CTENOPHORE POPULATION DYNAMICS: PATTERNS OF ABUNDANCE FOR *MNEMIOPSIS* IN U.S. COASTAL WATERS

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Abstract

The impact of gelatinous predators is directly related to their abundance. Therefore it is critical to understand and quantify the factors which control the abundance of these predators. An examination of plankton and environmental data for several coastal systems in the United States indicates that high biomasses of *Mnemiopsis spp.*, are associated with warm waters and an abundance of moderate sized copepods (i.e. *Acartia tonsa*). Field data suggest that temperature, food abundance, and predators may all be important in determining the observed patterns of ctenophore abundance. Currently there is insufficient quantitative information on processes which control growth and mortality rates to be able to make definitive conclusions about ctenophore population dynamics from field data or construct meaningful models.

Introduction

Mnemiopsis spp., *M. leidyi* and *M. mccradyi* are periodically abundant in the coastal waters of the United States from Cape Cod in the Northeast, along the Atlantic and Gulf Coasts, to southern Texas and may play an important role as zooplankton predators. A critical part of evaluating the impact of these gelatinous carnivores is an understanding of their population dynamics and the factors which control their abundance. Ideally, a discussion of population dynamics would include quantitative information on somatic growth, reproduction, and mortality, and how these rates vary over time to produce the observed biomass. Although there have been some experimental studies of growth rates for *M. mccradyi* (Reeve et al. 1989, Kremer and Reeve 1989), there is very little data on rates of egg production in the field (Baker 1973, Kremer 1975). Although both vertebrate and invertebrate predators have been identified, including the destruction of larval ctenophores by zooplankton (Stanlaw et al. 1981), rates of mortality cannot to date be quantified with any confidence.

In the absence of information on relevant rates, ecologists often attempt to infer process from measurements of stocks and how they vary with time. Therefore, in order to try to gain some insights into ctenophore population dynamics, I have tried to summarize and compare what is known about the pattern of abundance of *Mnemiopsis spp.* throughout their range in the United States. It is the goal of this study to compare the documented patterns of ctenophore abundance with other environmental variables such as temperature, prey biomass, and the presence of known predators, looking for patterns that suggest what factors control ctenophore biomass and their impact as gelatinous carnivores.

Due to time and logistical constraints, most the of the information for this paper has been derived from published papers supplemented by what was readily accessible to me through several colleagues. There is a vast resource of unpublished and "gray" literature that undoubtedly would add a lot of additional information. It has been beyond the scope of this investigation to conduct an exhaustive information search. Rather I have chosen to compare representative systems over the entire geographic range which have been relatively well studied . Some relevant studies are not discussed explicitly because patterns are similar to other systems (Mountford 1980) or because zooplankton data is lacking (Miller 1974). With only a few exceptions I have limited myself to studies in which investigators have quantified both the abundance of ctenophores and their zooplankton prey. I have used non quantitative and anecdotal data as useful supplements to assure me that my chosen examples are not atypical of their respective regions.

Examples from Various Regions

Data on ctenophore and zooplankton abundance and seasonality are summarized in Table 1 along with some hydrographic information. The following paragraphs discuss briefly each of the selected locations.

Narragansett Bay, Rhode Island is near the northern end of the range for *M. leidyi*. This temperate estuary (latitude 41° 30') has an annual temperature range of 1-25 C, and a fairly narrow salinity range (21-32‰) due to a modest influx of fresh water. The zooplankton biomass is dominated by two species of calanoid copepods, *Acartia hudsonica* during the colder temperatures, and *A. tonsa* during the summer and fall (Hulsizer 1976, Durbin and Durbin 1981). Large interannual variability is evident in the several years of data which are available for zooplankton abundance, but usually there is a high biomass in the late spring/early summer. Typically *M. leidyi* is at low to undetectable numbers during the winter and spring. There is a rapid biomass increase during the summer of several orders of magnitude, peaking in the late summer/early fall, with a period of high biomass lasting about 2 months (Kremer and Nixon 1976, Deason and Smayda 1982). In some years there have been measurable numbers of ctenophores collected during the early winter. particularly in years with a lower abundance of ctenophores during the summer (Deason 1982, Smayda 1988). A maximum seasonal biomass measured as displacement volume, averaging greater than 50 ml m^{-3} is typical for *Mnemiopsis* in Narragansett Bay. Biomass of ctenophores in the late summer has been shown to correlate directly with the biomass of crustacean zooplankton in the early summer (Deason and Smayda 1982). Additional sampling results from subsequent years (Smayda unpublished) can be used to investigate how well this relationship between ctenophore biomass and pre-existing food supply holds over a span of nearly 20 years. Modeling studies have shown that food availability is the key factor in determining

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the maximum ctenophore biomass (Kremer 1976, Kremer and Kremer 1982). Both butterfish, *Peprilus triacanthus* and the ctenophore *Beroe ovata*, are documented predators on *M. leidyi* (Oviatt and Kremer 1977, Kremer and Nixon 1976), and combined with reduced fecundity may be contribute to the rapid decline of ctenophores in the fall. *M. leidyi* in Narragansett Bay can also become heavily infected by a parasitic anemone (Crowell 1976).

Long Island Sound, which separates Connecticut and Long Island, New York (Lat. 41°) is deeper than the coastal estuaries, has a narrow range in salinity (24-29‰). The temperature range (0-24°) is typical of the northeastern U.S.. Generally, there are two biomass peaks in zooplankton, a spring peak dominated by *Temora longicornis*, and a summer-fall peak dominated by *Acartia tonsa*. Zooplankton stocks can be quite high (Deevey 1956) and there is large interannual variability in zooplankton abundance (Johnson 1987). the timing of seasonal stratification and de stratification may be critical in controlling the zooplankton stocks (Peterson 1986, Beckman and Peterson 1986). Typically there is a maximum abundance of ctenophores in the summer with average biomasses and interannual ranges similar to those in Narragansett Bay. The large shallow bays around Long Island are generally similar to Long Island Sound in their timing and magnitude of ctenophore abundance (Turner 1982, Park and Carpenter 1987, Monteleone 1988, Duguay et al. 1989).

Chesapeake Bay, Maryland is a large and complex estuarine system. Although ctenophores have been noted throughout most of the bay, this summary will focus on the mesohaline mid-bay region (38° 30') for which there are the most data (Olson 1987, VERSAR Inc. 1992, Purcell et al. in press). Temperatures typically range 2-26 C annually, and the salinity from 5-16‰. Annually there are two peaks in zooplankton abundance, a spring peak dominated by the copepod *Eurytemora affinis* and a summer peak which is generally larger dominated by *A. tonsa*. The lobate ctenophore, *M. leidyi*, is also most abundant during the summer, between June and September. The peak period for copepod and ctenophore biomass can co-occur, with both dropping off in the fall. Copepod production, as measured by egg production is typically high from mid-May to September (Purcell et al. in press) with females producing eggs at a rate of 30-120% of their body carbon per day. Ctenophore biomass appears to be somewhat less than measured in Narragansett Bay, based on a several year data set for both systems. The scyphomedusa, *Chrysaora quinquecirrha*, a known ctenophore predator, is common in the Chesapeake Bay and appears to influence the population dynamics of *Mnemiopsis* (Feigenbaum and Kelly 1984).

Biscayne Bay, in Southern Florida is a shallow subtropical estuary with a temperature range of 18-32 C and salinities ranging from mesohaline (<20‰) to hypersaline (>40‰), depending

on the season and location. For much of the bay there is no strong seasonal pattern in zooplankton biomass (Reeve 1970, 1975, Baker 1973), but there seemed to be a summertime low followed by a peak in the fall-winter, particularly in Card Sound. Baker (1973) found *M. mccradyi* in fairly high abundance most of the year in Central Biscayne Bay (70% average frequency of occurrence for 11 stations), with a pronounced summer low and peak in the fall. Fewer ctenophores were found in South Biscayne Bay (Reeve 1970) and none in Card Sound (Reeve 1975) which had similar depths, salinities and temperatures to the Central Bay, but where the zooplankton biomass was lower. In more recent years ctenophores have been abundant only in North Biscayne Bay (Reeve pers. comm.) presumably because zooplankton stocks to the south have been insufficient to support an actively reproductive ctenophore population. Baker's data indicated that ctenophores were not found in waters with zooplankton stocks of less than 3 mg C m^{-3}, while an experimentally based energetics model indicated that a stock of about 20 mg C m^{-3} was necessary for ctenophores to grow to reproductive size (Kremer and Reeve 1989). The population of *M. mccradyi* in Biscayne Bay seems to be right "at the edge" of sufficient food resources. Unfortunately, multi-year data do not exist for the various sub-regions of the Bay, and system-wide changes during the past twenty years have not been quantified.

Coastal waters along the Gulf of Mexico are generally less well studied than those waters described above. There are only a few published papers which quantify zooplankton biomass and document ctenophores. Both St. Andrews Bay, Florida (Hopkins 1966) and Corpus Christi Bay, Texas (Buskey in press) are shallow and have similar annual ranges in temperature and salinity (Table 1). *M. mccradyi* appeared to be in abundance only infrequently in St. Andrews Bay. In Corpus Christi, however, ctenophores were consistently present with several biomass spikes throughout the year and no particularly strong seasonality. Both *Chrysaora* and *Beroe* are present in these waters as well (Buskey pers. comm.). Along the coasts of Mississippi (Phillips et al. 1969) and Louisiana, ctenophores are present for much of the year and abundant at variable times, most consistently in the summer when they cause serious clogging and sampling problems for zooplankton monitoring studies (Gillespie 1971, Perry and Christmas 1973).

Discussion

Mnemiopsis spp. show a strong association with warm temperatures and waters dominated by the copepod *Acartia tonsa*, a fast growing ubiquitous species, typical of warm coastal environments. In the Northeast where the ctenophore populations die back to very low levels each year, there is a population explosion in the summer. Ctenophore peak biomass seems to be the greatest near the northern end of the range (Long Island Sound and Narragansett Bay) where the period of abundance is relatively brief (2-3 months). In waters where ctenophores are present nearly year round (eg. Corpus

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Christi and Biscayne Bay) there are generally lower peak biomasses. This pattern of ctenophore abundance may be partly due to relative food availability. Peak zooplankton stocks are generally higher and more seasonally pronounced in the northern systems than in the subtropical waters.

The influence of temperature on the population dynamics of *Mnemiopsis spp* has not been studied directly. Regional data suggest, however, that low temperatures severely retard growth and reproduction even though ctenophores have been observed to survive in cold water.

Large individual *Mnemiopsis spp* have been measured to produce thousands of eggs when freshly collected from the field (Baker 1973, Kremer 1976). Laboratory studies have shown rates of egg production to be influenced strongly by food availability (Reeve et al. 1989). Currently there are too little data to indicate the degree of food limitation for field populations of ctenophores. It is likely that egg production in the field is depressed when food stocks drop (Kremer 1975). Data from Biscayne Bay indicate that areas depauperate in prey zooplankton cannot support a population of *Mnemiopsis* and interannual comparisons from Narragansett Bay indicate that the biomass of copepods in the early summer and the subsequent ctenophore biomass are closely linked. Modeling efforts (Kremer 1976, Kremer and Kremer 1982) have indicated that food availability is the driving force which controls the peak abundance of ctenophore biomass. These models did not seriously consider the potential importance of predation, however.

The role of predators in controlling the biomass of ctenophores remains largely a subject of speculation. There are some examples from field abundance patterns that suggest the strong influence of invertebrate predators (eg. Kremer and Nixon 1976, Feigenbaum and Kelly 1984). Generally the patterns of ctenophores and their predators are not well known and the data are too thin to draw definitive comparisons. Taxonomic and life history differences among predators are also likely to be important. For example, the ctenophore *Beroe ovata* feeds only on other ctenophores and therefore is dependent on a high biomass of *Mnemiopsis* as a precursor. Given a suitable food supply, however, this predatory ctenophore can grow and reproduce rapidly and exert a strong predatory force. By contrast, the scyphomedusa *Chrysaora quinquecirrha* feeds not only on ctenophores but other jellies and crustacean zooplankton. Its life cycle requires a benthic polyp stage, and its population appears to be strongly correlated with interannual variations in salinity (Cargo and King 1990). The influence of fish predators is even more difficult to evaluate as feeding rates are very poorly known.

There is also evidence that ctenophore population growth rates may be strongly influenced by the composition of the zooplankton itself. Laboratory experiments indicate that the presence of large copepods can lead to very poor survival rates for newly hatched ctenophores (Stanlaw et al. 1981). Given the high reproductive potential of *Mnemiopsis spp*, it seems unlikely that this mechanism would serve to completely inhibit population growth in an otherwise favorable food environment, but high and

variable mortality of young stages must be taken into account in any serious analysis of ctenophore population dynamics. A preliminary model tried to take this into account (Kremer and Kremer 1988).

In summary, there are several critical questions which need to be evaluated regionally before the population dynamics of *Mnemiopsis* understood well. Among them are the following:

1. What is the importance of temperature in determining growth and reproductive rates for *Mnemiopsis spp* .?

2. What is the role of food limitation in limiting the abundance and biomass of *Mnemiopsis spp*.? To what extent are field populations of *Mnemiopsis spp* . food limited?

3. How important are predators in limiting the peak biomass and duration of high population abundance of *Mnemiopsis spp* .?

4. Are predators capable of "holding back" a population of *Mnemiopsis spp* . when food availability can support high rates of both somatic and reproductive growth?

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Table 1. Comparison of plankton patterns over the range of *Mnemiopsis spp.* in the United States.

Location	Avg. depth m	Temp. °C	Salinity ‰	ZOOPLANKTON BIOMASS mgC m^{-3} season	peak	peak range	CTENOPHORE BIOMASS ml m^{-3} season	peak	peak range	#years	references
Narragansett Bay, Rhode Island	9	1 - 25	25 - 32	June-July	70 [a]	30-110	Aug.-Sept.	50	6-100	>8	1
Long Island Sound Connecticut/New York	20-30	0-24	24-29	March-May July-October	100 [a,b]	20-200	July-Sept.	50	20-199	3	2
Chesapeake Bay (mid), Maryland	5-10	2-26	5-16	summer	90 [b]	30-180	June-Sept.	20	10-40	12	3
Biscayne Bay, Florida.	2	18-32	14-45	variable (fall to winter)	11 [c]		fall	30	-	1+	Baker 1973
St. Andrews Bay, Florida.	2-5	11-29	19-33	variable (late spring, fall)	25 [a] (12 av.)		variable (winter)	ND		2	Hopkins 1966
Corpus Christi Bay, Texas.	2.4	7-31	20-38	variable	50 (17 av.)		variable (summer)	15	8-20	1	Buskey 1993

a. >153 μm fraction, assuming C = 35% of dry weight, or 1 ml displ. vol = 60 mg C
b. converted from counts assuming 3μg C per copepodite/adult
c. >202 μm fraction, assuming C = 35% of dry weight

1. Hulsizer 1976, Kremer 1976, Kremer and Nixon 1976, Durbin and Durbin 1981, Deason 1982, Deason and Smayda 1982, Smayda 1988
2. Deevey 1956, Peterson 1985, Peterson 1986, Beckman and Peterson 1986, Johnson 1987
3. Lonsdale 1981, Olson 1987, VERSAR inc. 1992, Purcell et al. in press