

Patterns of abundance for *Mnemiopsis* in US coastal waters: a comparative overview

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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 prey copepods such as *Acartia tonsa*. Field data from several locations suggest that temperature, food availability, and predators may all be vital in determining the observed patterns of ctenophore abundance. Although currently there is insufficient quantitative information to make definitive conclusions about the control of ctenophore population dynamics in any of these systems, a comparison of patterns of abundance implies there may be a latitudinal gradient in the relative importance of temperature and food availability. In the north, where annual temperature cycles are likely to have the greatest influence, there is a relatively short, but intense, population explosion of *M. leidyi* in the late summer and early fall. In the warmer southern waters, the occurrence of *M. mccradyi* seems to be more closely linked to prey availability, and ctenophore biomass is generally lower. Predation may be of fundamental importance to the patterns of abundance for the two species of *Mnemiopsis* throughout their ranges, but presently is poorly documented in most systems.

Key words: ctenophore, *Mnemiopsis*, abundance patterns, population dynamics.

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Introduction

Mnemiopsis spp., *M. leidyi*, and *M. mccradyi* are periodically abundant in the coastal waters of the United States from Cape Cod in the north-east, along the Atlantic and Gulf Coasts, to southern Texas. A critical part of evaluating the impact of these gelatinous carnivores is to understand their population dynamics and the factors that control their abundance throughout the range. Ideally, a discussion of population dynamics would include quantitative estimates of somatic growth, reproduction, and mortality, in all locations, 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 and Baker, 1975; Reeve *et al.*, 1978, 1989; Kremer and Reeve, 1989), extrapolation of these laboratory results undoubtedly underestimates the somatic growth rates for field populations. There are presently very few data on rates of egg production by *Mnemiopsis* spp. for either the laboratory or field (Baker, 1973; Kremer, 1975; Reeve *et al.*, 1989), but reproductive rates for the two species are comparable. Existing results indicate that individual ctenophores are capable of producing

thousands of eggs per day, but there are very limited data on how fecundity varies seasonally in the field and how egg production correlates with temperature and food availability. Vertebrate and invertebrate predators on *Mnemiopsis* spp. have been identified (Dunnington and Mansueti, 1955; Phillips *et al.*, 1969; Miller, 1974; Kremer and Nixon, 1976; Oviatt and Kremer, 1977; Feigenbaum and Kelly, 1984), including the destruction of larval ctenophores by zooplankton (Stanlaw *et al.*, 1981), but rates of mortality cannot presently be quantified in any system.

In the absence of direct data on these relevant rates, some information about critical processes may be inferred from measurements of ctenophore stocks, how they vary with time and how they correlate with environmental variables. This review seeks some insights into ctenophore population dynamics over a latitudinal gradient by summarizing and comparing patterns of abundance of *Mnemiopsis* spp. throughout their ranges in the United States. Ctenophore abundance is analyzed within the context of several environmental variables, including temperature, prey biomass, and the presence of known predators to look for suggestions of factors that control ctenophore biomass in various locations.

This brief overview is limited to a comparison of systems that are representative of geographic areas. Some relevant studies have been omitted because patterns are similar to other systems (e.g. Mountford, 1980) or because zooplankton data are lacking (e.g. Miller, 1974). When appropriate, non-quantitative and anecdotal information has been used.

Examples from various regions

Data on ctenophore and zooplankton abundance and seasonality are summarized in Table 1 with hydrographic information. Summaries of annual patterns of temperature, prey zooplankton biomass, and ctenophore biomass are represented schematically in Figure 1.

Narragansett Bay, Rhode Island

Narragansett Bay, Rhode Island, is near the northern end of the range for *M. leidyi*. This temperate estuary (average latitude 41°35' N) has an annual temperature range of 1–25°C, with temperatures >20°C from June to September. The salinity range (21–32) is fairly narrow. 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 in zooplankton stocks has been documented, but zooplankton biomass is generally high from April through July (Fig. 1a). 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 (August–September), 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 averaging 50 ml m⁻³, measured as displacement volume, is typical for *M. leidyi* 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). Modeling studies also indicate that food availability is the key factor in determining the maximum ctenophore biomass (Kremer, 1976; Kremer and Kremer, 1982).

Both butterfish, *Peprilus triacanthus*, and the ctenophore *Beroë ovata* are documented predators on *M. leidyi* (Oviatt and Kremer, 1977; Kremer and Nixon, 1976), although *B. ovata* is not present regularly in Narragansett Bay. Late in the season, *M. leidyi* can become heavily infected by a parasitic anemone (Crowell, 1976), but the effect of these parasites on the ctenophores is unknown.

Long Island Sound

Long Island Sound (average latitude 41° N) is deeper than the coastal estuaries, has a relatively narrow range in salinity (24–29), and a temperature range (0–24°C) typical of the coastal waters of the north-eastern US. Temperatures >20°C occur from July until September. Generally, there are two biomass peaks in zooplankton, a spring peak dominated by *Acartia hudsonica* and *Temora longicornis*, and a summer–fall peak dominated by *A. tonsa* and *Parvocalanus crassirostris* (Deevey, 1956; Peterson, 1985). Zooplankton stocks can be quite high and there is large interannual variability in zooplankton abundance (Johnson, 1987).

Typically, there is a maximum abundance of *M. leidyi* in the summer (Beckman and Peterson, 1986), with average biomasses and interannual ranges similar to those in Narragansett Bay (Table 1). 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

Chesapeake Bay, Maryland, is a large and complex estuarine system. Although *M. leidyi* has been noted throughout most of the Bay, the mesohaline mid-bay region (38°30' N) is the best studied (Olson, 1987; Versar Inc., 1992; Purcell *et al.*, 1994). Temperatures typically range from 2–26°C annually with temperatures >20°C from June to October. Salinity in this region of the bay ranges from 5–16, with a strong seasonal pycnocline. Annually, there are two peaks in zooplankton abundance, a spring peak dominated by the copepods *Acartia hudsonica* and *Eurytemora affinis* and a summer peak dominated by *A. tonsa* (Olson, 1987; Versar Inc., 1992; White and Roman, 1992). *M. leidyi* is most abundant between June and September. In contrast to Narragansett Bay and Long Island Sound, the summertime peak period for copepod and ctenophore biomass may occur simultaneously, with both dropping off in the fall (Fig. 1b). Copepod production, as measured by egg production, is typically high from mid-May to September (Purcell *et al.*, 1994). Ctenophore biomass appears to be generally less than in Narragansett Bay, based on a data set for both systems over several years (Table 1). Common predators of ctenophores include the scyphomedusa, *Chrysaora quinquecirrha* (Feigenbaum and Kelly, 1984; Purcell, 1992; Purcell *et al.*, 1994), and harvestfish (Dunnington and Mansueti, 1955; Mansueti, 1963). *B. ovata* is found only in the high-salinity region near the mouth of the Bay (Burrell and Van Engel, 1976).

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

Location	Avg. depth (m)	Temp. (°C)	Salinity	Zooplankton biomass (mgC m ⁻³)			Ctenophore biomass (ml m ⁻³)			References
				Season	Peak	Peak range	Season	Peak	Peak range	
Narragansett Bay, Rhode Island Long Island Sound, Connecticut/New York	9	1-25	25-32	June-July	70*	30-110	Aug-Sept	50	6-100	>8
	20-30	0-24	24-29	March-May	100*†	20-200	July-Sept	50	20-199	3
Chesapeake Bay (mid), Maryland Biscayne Bay, Florida	5-10	2-26	5-16	July-October	90†	30-180	June-Sept	20	10-40	12
	2	18-32	14-45	Summer	11‡		Fall	30	—	1+
St Andrews Bay, Florida	2-5	11-29	19-33	Variable (fall to winter)	25*		Variable (winter)	nd		2
				(late spring, fall)	(12 av.)		Variable (summer)	15	8-20	1
Nueces Estuary, Texas	2.4	7-31	20-38	Variable	50 (17 av.)					Buskey (1993)

* >153 µm fraction, assuming C=35% of dry weight, or 1 ml displ. vol=60 mg C.

† Converted from counts assuming 3 µg C per copepodite/adult.

‡ >202 µm fraction, assuming C=35% of dry weight.

nd = no data.

1. Hulsizer (1976); Kremer (1976); Kremer and Nixon (1976); Durbin and Durbin (1981); Deason (1982); Deason and 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.* (1994).

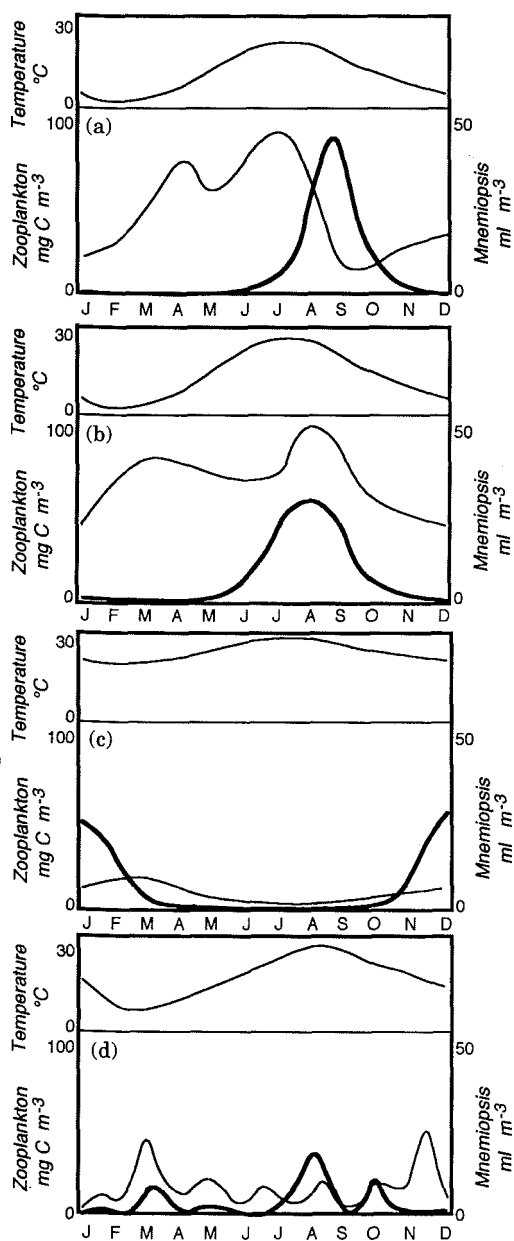


Figure 1. Schematic representations of annual cycles for temperature (upper portion), zooplankton biomass (light line), and *Mnemiopsis* biomass (heavy line) for four regions of the United States. (a) Northern (Narragansett Bay); (b) mid-Atlantic (Chesapeake Bay); (c) South Atlantic (Biscayne Bay). (d) Texas Bays (Nueces Estuary).

Biscayne Bay, Florida

Biscayne Bay, 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 only a weak seasonal pattern in zooplankton

biomass (Reeve, 1970, 1975; Baker, 1973; Brand, 1988), with a summertime low (Fig. 1c). In central Biscayne Bay (latitude 25°40' N), Baker (1973) found *M. mccradyi* in fairly high abundance most of the year (70% average frequency of occurrence for 11 stations), with a pronounced summer low and peak in the late fall/early winter. Fewer *M. mccradyi* 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 lower zooplankton biomass. In more recent years *M. mccradyi* have been abundant only in north Biscayne Bay (Reeve, pers. comm.). Bay-wide sampling from 1986–1987 documented that zooplankton stocks were generally higher in north Biscayne Bay (Brand, 1988), with most of the bay <5 mg m⁻³ ash-free dry weight (AFDW). Earlier field results (Baker, 1973) indicated that ctenophores were not found in waters with zooplankton stocks of less than 3 mg C m⁻³ (ca. 6 mg m⁻³ AFDW). The more recent field data (Reeve, unpublished; Brand, 1988) are consistent with earlier results (Reeve, 1970, 1975; Baker, 1973), indicating that the distribution and abundance of *M. mccradyi* correlate with times and areas of higher prey availability. The absence of small *M. mccradyi* during the summer (Baker, 1973) implies low reproduction during this period. Common predators on *M. mccradyi* include the ctenophore *Beroë ovata*, but sampling did not find them in sufficient number to be considered a major predatory force (Baker, 1973). Other predators and competitors have not been documented.

Coastal waters along the Gulf of Mexico

Coastal waters along the Gulf of Mexico are generally less well studied than those waters described above. There are only a few published papers that quantify both zooplankton biomass and document ctenophores. The subtropical waters of both St Andrews Bay, Florida (latitude 30°10' N), and the Nueces Estuary, Texas (latitude 27°50' N), are shallow and have similar annual ranges in temperature (10–30°C) and salinity (20–33) (Table 1). The zooplankton biomass in St Andrews Bay varied considerably during the two sampling years, one year without much seasonality, and the other year with clear biomass peaks in the late summer and following spring (Hopkins, 1966). *M. mccradyi* appeared to be in abundance only infrequently in St Andrews Bay. Along the coasts of Mississippi (Phillips *et al.*, 1969) and Louisiana, *M. mccradyi* 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). In the Nueces and Corpus Christi Bays there were biomass peaks of both microplankton and mesoplankton at several times during the year, without a strong seasonal pattern (Buskey,

1993). *M. mccradyi* were consistently present, with several biomass spikes throughout the year, also without strong seasonality (Fig. 1). In Texas coastal waters, the predators *Chrysaora quinquecirrha* and *Beroë ovata* were present but undocumented (Buskey, pers. comm.).

Discussion

Both *Mnemiopsis leidyi* and *M. mccradyi* show a strong association with warm water and environments dominated by the copepod *Acartia tonsa*, a fast-growing ubiquitous species, typical of coastal waters. In the north-east, *M. leidyi* undergoes a population explosion in the summer, dropping back to very low levels in the winter. 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 southern waters, *M. mccradyi* may be present nearly year-round (e.g. Nueces Estuary and Biscayne Bay), but biomasses are generally lower.

Species differences between *M. leidyi* and *M. mccradyi* might be expected to account for some of the observed patterns in abundance. Experimental results for the two species, however, were indistinguishable for several relevant ecological rates at comparable conditions. These measurements include respiration and excretion, egg production, feeding, and growth (Baker, 1973; Kremer, 1975, 1976, 1977, 1979, 1982; Reeve *et al.*, 1978, 1989; Kremer *et al.*, 1986; Kremer and Reeve, 1989). These experimental results imply that environmental variables, not intrinsic species differences, are responsible for biomass patterns observed over their latitudinal range. Considered together, the observed population dynamics of these two species of ctenophores in several coastal systems indicate that temperature, food availability, and mortality may work in a hierarchical fashion to control the timing and biomass of ctenophore abundance.

Temperature

Temperature appears to be of overriding importance in determining conditions suitable for population increase of *Mnemiopsis* spp. Although *M. leidyi* has been observed to survive in cold water, it is likely that both somatic growth and egg production are severely reduced at lower temperatures. Therefore, in northern systems, such as Narragansett Bay, Long Island Sound, and Chesapeake Bay, *M. leidyi* abundance does not increase substantially in the spring/summer until the waters are sufficiently warm, despite high biomass of prey zooplankton earlier in the season. In Narragansett Bay, near the northern end of the range, the annual peak copepod biomass clearly precedes the ctenophore peak biomass (Hulsizer, 1976; Durbin and Durbin, 1981; Deason and Smayda, 1982). Although no experimental

work has directly demonstrated the effect of temperature on growth and fecundity, studies of respiration and excretion with *M. leidyi* measured a high Q_{10} of about 4 over a temperature range from 10–26°C (Kremer, 1977), indicating that metabolic rate is very sensitive to temperature.

When temperatures are sufficiently warm and prey are abundant, the abundance and biomass of *M. leidyi* can increase rapidly (Fig. 1a, b), but field patterns suggest that the annual temperature cycle in northern latitudes severely restricts the period of rapid somatic growth and high reproduction to a few months during the warmest period of the year. The warmer waters inhabited by *M. mccradyi* show a very different seasonal pattern, where temperature is much less important to the population dynamics.

Food availability

Food availability appears to set an upper limit on the maximum biomass of *Mnemiopsis* spp. through a direct effect on both fecundity and somatic growth. Large individuals of both species, freshly collected from the field, have been shown to produce up to several thousand eggs per day, and maximum fecundity as a function of ctenophore size is comparable for the two species (Baker, 1973; Kremer, 1976). Laboratory studies of *M. mccradyi* have shown rates of egg production to be influenced strongly by food availability (Reeve *et al.*, 1989). Currently, there is only circumstantial evidence to demonstrate the effect of food limitation on field populations of *Mnemiopsis*. For Narragansett Bay, egg production by *M. leidyi* declined later in the season when food stocks dropped (Kremer, 1975), and small *M. mccradyi* were absent from Biscayne Bay during the summer when zooplankton was at a minimum (Baker, 1973).

Combined field and laboratory evidence from numerous sources indicates clearly that high prey biomass is a necessary precursor of high biomass of *Mnemiopsis*. Data from sub-regions of Biscayne Bay have shown that areas poor in zooplanktonic prey are unable to support a population of *M. mccradyi*. Interannual comparisons from Narragansett Bay (Deason and Smayda, 1982) indicate a close linkage between the annual maxima of prey zooplankton in the early summer and the subsequent biomass of *M. leidyi*. Modeling has further verified the tight coupling between prey availability and ctenophore biomass (Kremer, 1976; Kremer and Kremer, 1982; Kremer and Reeve, 1989).

Experimental results for feeding and growth rates are similar at comparable temperatures for both *M. leidyi* and *M. mccradyi* (Reeve and Baker, 1975; Kremer, 1975; Reeve *et al.*, 1978, 1989; Kremer, 1979), but field sampling has shown maximum seasonal biomass is generally higher for *M. leidyi* than *M. mccradyi* (Fig. 1). The

higher maximum biomass of ctenophores correlates with higher zooplankton stocks.

Predation

The role of predators or competitors in controlling the biomass of *Mnemiopsis* spp. remains largely a subject of speculation. There are some examples from field abundance patterns that suggest the strong influence of invertebrate predators (e.g. Kremer and Nixon, 1976; Feigenbaum and Kelly, 1984). Generally, the patterns of ctenophores and their predators are not well known and the data are inadequate to draw definitive comparisons. Taxonomic and life history differences among predators are also likely to be important. For example, although the ctenophore *Beroë ovata* feeds on other ctenophores (Burrell, 1968; Greve, 1970; Swanberg, 1974), given a suitable food supply, this predatory ctenophore can grow and reproduce rapidly and exert a strong predatory force (Kremer and Nixon, 1976). By contrast, the scyphomedusa *Chrysaora quinquecirrha* feeds not only on ctenophores but also on medusae and crustacean zooplankton (Purcell, 1992), and therefore functions both as a predator and competitor for *Mnemiopsis* spp. The life cycle of *C. quinquecirrha* requires a benthic polyp stage, and the abundance of medusae appears to be strongly correlated with interannual variations in salinity (Cargo and King, 1990). *C. quinquecirrha* is not found in the more northern range of *M. leidyi*, and is poorly documented for the Gulf Coast. In regions of Chesapeake Bay, however, it seems to have an important predatory role (Feigenbaum and Kelly, 1984; Purcell, 1992), although the impact on the ctenophore population has not been quantified.

The influence of fish predators is even more difficult to evaluate quantitatively. Stromateoid fish of the genus *Peprius* have been documented to feed on *Mnemiopsis* spp. in the United States over a broad latitudinal range (Dunnington and Mansueti, 1955; Phillips *et al.*, 1969; Oviatt and Kremer, 1977). The predatory impact of this fish has not been assessed quantitatively, except in Narragansett Bay where removal rates of about 5% day⁻¹ of the total number of *M. leidyi* were estimated (Oviatt and Kremer, 1977). Predation rates of this magnitude would be expected to have little effect on a rapidly growing population of *Mnemiopsis*, but could account for a major fraction of the observed population decline when somatic and reproductive growth are low (Kremer, 1976).

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 copepods (*Undinula vulgaris*) 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 inhibit population growth completely in an otherwise favorable environment with sufficient food and warm temperature. Nevertheless, high and variable mortality of young stages of ctenophores must be taken into account in any serious analysis of ctenophore population dynamics.

Population dynamics: summary and geographic consequences

Different patterns of abundance for *Mnemiopsis* spp. are evident when examining the full latitudinal range in the United States. In northern waters, the annual temperature cycle serves to drive strong seasonal plankton patterns (Fig. 1a, b). *M. leidyi* is abundant only during a limited period in the summer and measured biomass is highest near the northern end of the range. Food availability appears to be of less importance than temperature in determining the annual abundance cycle of *M. leidyi*, but is likely to contribute to inter-annual variability in ctenophore biomass. Predation pressure also has been documented to control the biomass of *M. leidyi*. In Narragansett Bay, the presence of *Beroë ovata* during one sampling season strongly affected the biomass pattern of *M. leidyi* (Kremer and Nixon, 1976), and butterfish represent a major predatory influence in the late summer (Oviatt and Kremer, 1977). In the Chesapeake Bay, the predatory scyphomedusa *Chrysaora quinquecirrha* has been documented to be of major importance regionally (Feigenbaum and Kelly, 1984; Purcell, 1992).

In subtropical systems to the south (e.g. Biscayne Bay and Nueces Estuary), the influence of temperature is diminished and seasonality is less pronounced. In these systems, the biomass of *M. mccradyi* appears to be directly linked to food availability. In these systems, predation on ctenophores has not been evaluated. It seems reasonable to hypothesize, however, that a tight coupling exists between food availability, ctenophore biomass, and predation pressure, resulting in biomass peaks of *M. mccradyi* that are generally lower than maxima of *M. leidyi* to the north.

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