect medusa abundance as measured by visual counts over short time scales is by affecting their vertical distribution. If an environmental condition either influences or inhibits vertical swimming behavior, it affects the proportion of medusae available for visual count. Residuals from the linear relationship between visual count and vertical net haul (Chapter 2) illustrate differences in depth distribution. Residuals plotted with respect to wind speed show more variability, both positive and negative, at wind speeds below 6 m s^{-1}, meaning that under low wind conditions, depth distribution varies more than under high wind conditions (Fig. 4.4a). I hypothesize that either high wind speeds physically homogenize the depth distribution or inhibit swimming behaviors that may lead to high residuals.

Residuals plotted with respect to water temperature show two unsurprising patterns (Fig. 4.4d). At temperatures between 20°C and 30°C, both high positive and high negative residuals are present. Gatz et al. (1973) illustrates that pulsation rate of *C. quinquecirrha* medusae is higher at higher temperatures. Since pulsation is the swimming motion, it is reasonable to hypothesize that the more rapid swimming motion under warmer conditions would facilitate aggregation at any depth. At low temperatures, on the other hand, all of the high residuals are positive, meaning that when high abundances of medusae are present at low temperatures, they are found

deeper in the water column than expected based on the relationship between visual counts and vertical net hauls. This is consistent with the finding that pulsation rate slows and medusae sink at temperatures below 15°C (Gatz et al. 1973; Sexton et al. 2010).

Although there is a cyclic pattern in medusa abundance that is related to the lunar cycle, no discernible pattern is present in the residuals from the regression model of abundance as measured by visual counting versus vertical net hauls (Fig. 4.4b). This does not negate either the physical or behavioral hypothesis for the mechanism that causes the cyclic pattern as described above, but does suggests that the mechanism must work to move medusae horizontally rather than vertically.

The pattern of residuals plotted with respect to salinity is more puzzling. Based on the optimal range of salinity for high abundances of medusae, which is from 10 to 16 as reported by Decker et al. (2007), I would expect to see high positive and high negative residuals distributed throughout this range. Instead, high positive residuals occur in a very narrow range from 12 to 14, and high negative residuals occur over a more diffuse range below a salinity of 12 (Fig. 4.4c). When the residuals are separated by year (Fig. 4.5), it becomes clear that all of the high positive residuals occurred in 2005, and the majority of high negative residuals occurred in 2006, while the residuals from the remaining years are typically low. Since 2005 and 2006 had higher total abundance than the other years in the time series, it is not surprising that they would also produce all of the high residuals because the magnitude of the residuals depends on total abundance. It is not clear, however, why the residuals from 2005 are positive while the residuals from 2006 are negative. There were no striking

103

differences in the environmental conditions between these two years, and in fact, 2005 and 2006 are more similar to each other in terms of the timing, duration, and magnitude of the medusa bloom than either of them is to any other year.

In summary, several relationships have been identified that explain variability of *C. quinquecirrha* abundance on intra-annual time scales. The short term changes in abundance observed in the time series of visual counts can be attributed to biological factors, including the organism's life cycle and behavior, and physical factors including currents and seasonal temperature changes. The appearance of a cyclic pattern related to the time between successive peaks in strobilation indicates that the rate of strobilation is significant in determining the total medusa abundance. A second cyclic pattern related to the spring-neap cycle indicates that medusae are moving far enough horizontally, through swimming behavior, advection, or both, to cause localized changes in abundance. Finally, apparent changes in abundance can be caused by changes in vertical distribution of medusae.

Such information may be useful for improving our ability to predict the abundance of this nuisance species through the season. For example, predictions could be updated to reflect the pattern of population growth in order to improve predictions early in the season. The change in abundance related to the spring-neap cycle suggests that a large number of medusae are moving from one location to another on a predictable cycle. If the spatial pattern of movement could be identified, it would allow for predictions over smaller spatial scales. Information about the conditions that influence vertical distribution may allow for prediction of locations

where medusae are likely to be present, but not visible at the surface such as the end of the season when water temperature decreases.

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Tables

Table 4.1: Coefficients calculated for regression models for each year of the time series of visual counts of medusae. r^2 of the Gaussian model represents the r^2 value calculated for the simple initial Gausian model (Eq. 1). All other values were calculated for the combined Gaussian and periodic model (Eq. 2)

	2005	2006	2007	2008	2009	2010
Amplitude	0.41	0.22	0.16	0.06	0.15	0.02
Mean	257.20	234.50	239.10	240.60	213.80	227.30
SD	-23.42	-33.94	-3.16	-21.26	-20.06	-17.41
$\mathbf{A_1}$	-0.07	0.03	-0.01	0.01	-0.01	0.01
$\mathbf{\Phi_1}$	157.50	320.90	331.10	318.90	389.50	324.30
$\mathbf{A_2}$	0.03	-0.06	-0.01	0.02	-0.04	-0.01
$\mathbf{\Phi_2}$	153.50	155.10	153.90	154.80	157.60	185.00
$\mathbf{r^2}$ **of Gaussian**	0.39	0.28	0.49	0.28	0.41	0.21
$\mathbf{r^2}$ **of Gaussian + periodic**	0.45	0.38	0.52	0.44	0.53	0.32

Table 4.2: r^2 values and sign of the slopes from the regression equation between each of the listed variables and the five point moving average of abundance as measured by visual count over 183 m^2 (count = a*variable + b). NS indicates that the relationship between abundance and the environmental variable is not significant (p<0.05). Difference in temperature and difference in salinity represent the difference between the measurement made at the water surface and the measurement made at 1 m depth.

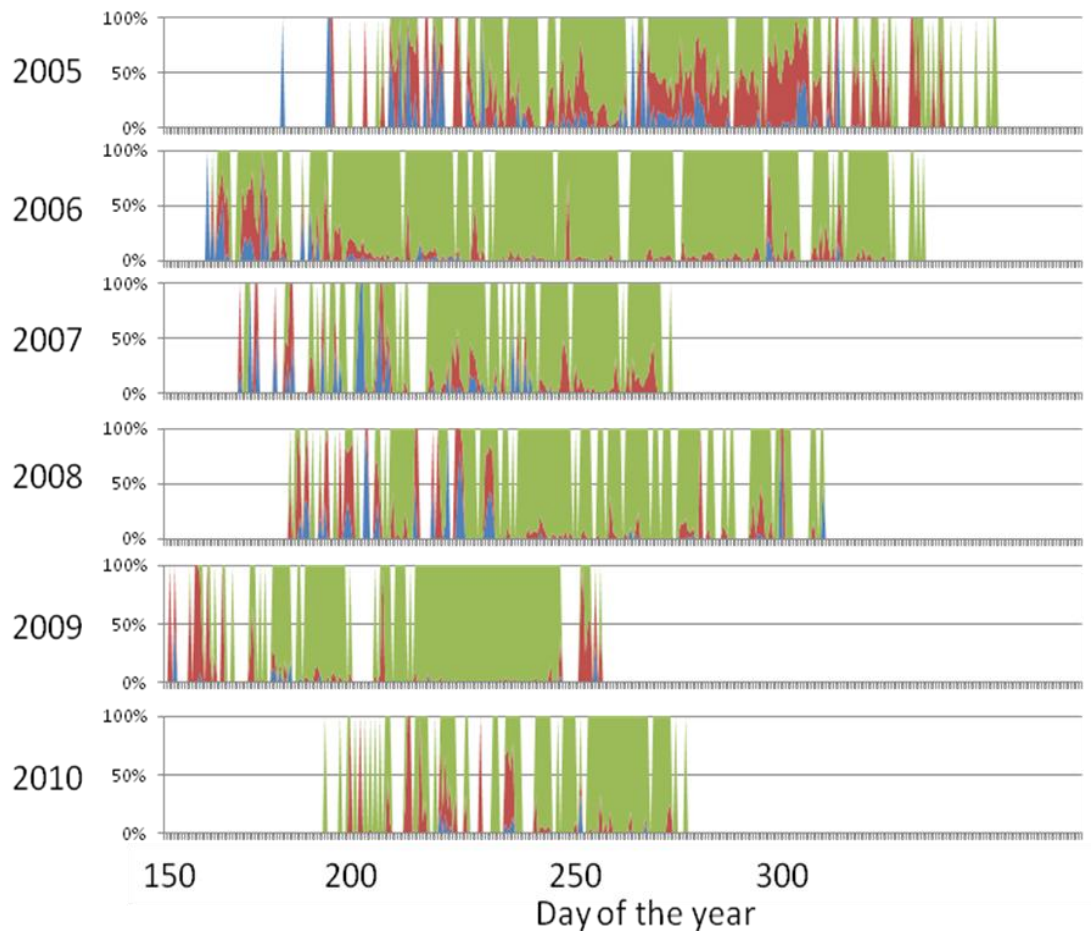| Variable	slope	r^2
Light		NS
Temperature	+	0.03787
Salinity	+	0.0293
Difference in temperature		NS
Difference in salinity		NS
Wind speed	-	0.01057
Wind direction		NS
Moon illumination	+	0.01105
Expected tide		NS
Observed tide		NS

Figure 4.1: Relative abundance of three size classes of medusae, less than 4 cm bell diameter (blue), 4 to 8 cm bell diameter (red), and greater than 8 cm bell diameter (green).
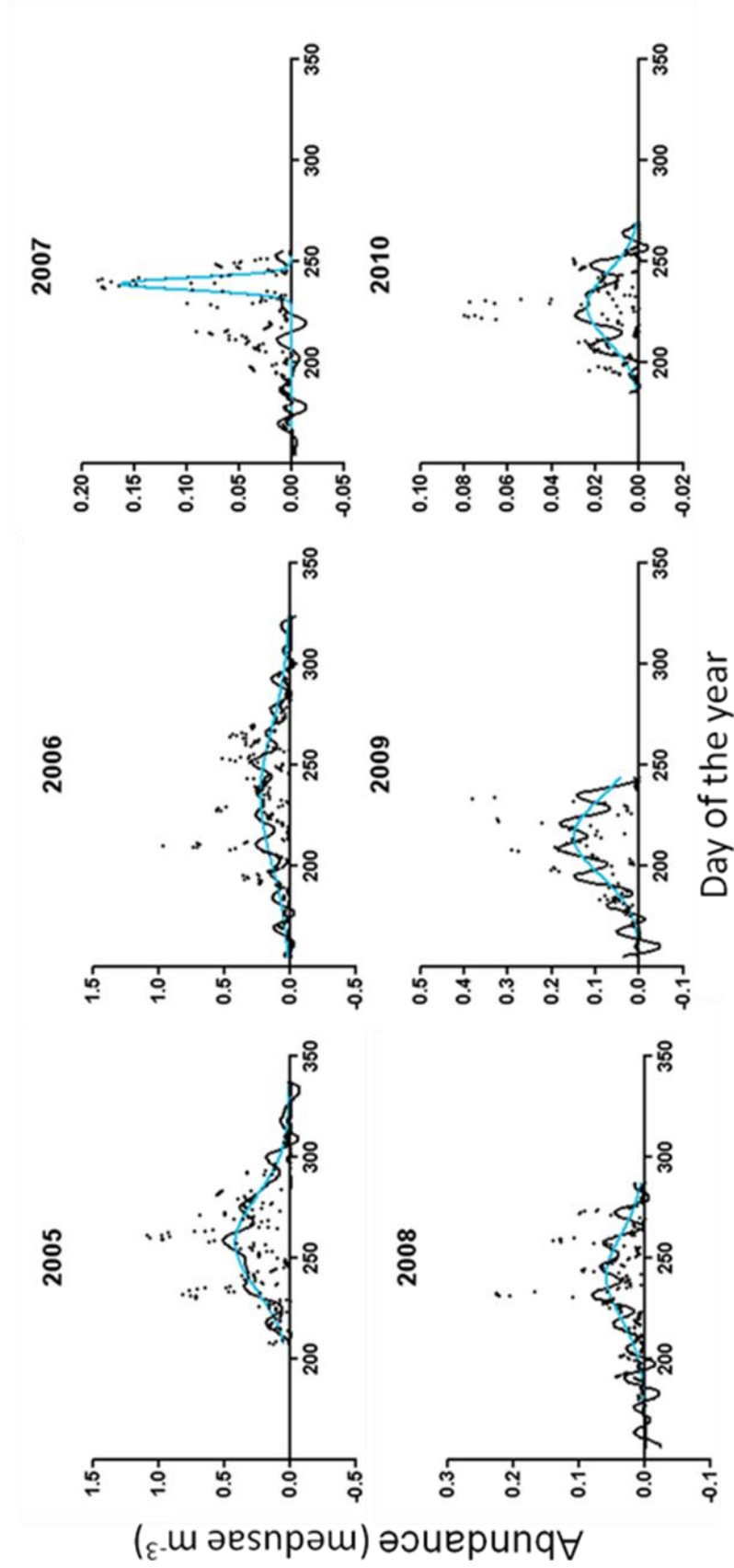
Figure 4.2: Time series of visual counts over 183 m2 for each year from 2005-2010 with Gaussian model (blue) and Gaussian plus periodic model (black).

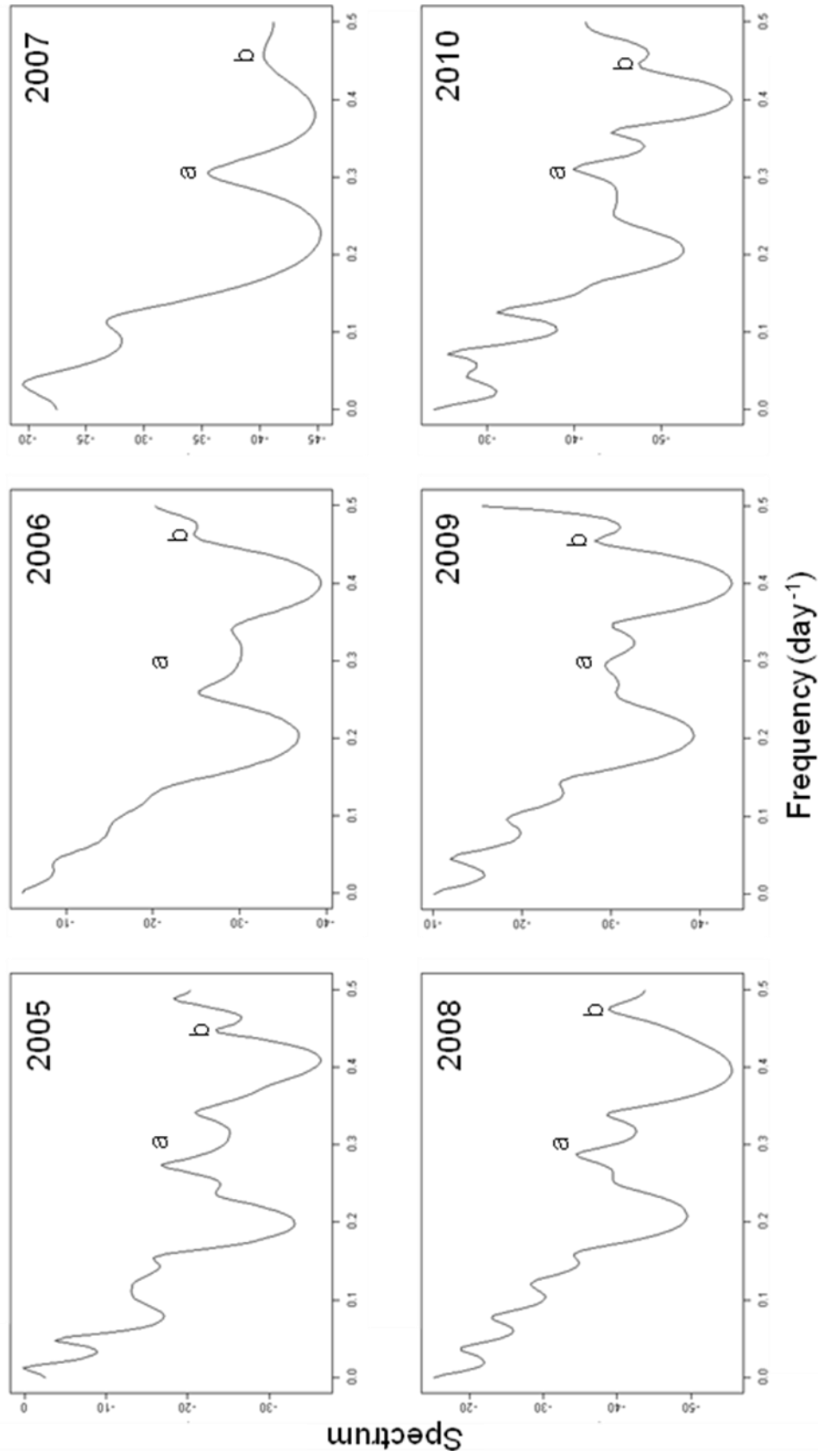**Figure 4.3**: Smoothed periodograms of residuals from Gaussian model of time series of visual counts over 183 m2 area from 2005-2010. Letters indicate features with the same period in each year (a = 21 days, b = 13.66 days).
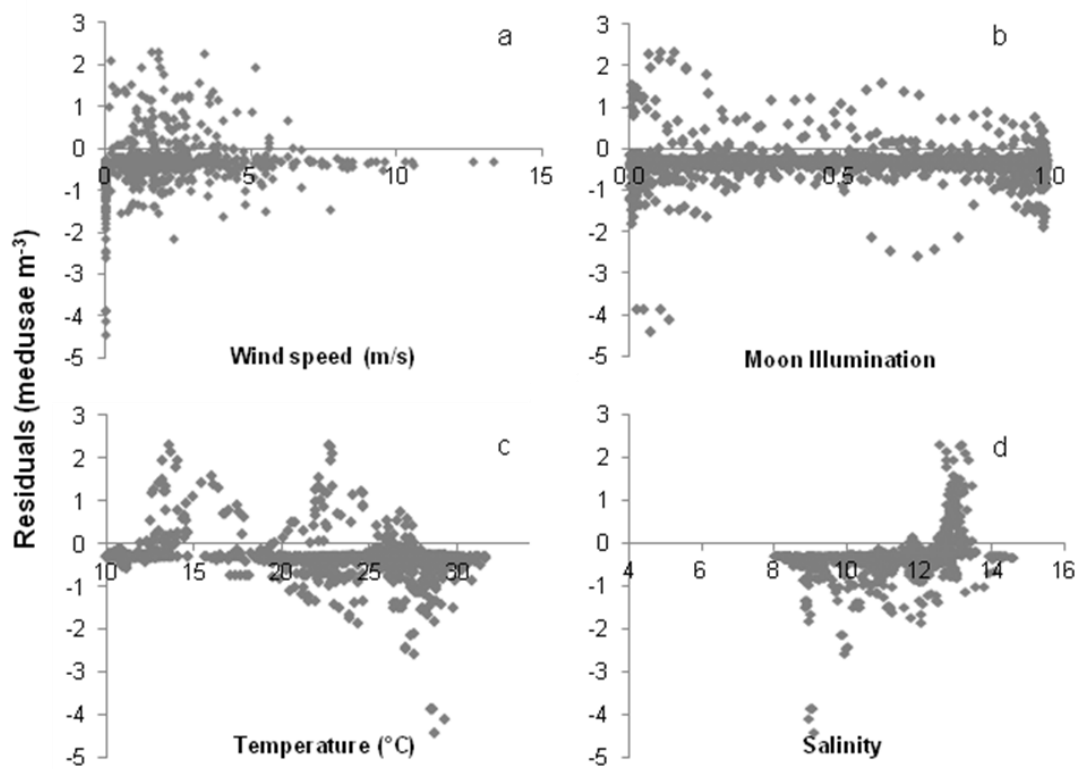
Figure 4.4: Residuals from linear regression of visual counts versus net hauls plotted with respect to wind speed (a), moon illumination (b), temperature(c), and salinity (d) at the time of each count.

Figure 4.5: Residuals from linear regression of visual counts versus net hauls plotted with respect to salinity in 2005 (red), 2006 (yellow), and all other years (blue).

Chapter 5: Response of *Chrysaora quinquecirrha* medusae to low temperature

CHAPTER CITATION:

Sexton, M. A., R. R. Hood, A. M. Liss, J. Sarkodee-adoo, 2010. Repsonse of

Chrysaora quinquecirrha medusae to low temperature. Hydrobiologia

645:125-133.

Abstract

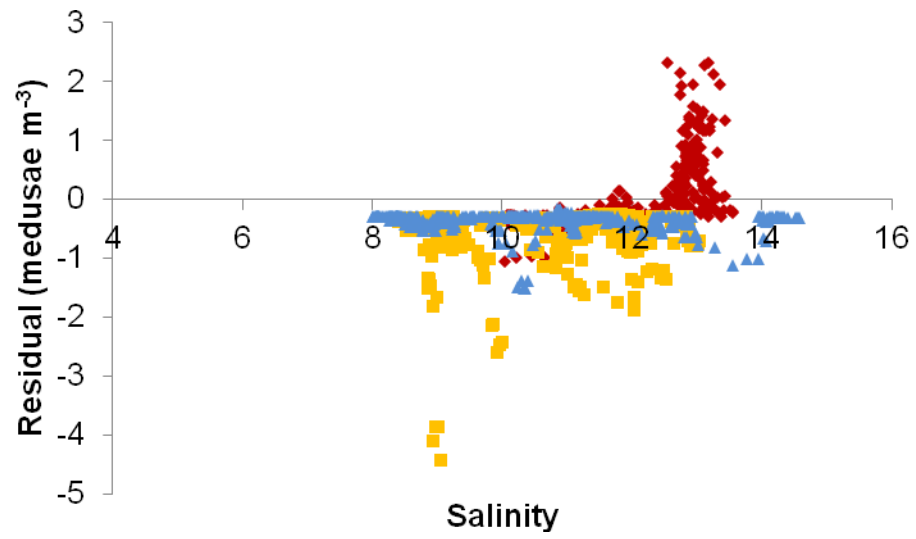Because of their high abundance in Chesapeake Bay, *Chrysaora quinquecirrha* medusae may be an important reservoir of organic matter. The timing and location of the decomposition of biomass from medusae may have implications for carbon cycling in the bay. Our objective was to identify the cause of *C. quinquecirrha* medusa disappearance in order to better understand when and where decomposition occurs. A time series of visual surface counts and vertical net hauls in the Choptank River, a tributary of Chesapeake Bay, showed that as temperatures approached 15°C, *C. quinquecirrha* medusae disappeared from the surface, but persisted in net hauls until temperatures reached 10°C. To test if medusae sink upon cooling, I exposed *C. quinquecirrha* medusae to low temperatures in large static tanks and measured their depth and pulsation rates twice daily for at least six days. This procedure was repeated three times through the 2008 jellyfish season. On average, individuals exposed to temperatures below 15°C were found deeper and pulsed slower than those in the warmer control tank. This suggests that low temperatures cause the medusae to sink before cooling to the limit of their physiological tolerance and may have implications for the deposition of organic matter associated with the seasonal disappearance of medusae from Chesapeake Bay.

Introduction

The medusa stage of *Chrysaora quinquecirrha* (Desor 1848) is seasonally abundant in the mesohaline Chesapeake Bay and its tributaries. It has been shown to

117

affect populations of other gelatinous zooplankton, copepods, and ichthyoplankton (for example Feigenbaum and Kelly 1984; Purcell 1992; Cowan and Houde 1993). Feigenbaum and Kelly (1984) suggest that *C. quinquecirrha* influences the trophic structure of the bay through its predation on *Mnemiopsis leidyi* (A. Agassiz 1865). By controlling the population of the voraciously feeding ctenophore, high abundances of *C. quinquecirrha* can positively affect secondary production (Purcell et al. 1994b; Purcell and Decker 2005). A direct effect on fish populations is medusa predation on fish eggs and larvae, which can account for high percentages of mortality (Purcell et al. 1994a). In addition to important trophic interactions, *C. quinquecirrha*'s painful sting has negative influences on recreational activities. For these reasons, it is desirable to understand and predict the occurrence of *C. quinquecirrha*.

Several studies have addressed the environmental factors that determine abundance and distribution of *C. quinquecirrha* medusae in Chesapeake Bay (for example, Cargo and King 1990; Purcell and Decker 2005; Breitburg and Fulford 2006; Decker et al. 2007) and the conditions that cue strobiliation (for example Cargo and Schultz 1967; Cargo and Rabenold 1980; Purcell et al. 1999); however, the mechanisms of the seasonal disappearance of *C. quinquecirrha* have not been well studied. The day of final occurrence on the Patuxent River, as measured by a time series of average weekly visual counts, usually has been in early November (Fig. 1, median = 311, November 7; D. G. Cargo, unpublished data).

Because of their tendency to form blooms, jellyfish sometimes have important influences on nutrient cycling (Pitt et al. 2009). Several studies have shown that jellyfish can be important to the local carbon cycles. Titelman (2006) identified a shift

in the bacterial community when decaying gelatinous matter was the carbon source because bacteria varied in their ability to utilize it. Gelatinous biomass accounted for a large amount of fixed carbon during summer in the mesohaline portion of the York River, a tributary of Chesapeake Bay (Condon and Steinberg 2008). They suggested that this carbon can be released to the water column, especially during starvation, or to the benthos from gelatinous matter on the sediment. Once on the bottom, Billet et al. (2006) showed that jellyfish carcasses provided a significant input of organic matter to the sea floor, and West et al. (2009) suggested that decomposition of gelatinous biomass can affect sediment nutrient cycling, including causing a significant increase in sediment oxygen demand. Thus, carbon from *C. quinquecirrha* may play an important role in carbon cycling in the mesohaline Chesapeake Bay. The time that *C. quinquecirrha* medusae disappear each year has implications for the timing and location of release of organic matter from gelatinous zooplankton.

I addressed temperature as one possible cause of the annual disappearance of medusae. Gatz et al. (1973) showed that pulsation rate, the swimming activity of the medusae, decreased with temperature, until pulsation stopped completely at 10°C. This relationship between pulsation rate and temperature may cause *C. quinquecirrha* to sink to the bottom because the negatively-buoyant medusa cannot swim as strongly away from the bottom. I compared visual surface counts to vertical net hauls in the Choptank River, a tributary of Chesapeake Bay, in 2005 and 2006 to determine whether the vertical distribution of medusae changes as temperatures approach 15°C. In order to clarify this point further, a large tank experiment was used to determine the effect of low temperature on depth of *C. quinquecirrha* medusae. I hypothesize

119

that *C. quinquecirrha* exposed to temperatures between 10°C and 15°C in large tanks

will be deeper and pulse slower than *C. quinquecirrha* exposed to warmer

temperatures.

Methods

Visual counts and vertical net hauls for *Chrysaora quinquecirrha* medusae

were conducted twice daily from the dock at the Horn Point Laboratory, Cambridge,

Maryland, USA on the south side of the Choptank River (38° 35.610'N, 76°

7.725'W). Counts were taken daily at 0700 and 1900 from 6 June 2005 to 15

September 2005. The count area was defined as the 3 m on the east side of the dock

along its entire 61 m length forming a 183 m^2 transect. Consistency in the count area

was ensured each day by carrying a 3-m PVC measuring rod with a weighted line on

the far end while counting medusae inside the weighted line. Secchi depth measured

at the time of each count was used to estimate the depth to which medusae could be

seen during the visual count. Densities of *C. quinquecirrha* (medusae m^{-3}) were

calculated from the numbers in the area count visually divided by the water volume

searched (area x Secchi depth). Immediately after each visual count, a vertical haul

from bottom to surface was made with a net (9-m^2 mouth area, 1.6-cm nylon mesh).

Water depth was measured at the time of each net haul in order to calculate volume

sampled and density of medusae. On 16 September 2005, the sampling times were

adjusted so that the morning count and net haul occurred immediately after sunrise

and the evening net haul occurred 20 min before sunset. In subsequent years,

observations began on 1 June and followed the sunrise/sunset schedule through the

entire season. Counts and net hauls continued on this schedule until no medusae were observed at the surface along the transect or the surrounding area or collected in the net for 10 consecutive days.

Calculations of the importance of carbon from *C. quinquecirrha* medusae (CQC) relative to other measures of carbon in Chesapeake Bay were made from visual counts and literature values. Two measures of abundance were included: the highest weekly average on the Choptank River from the years 2005-2008, as described above, and the average July-August count on the Patuxent River from Cargo and King (1990). Patuxent River counts were assumed to have a visible depth of 1 m in order to calculate a density in the count area (medusae m^{-3}). The carbon represented by the densities of *C. quinquecirrha* medusae was calculated using the equation from Purcell and Decker (2005):

$$C = 2.15*10^{-4} \, \text{Diam}^{2.903}$$

An average diameter of 33 mm was assumed based on average diameters in late August reported in Purcell (1992) and used to calculate carbon per individual. This allowed for calculation of the concentration of CQC in the water column, potential CQC flux to the sediment, and CQC deposition rate.

Timing of medusa disappearance in Fig. 1 was from a time series of weekly mean visual counts made at the Chesapeake Biological Laboratory in Solomons, Maryland, USA from 1960 to 1995. Average July-August counts from 1960 to 1986 from this series are published in Cargo and King (1990), but dates of final occurrence were not published. Counts were made by D. G. Cargo with assistance from M. Wiley

and H. Millsap until 1991. Wiley continued the counts in 1992 and 1993, and Millsap continued them in 1994 and 1995.

In order to determine whether cold temperatures cause medusae to sink, two 10,000-l tanks were filled with 1-µm filtered Choptank River water. Tanks of 2.3 m depth were chosen to simulate the water depth at the dock where counts and net hauls were made, and where water depth ranged from approximately 1.5 m to 3 m depending on tide. I assumed that interaction with the bottom of the tanks would simulate that occurring in situ. One tank was designated the treatment tank, and the other was the control tank. The treatment tank was cooled to 13°C and the control tank was cooled to 16°C. In order to avoid damaging the medusae, the pumps were turned off after initial chilling to the starting temperatures. Temperature was measured twice daily throughout the experiment. The first two trials were terminated after 6 days when the temperature at the bottom of the tanks reached 16°C. The third trial was allowed to continue beyond 6 days despite the increase in temperature. Because changes in light were shown to cause vertical migration in *C. quinquecirrha* (Schuyler and Sullivan 1997), lights remained off throughout the experiment, and tanks were draped with dark plastic to block out ambient light. Because many of the zooplankton prey of the medusae migrate vertically, food was not introduced to the tanks in order to eliminate the vertical position of prey as a variable that could influence the vertical position of the medusae.

Chrysaora quinquecirrha medusae were dipped in buckets from the Tred Avon River at Oxford, Maryland, USA immediately before being placed in the tanks and the bell diameter at maximum expansion was measured. The medusae were

transported from the river to the laboratory in buckets, and small volumes of water from the chilled tanks were added to the buckets every 0.5 h for 2-3 h to decrease temperature slowly. When the temperatures in the buckets were within 1-2°C of the tank temperatures, twenty medusae were distributed equally between the two tanks to obtain similar size distributions in both tanks and allowed to acclimate 24 h before observations began. Although Gatz et al. (1973) suggested that temperature acclimation to a similar temperature difference occurs within 3 h, Schuyler and Sullivan (1997) reported behavioral changes after the first day of residence in a large tank. Those changes were presumed to be the medusae resuming normal behavior after the stress of capture and transport. For this reason, the conservative acclimation time of at least 24 h was used here.

After 24 h, the depth at which each medusa was swimming was determined by use of a dive light and sounding line. At the same time, the number of swimming pulses in 15 sec was counted for each individual. Water temperature also was measured at the surface, 1 m, 2 m, and bottom to calculate a depth-integrated temperature for each tank. These measurements were taken twice daily, and the procedure repeated three times (trials). The first two trials ran for 6 days and the third for 9 days. Although the successive measurements were made over the course of time, they were assumed to be independent because the time between measurements was sufficient for the individuals to travel from top to bottom nearly one hundred times based on a swimming speed of 0.6 cm s^{-1}, which was the most frequent swimming speed observed in the absence of food by Matanoski et al. (2001). Average depths and pulsation rates observed in the treatment and control tanks were compared

using a Wilcoxon two sample test because the distributions of the paired measurements were non-normal. Trends in depth and pulsation with respect to depth-integrated temperature were addressed with least squares regression using S-plus 8.0 statistical software (Sokal and Rolf 1995).

Results

Results from the time series of visual counts and vertical net hauls on the Choptank River showed that *C. quinquecirrha* medusae disappeared from the visible surface layer before they disappeared from the entire water column (Fig. 5.2). Disappearance from the visible layer coincided with the seasonal decrease in water temperature to 15°C, but complete disappearance from the water column coincided with the decrease in temperature to 10°C (Figs. 5.2 and 5.3).

In all three trials of the tank experiment, medusa average depth was deeper and the average pulsation rate was slower in the cold treatment tank than in the control (Fig. 5.4). Average pulsation rates ranged from 26 to 36 pulses min^{-1} in the control tank, and from 11 to 28 pulses min^{-1} in the cold treatment. These rates are consistent with those observed by Gatz et al. (1973) in similar temperatures. Results were significantly different according to a one-sided Wilcoxon two sample test with $p<0.05$ for all trials (Trials 1 and 2, n=12 for both groups; Trial 3, n=18). For depth, t_s=-4.1312, -4.130, and -4.411, and for pulsation, t_s=3.903, 4.066, and 2.929 for Trials 1, 2, and 3, respectively.

In the first and second trials, there were no overlaps between the cold treatment and the control for average depth or average pulsation rate (Fig. 5.5). In the

third trial, which lasted three days longer than the previous trials, the average depths

began similarly to the other trials, but approached one another over time; however,

the grand average of all depths over the course of the trial remained significantly

deeper in the cold treatment tank than in the control. The relationships of depth and

pulsation rate to depth-integrated temperature showed similar patterns in the first and

second trials with deeper occurrences and slower pulsation rates in the cold

treatments than the controls. In the third trial, where the temperature in the cold

treatment tank approached that of the control tank, average depth and pulsation rate

increased as temperature increases. Least squares linear regression showed significant

relationships between temperature and depth (=0.501, p<0.05) and pulsation rate

(=0.896, p<0.05) (Fig. 5.6).

Discussion

Because the last medusae have been observed most frequently near or after the

beginning of November (Fig. 5.1) when water temperatures are decreasing (Fig. 5.3),

low temperature is a likely cause of the seasonal disappearance of *C. quinquecirrha* in

most years. In some years, disappearance occurred long before the water temperature

began to decrease toward the minimum tolerated by *C. quinquecirrha* medusae. In 7 y

of the 35-y time series, the day of final occurrence was at least 50 days earlier than

the median day of final occurrence (Fig. 5.1). Possible mechanisms for these

unusually early disappearances include starvation due to low food availability;

mortality due to higher than normal rates of disease, parasitism, or predation; or an

early cessation of strobiliation accompanied by normal senescence (see Appendix 1).

Additionally, unusually low abundance and relatively early disappearance of medusae in 1972 have been attributed in part to Hurricane Agnes (Cargo 1976); therefore, suboptimal salinity and temperature and physical flushing should also be considered as possible mechanisms. More inquiry is necessary to determine which of these mechanisms may be at work in years with early disappearance. While the reasons for early disappearance in some years are still unclear, results from this study explain the cause of *C. quinquecirrha* medusa disappearance in most years. Throughout the season, densities found in the net were higher than those measured by the visual counts (Fig. 5.2b). I interpret this difference to be caused by a non-uniform vertical distribution of *C. quinquecirrha* in the water column. After day 300 when temperatures began to cool below 15°C, densities measured by the net remained as high as in warmer temperatures while those measured by visual counts declined. This indicates that the already vertically stratified distribution had moved farther from the surface at the time of cooling. The experimental results show that temperatures below 15°C cause medusae to reside near the bottom (Figs. 5.4-5.6), as was suggested by the field observations (Figs. 5.2 and 5.3). Thus, the living medusae would be deposited on the sediment surface and pulsation rate would continue to slow until the temperature reaches 10°C, the limit of their temperature tolerance, as reported by Gatz et al. (1973).

Calculations of the amount of *C. quinquecirrha* carbon (CQC) present, annual flux, and deposition rate based on abundance observed in the Choptank and Patuxent rivers showed that medusae contribute organic matter to the tributary carbon cycles (Table 5.1). Literature values of dissolved organic carbon (Fisher et al. 1998), total

126

annual carbon flux (Kemp et al. 1997), and rate of deposition from the spring bloom (Hagy et al. 2005) from the mesohaline portion of Chesapeake Bay were compared with the calculated values (Table 5.1). Although the total flux from *C. quinquecirrha* deposition may be small relative to the total annual flux of carbon to the sediment, the calculated deposition rate—as much as 1% of deposition from the spring bloom— shows that the end-of-season deposition may represent a sudden pulse of carbon to the sediments. While the in situ observations of the end-of season disappearance of medusae and the tank experiments suggest that biomass from medusae is deposited on the bottom, the question remains whether this biomass decomposes in place or is further transported along the bottom by currents. I have assumed that carbon from *C. quinquecirrha* remains in the tributaries; however, further study is needed to understand the fate of this carbon once it reaches the sediment surface.

West et al. (2008) showed that the deposition of gelatinous organic matter can double sediment oxygen demand. In Chesapeake Bay and its tributaries where summer hypoxia and anoxia are increasingly common (Kemp et al. 2005), sources of increased oxygen demand are a serious concern. However, if low temperature causes the deposition organic matter from *C. quinquecirrha* medusae as our results suggest, it occurs late in the year when cool temperatures and reduced stratification result in a well-mixed and oxygenated water column. In fact, because they have few predators, medusae may be a reserve of organic matter that is not respired until late in the season when the threat of anoxia is gone.

The role of jellyfish as predators has been well studied (for example Cowan and Houde 1993; Behrends and Schneider 1995; Mills 1995), but because of low

apparent removal by predators, the fate of jellyfish biomass is only beginning to be addressed. Excretion from live gelatinous organisms can provide a fraction of the nutrients necessary to fuel primary production (Nemazie et al. 1993; Pitt et al. 2009). In addition to inorganic nutrients, jellyfish release dissolved organic matter to the water, which can fuel bacterial production. Riemann et al. (2006) showed that increased bacterial production coincided with the depth of highest abundance of jellyfish in a Norwegian fjord, presumably as a result of the DOM released by the jellyfish. This suggests that jellyfish are an important link to lower trophic levels (Riemann et al. 2006). Dead jellyfish biomass fueled bacterial production, but not all members of the bacterial community could utilize it, thus the jellyfish played a role in structuring the bacterial community (Titelman et al. 2006; Tinta et al. 2010). Therefore, *C. quinquecirrha* medusa biomass accumulating at the sediment surface at the end of the season may directly increase bacterial production and may also influence the bacterial community composition at that time.

Jellyfish are known for their ability to reach high abundances quickly (Mills 2001). These blooms can have great effects on the ecosystem through trophic interactions (for example Feigenbaum and Kelly 1984) and nutrient cycling (Pitt et al. 2009). The demise of such blooms can be equally important as nutrients are released through decomposition, as suggested above. In order to understand the role of decomposing gelatinous biomass on nutrient cycling, it is necessary to understand what factors cause the demise of jellyfish blooms. This type of information may lead to the ability to predict when and where decomposing gelatinous biomass will provide nutrients for bacterial production. Anthropogenic impacts are accumulating

throughout most marine and estuarine systems; therefore, it is likely that some of the factors that cause the death of jellyfish blooms and their subsequent role in carbon cycling have been or will be impacted. For example, Yamamoto et al. (2008) showed that jellyfish carcasses can be an important source of food to benthic scavengers in the Sea of Japan. Since fishermen cut up the jellyfish caught in their nets, they may alter the timing or rate of deposition of jellyfish carcasses to the sea floor. Understanding how these impacts will continue to affect jellyfish blooms, like that of *C. quinquecirrha* in Chesapeake Bay, may be important to understanding how nutrient cycling will respond to environmental changes.

In summary, the results indicate that low temperature causes medusae to sink in the water column. This information implies that gelatinous organic matter is delivered to the sediment when water temperature cools to 15°C. Although the medusae represent an appreciable amount of carbon, when low temperatures coincide with their demise, biomass deposition is unlikely to contribute to oxygen depletion. The results of this study show that in most years, when medusae disappear as water temperature decreases, the biomass from these organisms may be deposited onto the sediment surface where they will be decomposed.

during the summers of 2007 and 2008 respectively. I gratefully acknowledge Laura

Murray, Court Stevenson, and the Horn Point Laboratory for the use of equipment

necessary to this experiment. Comments from the editor and two anonymous revieIrs

were responsible for significant improvements to earlier drafts of this work.

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Table 5.1 Carbon from *Chrysaora quinquecirrha* (CQC) expressed as concentration, flux, and deposition rate and as percentages of the dissolved organic carbon (DOC), annual total organic carbon flux (TOC) to the sediment, and deposition from the spring bloom in the Choptank and Patuxent river estuaries of Chesapeake Bay.

	Measure of medusa abundance	CQC (mgC m^{-3})[c]	% of water column [DOC][d]	Annual CQC flux (mgC m^{-2})[e]	% Annual TOC flux[f]	CQC deposition rate (mgC m^{-2} d^{-1})	% deposition from spring bloom[g]
Choptank[a]	mean	1.59	0.79	72.51	0.12	3.37	0.66
	minimum	0.66	0.33	28.36	0.05	1.32	0.25
	maximum	24.97	1.04	112.37	0.18	5.23	1.02
Patuxent[b]	mean	1.38	0.69	12.57	0.02	0.58	0.11
	minimum	$3*10^{-3}$	$1.5*10^{-3}$	0.17	$2*10^{-4}$	$8*10^{-3}$	0.02
	maximum	0.22	0.11	77.79	0.13	3.62	0.71

[a]Measures of abundance on the Choptank River represent the highest weekly average abundance (no. m^{-3}) from twice daily visual counts at the Horn Point Laboratory dock on the Choptank River each year from 2005-2008. Secchi depth was used to estimate volume sampled.

[b]Measures of abundance on the Patuxent River represent the highest average of daily visual counts at the Chesapeake Biological Laboratory on the Patuxent River each year from 1960-1986. Visible depth was assumed to be approximately 1 m to estimate the volume sampled (D. Cargo, unpublished data).

[c]Concentrations of carbon from *C. quinquecirrha* were based on relationships between bell diameter, dry Iight, and carbon content from Purcell and Decker (2005) applied to abundance estimates from this study and Cargo and King 1990).

[d][DOC] of 200 μM was the dissolved organic carbon concentration in Chesapeake Bay at salinities ranging from 10-16 in September 1990 (Fisher et al. 1998).

[e]Flux was calculated from CQC using average depths of each river (Fisher et al. 2006).

[f]Annual TOC flux into the sediment of 61.2 g C m^{-2} for Chesapeake Bay (Kemp et al. 1997).

[g]Carbon deposition rate from the spring bloom in Chesapeake Bay was calculated to be 0.51 g C m^{-2} d^{-1} by Hagy et al. (2005). Carbon deposition rate of CQC was based on the average observed time for water temperature to drop from 15°C to 10°C in the Choptank River.
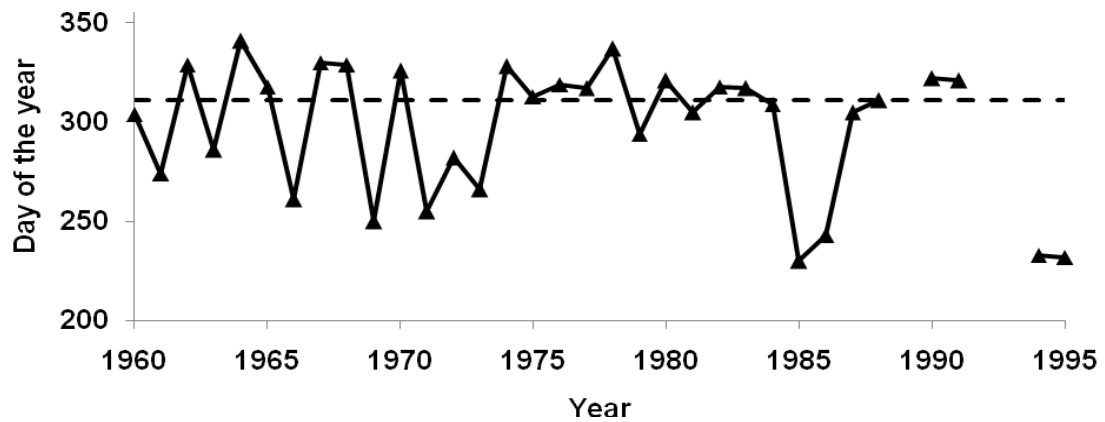
Fig. 5.1 Day of last occurrence of *Chrysaora quinquecirrha* medusae from visual

counts made at the Chesapeake Biological Laboratory on the Patuxent River,

Solomons Island, Maryland from1960-1995. Dashed line indicates the median day of
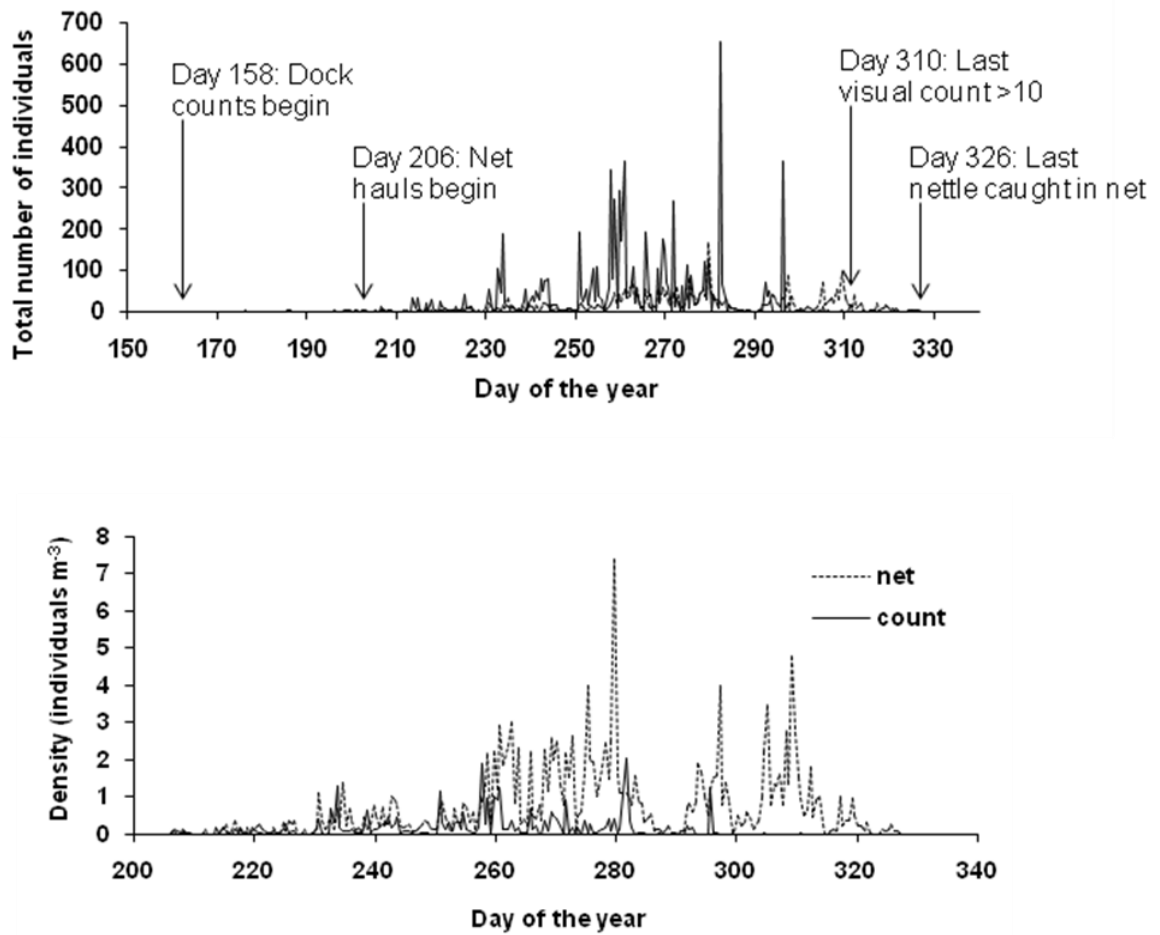
last occurrence (m=311, 7 November).

Fig. 5.2 Abundance (a) and density (b) of *Chrysaora quinquecirrha* medusae as measured by visual surface counts (solid) and vertical net hauls (dashed) in 2005 made from the Horn Point Laboratory dock, Cambridge, Maryland.
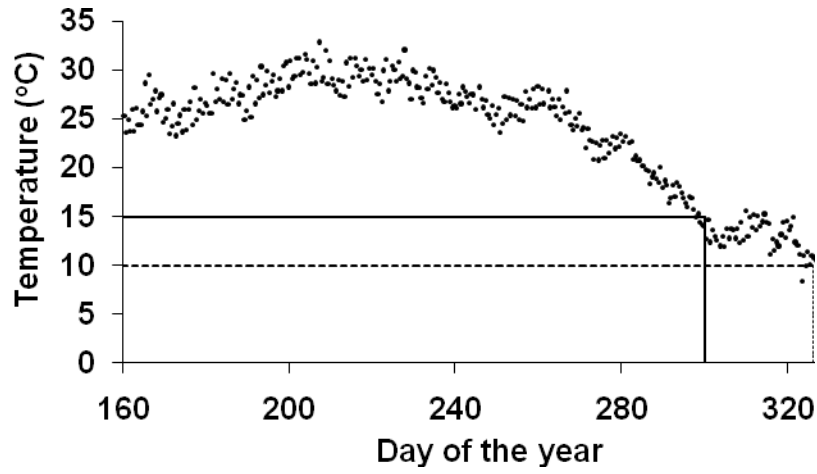
Fig. 5.3 Time series of water temperature measured at the Horn Point Laboratory dock, Cambridge, Maryland in 2005. Dashed lines indicate the temperatures on the dates disappearance of *Chrysaora quinquecirrha* medusae from the surface (solid) and disappearance from the net hauls (dashed) shown in Fig. 2.
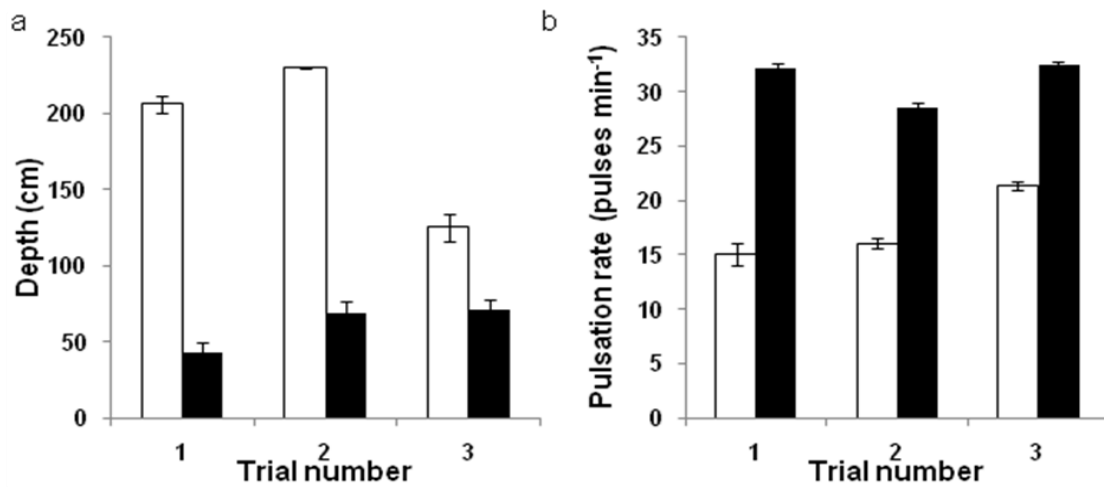
Fig. 5.4 Average depth (a) and pulsation rate (b) of *Chrysaora quinquecirrha* medusae for each trial. Average depths and pulsation rates were significantly different in the cold treatment tank (open bars) than in the control (dark bars) in all trials. Error bars represent standard error.
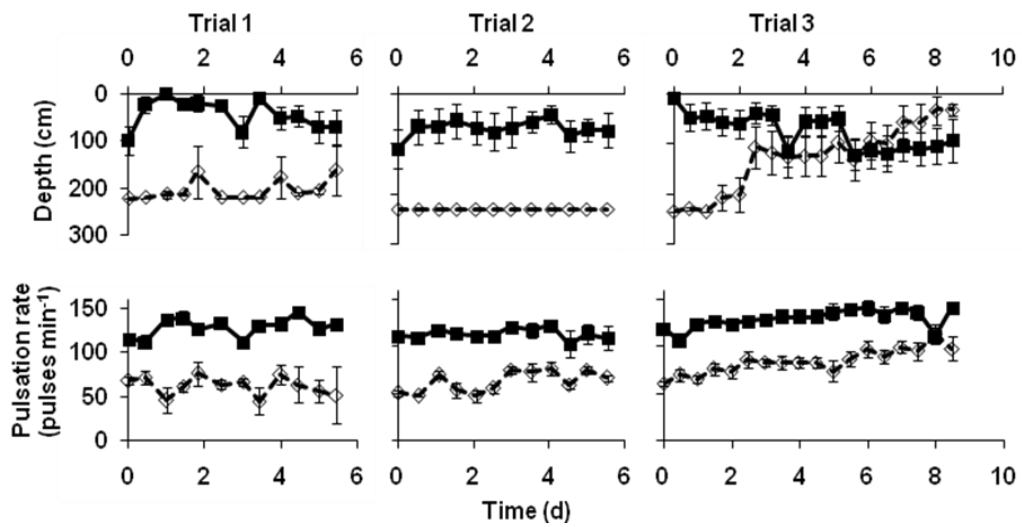
Fig. 5.5 Time series of average depth (top row) and pulsation rate (bottom row) of

Chrysaora quinquecirrha medusae as measured twice daily in the cold treatment

(open symbols) and the warmer control (filled symbols) tanks. Error bars represent
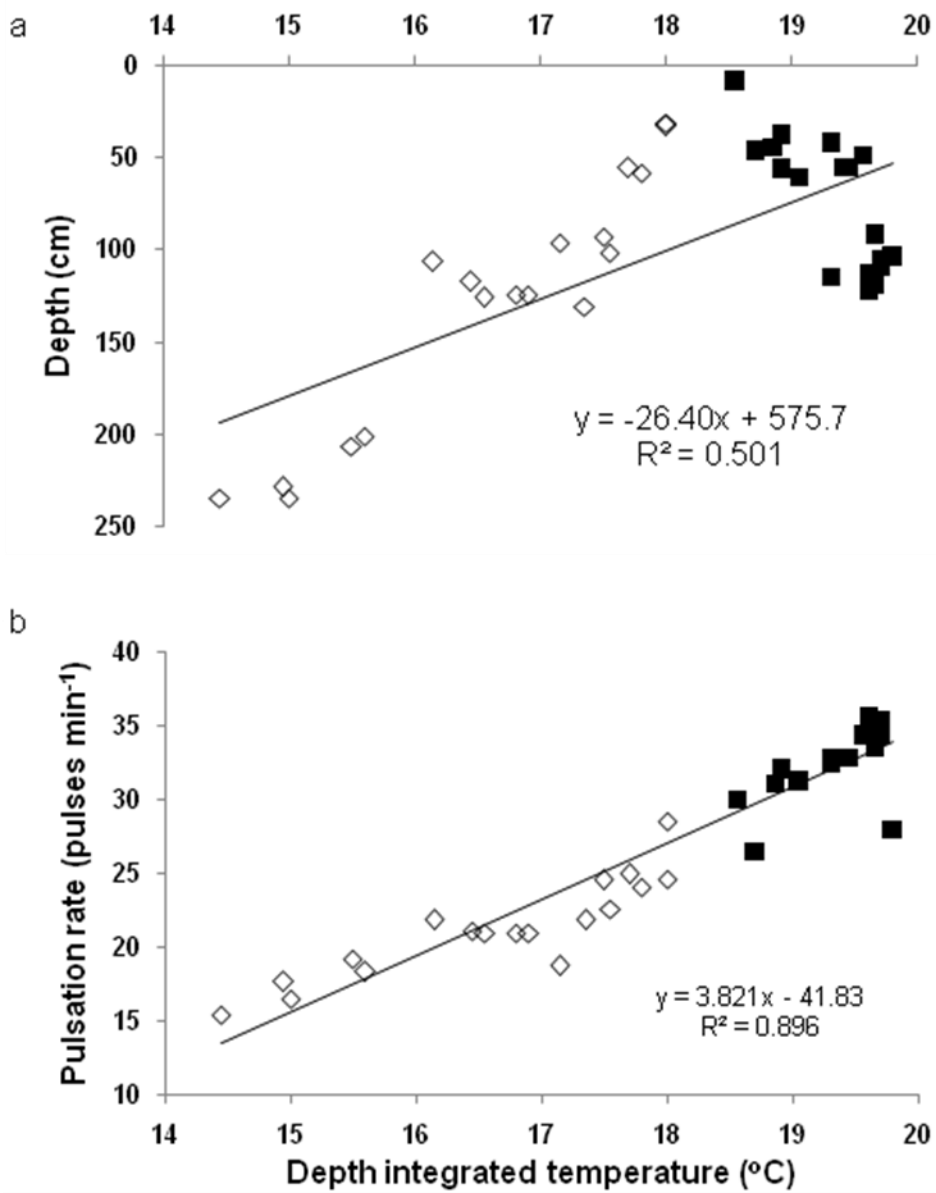
standard error.

Fig. 5.6 Least squares linear regression lines calculated for average depth (a) and pulsation rate (b) of *Chrysaora quinquecirrha* medusae from Trial 3 with respect to depth-integrated temperature. Open points are from the cold treatment and filled points are from the control.

Appendix 1

Observations of early disappearances of *Chrysaora quinquecirrha* medusae that could not be explained by decreasing temperature led to the development of several hypothesized causes of early disappearance: starvation, senescence, predation, or disease. Field observations in 2007 indicated that approximately two weeks prior to the final observation of any medusae in the visual counting area, oral arms were no longer present on the majority of medusae, and medusa diameter began to decrease. Similar observations of missing oral arms preceded early disappearances in 2009 and 2010. Two of the hypotheses, starvation and senescence, were examined using tank experiments in 2009 and 2010 to determine whether lack of prey or natural aging caused a loss of oral arms and early disappearance similar to that observed in the field.

The experiment was conducted using 1.2 m^3 tanks filled with 1-µm filtered water from the Choptank River. Water was completely changed once each week throughout the experiment. In 2009, each of nine tanks was randomly assigned to either the fed or the starved treatment with four tanks in the fed group and five tanks in the starved group. In 2010, only eight tanks were available, and each was again randomly assigned to either the fed or starved group with four tanks in each group. On the first day of each experiment, medusae were captured from the pier in Cambridge, Maryland, USA and assigned randomly to the tanks with two medusae in each.

Oral arm length and total volume of each medusa was measured on the first day of each of the two trials. Oral arm length was measured by lifting the medusa out

142

of the water, gently supporting the bell from beneath but allowing the oral arms to trail below it. The length of the trailing oral arms was quickly measured while the animal was held out of the water. Volume was measured by placing the animal in a 1-L graduated cylinder with a known volume of water. These measurements were repeated twice weekly throughout the experiment in 2009 and once weekly in 2010. Measurements continued on these schedules until all of the medusae had died.

The medusae in the fed group were fed commercially available fish food flakes with a high fishmeal and shrimp-meal content. The medusae were gently dipped from their tanks and placed in approximately 2 L of water. A slurry of fish flakes and water was then applied to their oral arms with a large pipette until the oral arms became saturated with food. Within approximately 30 minutes, the brightly colored food would be visible inside the bell of the medusae. Once most of the food had been transferred from the oral arms into the mouth, the medusae were placed back in their tanks. In 2009, they were fed twice weekly, and in 2010 they were fed four times a week.

Least squares linear regression was used to characterize the trends in mean oral arm length, mean total volume, and the ratio of mean oral arm length to mean total volume over time (Sokal and Rohlf 1995). All means were calculated based on measurements of all of the individuals in an experimental group. Analysis of covariance (ANCOVA) was used to compare the rates of decrease in mean length and mean volume between the fed and starved groups.

Finally, timing of medusa disappearance from a time series of Weekly mean visual counts made at the Chesapeake Biological Laboratory in Solomons, Maryland,

USA on the Patuxent River from 1985 to 1995 were compared with the September

zooplankton abundance as measured by the Chesapeake Bay Program for the same

years. Average July-August counts from 1960 to 1986 from this series are published

in Cargo and King (1990), but dates of final occurrence were not published. Counts

were made by D. G. Cargo with assistance from M. Wiley and H. Millsap until 1991.

M. Wiley continued the counts in 1992 and 1993, and H. Millsap continued them in

1994 and 1995. Counts of mesozooplankton collected by the Chesapeake Bay

Program Maryland Mesozooplankton Monitoring Project at the Patuxent River station

LE1.1 were downloaded from http://www.chesapeakebay.net/data_plankton.aspx

(collection methods described in EPA 2007). Least squares linear regression was used

to determine whether there is a relationship between the timing of medusa

disappearance and the abundance of mesozooplankton prey in late summer.

   The size of medusae in both groups decreased with respect to both oral arm

length and total volume over the duration of the experiment (Figs. A.1a,b and

A.2a,b). Least squares linear regression indicated that these trends of decreasing

length and volume over time represent a significant relationship ($p < 0.05$; Table A1).

In 2009, there was no significant difference between the slopes of the fed and starved

groups' oral arm length (ANCOVA; Table A.1a); however in 2010, the length of the

oral arms of medusae in the fed group decreased at a faster rate than those in the

starved group (ANCOVA; Table A.1b). There was no significant difference in the

rate of decreasing volume between the fed and starved groups in either year

(ANCOVA; Tabel A.1a,b). The slope of the regression line for the ratio of oral arm

length to total volume, on the other hand, only showed a significant difference from zero in the starved group in 2009 (Figs. A.1c, A.2c and Table A.1).

Comparison of the timing of medusa disappearance with mesozooplankton abundance in late summer indicated that the relationship between them is inverse with high mesozooplankton abundance in years with early medusa disappearance (Fig. A3). Least squares linear regression indicates that this relationship is statistically significant (p = 0.03667, r^2 = 0.6157).

The decrease in size was expected for the starved group, but the decrease in the size of those individuals in the fed group indicated that they were not receiving enough food. In 2010, frequency of feeding was increased in order to avoid or at least slow degrowth. That the pattern of decreasing length and volume continued in the fed group in 2010 indicates that the increased food supply was not sufficient to maintain the medusae. Additionally in 2009, it was evident that the medusae suffered physical damage to both the bell and oral arms when they were removed from the tanks and measured. The frequency of measurement was decreased in 2010 in an attempt to minimize the effects of this damage, but the unequal frequency of measurement and feeding means that the fed group was handled more frequently than the starved group. The effects of this increased handling may explain the fact that the rate of oral arm length decrease was greater in the fed group (ANCOVA, Table A.1).

While these flaws affect the results of the experiment, the results do provide some insight into the mechanisms by which the annual *Chrysaora quinquecirrha* bloom disappears. In both trials of this experiment, the ratio of oral arm length to total volume showed no significant negative trend in the fed group. Coincidentally, in both

145

years, medusae disappeared from the Choptank River at least 50 days before all of the experimental medusae died in the tanks. Since the experimental medusae were taken from the Choptank River population, it is reasonable to assume that if senescence was the cause of the decline of the bloom, the experimental medusae would also have died at the same time and would have been expected to show the same symptoms as those that remained in the natural population. While I cannot rule out the possibility that the medusae would have eventually exhibited natural senescence if they had been provided sufficient food in the laboratory, loss of oral arms does not appear to be a symptom of natural senescence. Further support for this conclusion can be found in a population genetics model based on corals. Orive (1995) indicates that organisms with complex life histories that include an asexual reproductive stage like the polyp stage of cnidarians are unlikely to evolve natural senescence.

While the ratio of oral arm length to total volume did show a significant negative trend in 2009, it never reached zero in any group before all of the medusae from the group had died. Visual observation of the natural population indicates that oral arm length approached zero over an approximately two week period immediately prior to disappearance in 2007, 2009, and 2010 (unpublished observation). This difference between the natural population and those starved in this experiment indicate oral arm loss is not a symptom of starvation.

I conclude that the loss of oral arms by *Chrysaora quinquecirrha* medusae and associated early disappearance in 2007, 2009, and 2010 were most likely not related to either a natural senescence or starvation. Any biological or environmental factors that did contribute to the loss of oral arms were excluded from our experimental

tanks. Remaining hypotheses not addressed by this experiment include infection with a disease or parasite or an unusually high rate of predation. Further inquiry is needed to address these possibilities.

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Tables

Table A.1: Statistical results of linear regression and ANCOVA for fed and starved medusae mean oral arm length, mean total volume, and mean ratio of length to volume in 2009 (a) and 2010 (b). Slope, r^2, and p-value all refer to the results of the linear regression analysis of the variable for on group over time. The final row of each table expresses the results of the ANCOVA test for difference of slopes between the two groups for each variable.

A: 2009	length		volume		length/volume	
	fed	**starved**	**fed**	**starved**	**fed**	**starved**
slope	-0.3634	-0.4110	-0.2800	-0.4033	-0.0074	-0.0154
r^2	0.7067	0.9230	0.5000	0.8156	0.2450	0.5225
p-value	$4.54*10^{-5}$	$4.87*10^{-8}$	0.0022	$9.65*10^{-6}$	0.0512	0.0079
ANCOVA	no significant difference		no significant difference		no significant difference	

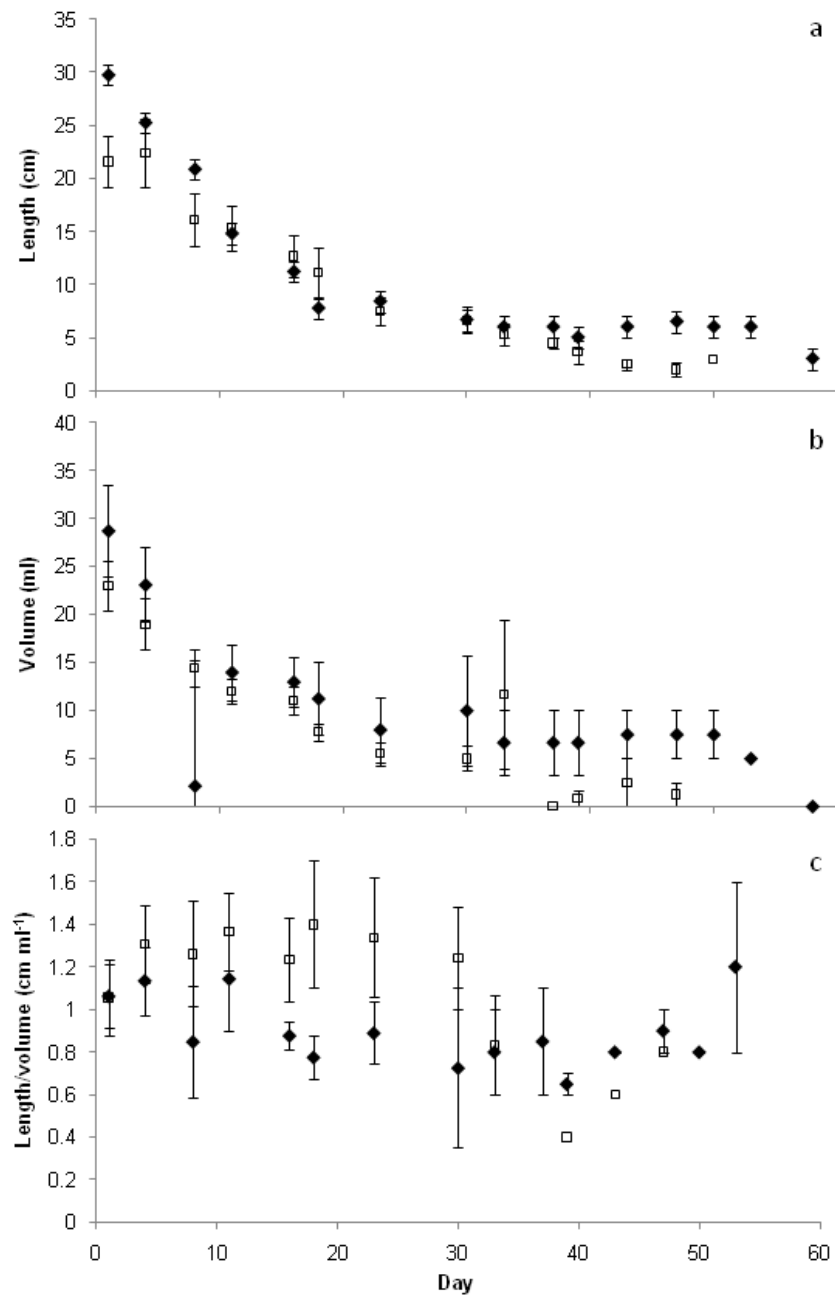| B: 2010	length		volume		length/volume	
	fed	**starved**	**fed**	**starved**	**fed**	**starved**
slope	-0.5923	-0.5308	-0.3617	-0.5951	-0.0117	-0.0052
r^2	0.9720	0.9385	0.8290	0.8350	0.3813	0.0532
p-value	$1.77*10^{-7}$	$7.43*10^{-5}$	0.0003	0.0015	0.0572	0.5828
ANCOVA	significantly different slopes		no significant difference		no significant difference	

Figures

Fig. A.1: Mean oral arm length (a), mean total volume (b), and ratio of mean oral arm length to mean total volume over time. Day 1 = 24 Aug. 2009. Shaded points represent the means from the fed group, and open points represent means from the starved group. Error bars represent standard error of the mean.

Figure A.2: Mean oral arm length (a), mean total volume (b), and ratio of mean

oral arm length to mean total volume over time. Day 1 = 8 Sept. 2010. Shaded

points represent the means from the fed group, and open points represent means

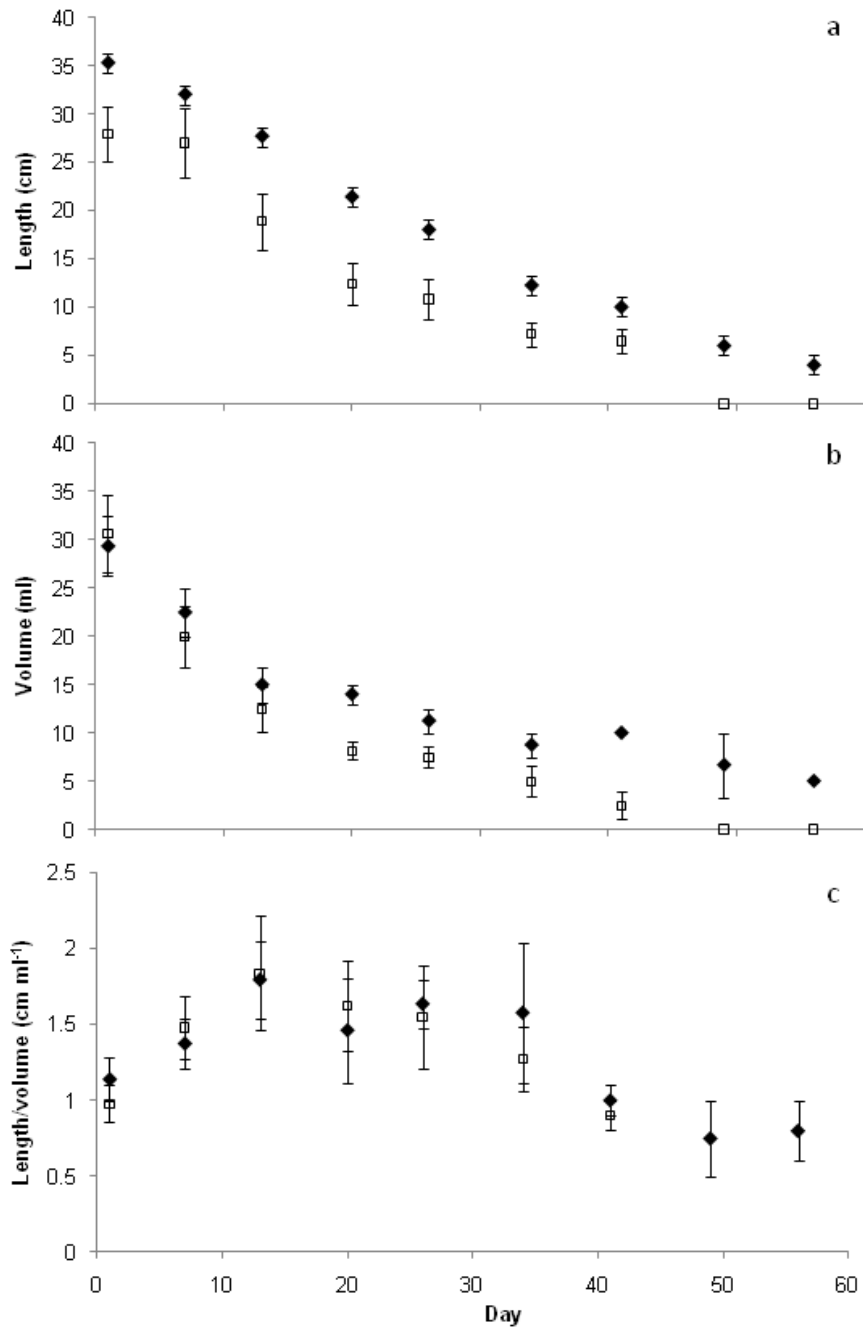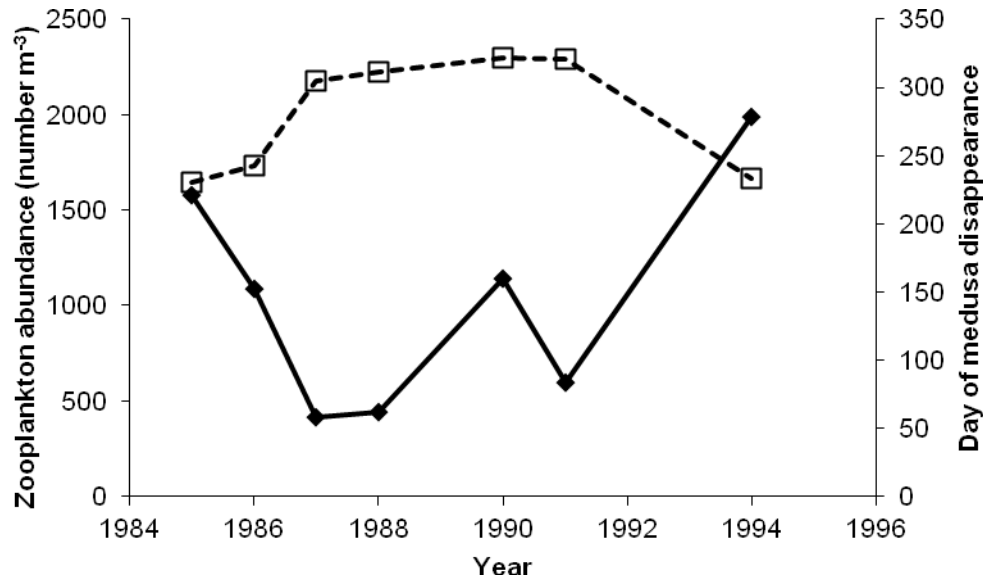from the starved group. Error bars represent standard error of the mean.

Figure A.3: Mesozooplankton abundance in the Patuxent River as measured by the Maryland Mesozooplankton Monitoring Project at the Patuxent River station LE1.1 (open points, dashed line), and annual day of *Chrysaora quinquecirrha* medusa disappearance at the Chesapeake Biological Laboratory, Solomons, MD, USA (dark points, solid line).

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