

Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island

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Abstract

The lobate ctenophore *Mnemiopsis leidyi* occurs throughout Narragansett Bay, Rhode Island, during warm summer months but is often undetectable in the central portion of the bay during winter months. During 2 yr of weekly sampling, we found that *M. leidyi* populations in a shallow embayment, Greenwich Cove, either overwintered or were only briefly absent during winter. The Greenwich Cove population reproduced weeks earlier and reached higher average and peak population concentrations than open-bay populations. Shallow embayment populations such as that in Greenwich Cove probably serve as source populations that inoculate the main region of the bay by advective transport in the spring months. We propose that earlier occurrences of *M. leidyi* during recent years are due to amplification of pulsed spring warming events that permit early reproduction in the shallow embayments that serve as source regions for *M. leidyi* in Narragansett Bay. We further suggest that the source-sink perspective we describe is relevant not only to Narragansett Bay but other temperate regions of the world persistently occupied by *M. leidyi*.

The importance of *Mnemiopsis leidyi* as a planktonic predator has been documented by a large body of research on its feeding capabilities (Kremer 1975; Reeve et al. 1978; Waggett and Costello 1999) and trophic impacts (Kremer 1979; Shiganova et al. 2001; Sullivan et al. 2001). These predatory capabilities underlie the importance of recent range expansion patterns for *M. leidyi*. Invasion of regions outside its historical distributions have resulted in dramatic planktonic community alterations in regions such as the Black Sea (Shiganova et al. 2003) and Sea of Azov (Studenikina et al. 1991). Although perhaps less acclaimed than these spatial range expansions, records of temporal range expansion within its endemic range can also cause important changes in planktonic community dynamics (Sullivan et al. unpubl. data). For example, within Narragansett Bay, peak occurrence of *M. leidyi* has shifted approximately 2 months earlier than the historic mean (Sullivan et al. 2001). However, the historically dominant summer copepod, *Acartia tonsa*, has not experienced a similar phenological shift, with the result that the seasonal timing of predator (*M. leidyi*) and prey (*A. tonsa*)

overlap differently than during the past. One result of this change is that *A. tonsa* has been almost eliminated from the plankton during recent summers in Narragansett Bay as a result of predation pressure from *M. leidyi* (Sullivan et al. unpubl. data). The long-term trophic consequences of near removal of copepods from Narragansett Bay during summer months, historically a period of high copepod abundance, are not yet clear. However, there is evidence of reduction in numbers of some species of larval fish in recent years (Keller et al. 1999) and increases in summer values of chlorophyll *a* (Chl *a*) (Sullivan et al. unpubl. data).

Despite the potentially important consequences of phenological shifts by *M. leidyi*, the mechanisms underlying *M. leidyi* seasonality are not well documented. Metabolism and growth of *M. leidyi* are clearly influenced by temperature (Kremer 1977), and climatic change has been suggested (Sullivan et al. 2001) to underlie recent alterations in *M. leidyi* seasonality. The relationship is supported by a positive correlation between periods of seasonal advance in *M. leidyi* abundance and average sea surface temperature increases. However, the overall change in average annual temperature of 2°C over the last 50 yr in Narragansett Bay (Hawk 1998) appears relatively small to result in such dramatic seasonality alterations. Likewise, it remains unclear why this level of warming has substantially altered *M. leidyi*'s seasonality but not that of other co-occurring species.

We designed this program in order to describe seasonal patterns in abundance and to clarify the mechanisms enabling temporal range expansion by *M. leidyi*. Previous research indicated that a general inshore–offshore gradient characterized the summer increase in *M. leidyi* abundance and that seasonal population growth occurred first at interior regions of Narragansett Bay (Kremer and Nixon 1976). Our choice of sample locations reflected this

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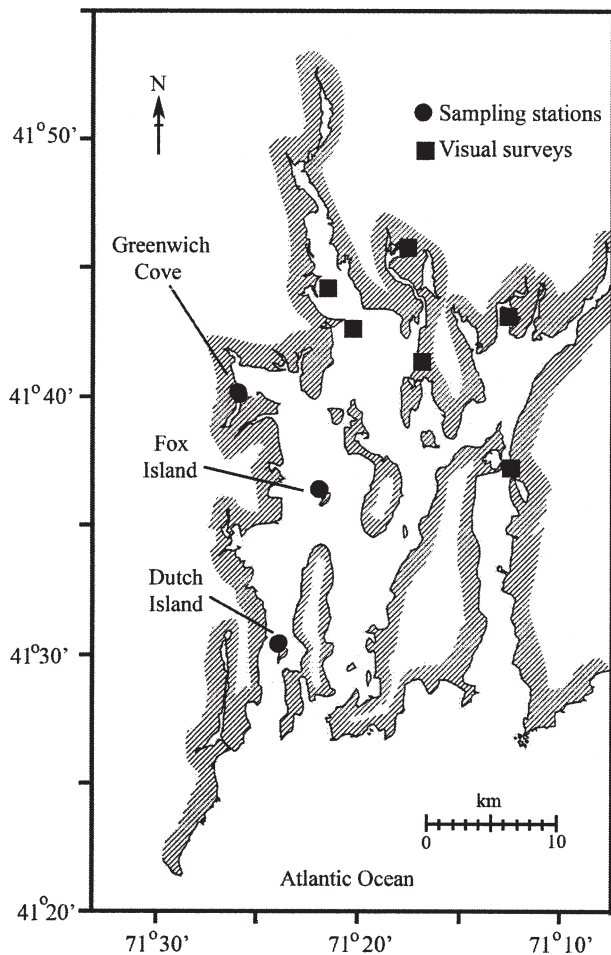


Fig. 1. Locations of weekly sample stations and presence/absence visual surveys in Narragansett Bay, Rhode Island. *M. leidyi* were found to be present throughout the winter of 2001–2002 at all the visual survey stations.

gradient and the parameters we measured were intended to clarify the basis for interstation differences in population dynamics of *M. leidyi*.

Methods

Sample locations and frequency—Our sample locations (Fig. 1) represented a gradient spanning conditions from the mouth of Narragansett Bay to a sheltered embayment with restricted exchange to the main body of the bay. The Dutch Island site was near the mouth of Narragansett Bay and the Fox Island site further within the bay, but still within a central water volume of Narragansett Bay (Pilson 1985). Greenwich Cove is a highly sheltered embayment with extensive marina and recreational boat mooring activity. Our goal was to sample along an inshore to midbay gradient at several stations within a sufficiently short time duration to allow reasonable comparison among stations. We chose a 3–4-h time duration for total sampling. The time intervals between sampling events were intended to be short enough to capture what preliminary evidence indicated were events occurring on a timescale of

Table 1. Summary of sample types and methods used during the survey.

Sample variable	Method
Temperature	YSI multiparameter sonde
Salinity	YSI multiparameter sonde
Chl <i>a</i>	Niskin collection, fluorometry
Mesozooplankton composition and concentration	64- μm net collection, formalin preservation, visual enumeration
<i>M. leidyi</i> abundance (<1.0-, >1.0-cm size fractions)	64- and 1,000- μm net collection
<i>M. leidyi</i> egg production	Direct visual enumeration of individuals maintained for either 24 or 48 h

several weeks. Consequently, we sampled all three sites on a weekly basis for 2 yr (November 2001–October 2003). Inclement weather caused incomplete sampling once during the 2001–2002 season and four times during the 2002–2003 season. Additionally, visual sampling for presence or absence of *M. leidyi* was performed at six additional sites during winter of the 2001–2002 season and ice-free periods of the 2002–2003 winter period.

Sample variables—A range of variables (Table 1) was measured on each sample date at each site. Physical variables (temperature and salinity at 1-m depth intervals) were measured with a YSI Model 600SLM multiparameter sonde. Water column stability was calculated by the index *E* (Knauss 1997):

$$E = \frac{\alpha(T_s - T_b)}{D} + \frac{\beta(S_s - S_b)}{D}$$

where α and β are constants (1.5 and -7.6 , respectively); T_s and T_b are temperatures at surface and bottom, respectively; S_s and S_b are surface and bottom salinity; and D is the depth of the sample location.

Samples for Chl *a* were collected from a 2-liter Niskin bottle and/or a surface bucket. Typically, three depths were sampled when the water column was well mixed. Additional depths were added when the water column was stratified. Chl *a* samples were collected onto GF/F filters, extracted in 90% spectranalyzed acetone, and analyzed by fluorometry (Knap et al. 1996). Mesozooplankton were collected by vertical tows of a 25-cm-diameter, 64 μm mesh net equipped with a flow meter. Vertical tows sampled the entire water column with the volume filtered varying between 0.4–1.0 m^3 , depending on station depth. The samples were preserved in 5% formalin buffered with sodium borate. Subsamples containing at least 200 individuals were counted under a dissecting microscope at $\times 50$ magnification.

M. leidyi were collected by two oblique tows with a 0.5-m-diameter net (1-mm mesh) equipped with a flow meter. Tow duration ranged 3–10 min and was adjusted to collect sufficient numbers of ctenophores for appropriate statistical analyses. These oblique tows sampled the entire water column and volume sampled varied from 0.9 m^3 to

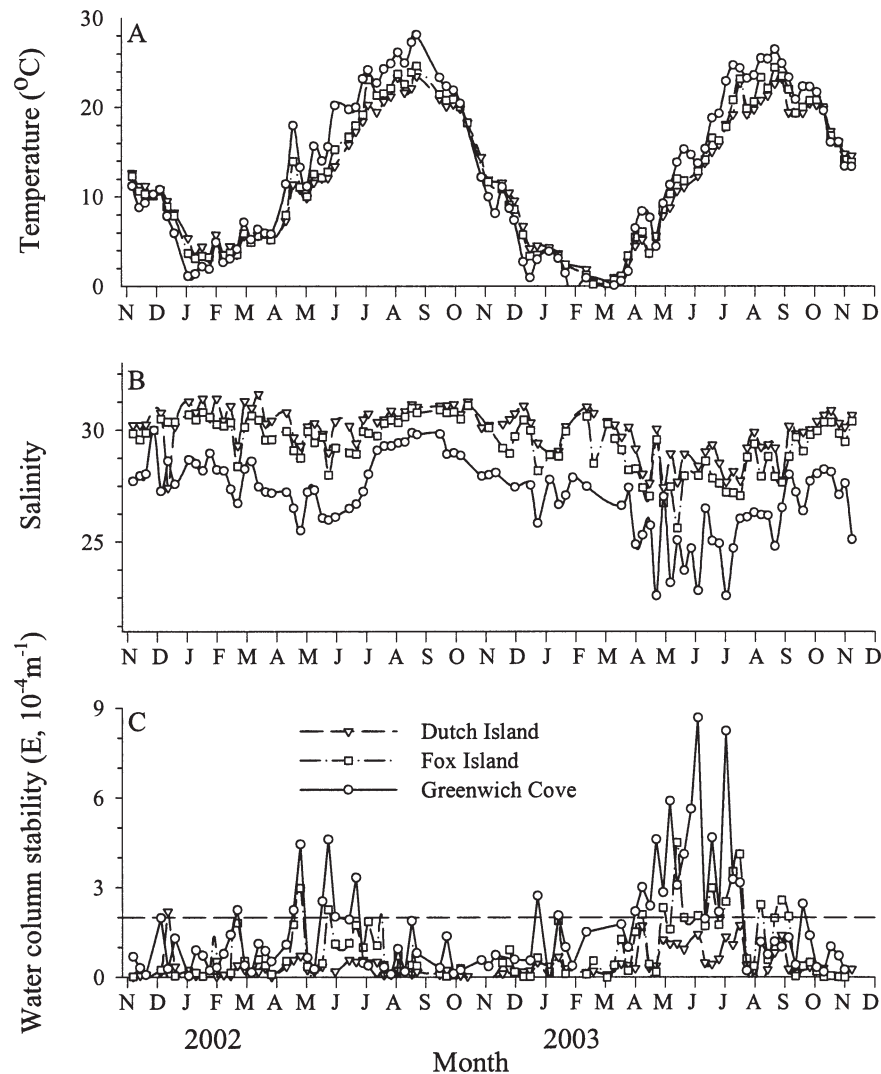


Fig. 2. Physical characteristics, (A) temperature, (B) salinity, and (C) water column stability of sample sites during field study. Dashed line in (C) represents the threshold value of $E (=2.0 \times 10^{-4} \text{ m}^{-1})$ above which the water column is considered essentially stratified (Knauss 1997).

79.0 m³, depending on station depth and abundance of ctenophores (when *M. leidyi* was very abundant, the volume sampled was kept low to prevent net clogging, but when abundances were low in winter, the tow durations were longer). The shallow depth and fixed sample platform at Greenwich Cove made such tows impractical at that station, so vertical tows were collected from the bottom to the top of the water column.

The contents of the tow were counted and measured immediately (when possible) or returned to the laboratory in a covered bucket for live measurements. *M. leidyi* egg production was measured on individuals collected by hand and between 2 and 8 cm total length. A minimum of 5 but usually 15–35 individual animals were collected per station, returned to the laboratory in coolers, isolated in individual dishes in 300 mL of filtered seawater, and incubated for 24 h at the temperatures of their capture locations. At temperatures below 10°C, ctenophores were incubated for 48 h, and the total egg production was divided by 2 to

obtain a daily rate. *M. leidyi* do not cannibalize their eggs (Kremer 1975), and container size during these short incubations did not affect egg production rate (B. K. Sullivan unpubl. data).

Statistical comparisons between stations and years made use of the Statistica (Statsoft) software package. Repeated-measures analysis of variance (RM ANOVA) comparisons were used for variables that were measured repeatedly at each station on each sample date (e.g., *Mnemiopsis* population concentrations, temperature, zooplankton concentrations). Standard ANOVA was used for comparisons of variables that were not repeatedly measured at each station on each sample date (e.g., date of peak *Mnemiopsis* appearance, maximum or minimum yearly temperature).

Results

Physical characteristics of the sample sites—Seasonal variations in temperature and salinity were similar in

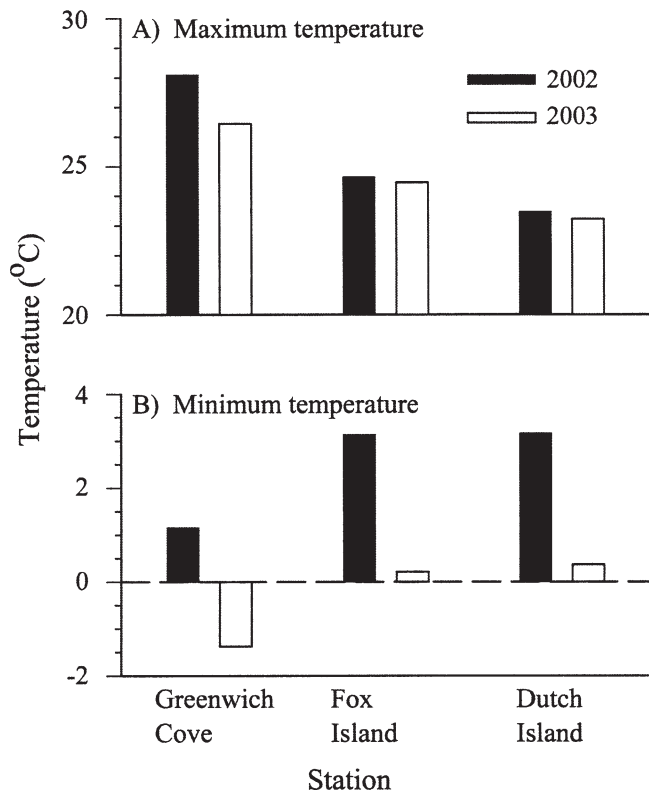


Fig. 3. (A) Maximum and (B) minimum sea surface temperatures at sample stations during the 2 yr of weekly sampling.

general pattern for all stations but more extreme at the innermost station, Greenwich Cove, and least variable at the outermost station near Dutch Island (Fig. 2). The Fox Island station values typically lay between these two extremes but were most similar to those of the Dutch Island station. Although Fox and Dutch stations were frequently similar in many respects, the fact that they were characterized by different water masses was demonstrated by significantly different salinity and Chl *a* values for both winter and summer months from the two sites (ANOVA, $p < 0.05$). The 2 yr of sampling, designated by their summer periods as 2002 and 2003, were historically warm and cold years, respectively (NOAA 2004). Interannual variations in maximum and minimum temperature were most pronounced at Greenwich Cove (Fig. 3). In contrast, the modifying effect of closer proximity to the Atlantic Ocean was evident at the Dutch Island and, to a lesser extent, the Fox Island stations.

The timing and patterns of spring warming varied systematically across stations. Warming occurred earlier inshore than offshore during both sample years (Fig. 4; Table 2). We used the dates at which the 5°C, 10°C, 15°C, and 20°C thresholds were reached as an index of the temporal variations of spring warming. The lowest temperature threshold, 5°C, varied little between stations in any year (Fig. 4; Table 2). Consequently, the average difference at which the 5°C threshold was surpassed was small (<5 d), between the innermost (Greenwich Cove) and outermost stations (Dutch Island). However, this difference

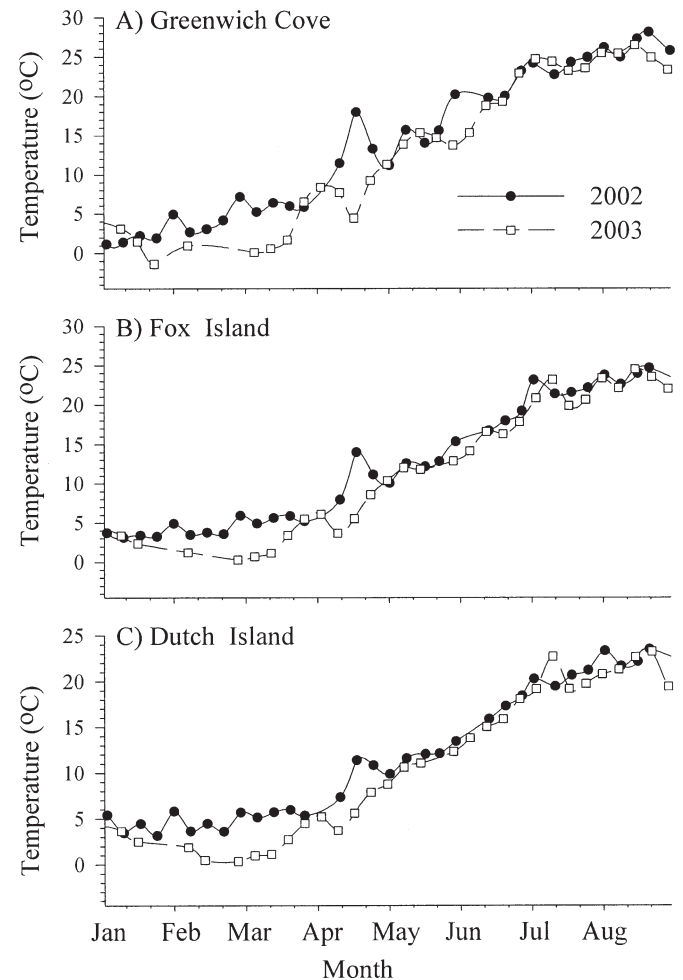


Fig. 4. Temperature records comparing spring warming patterns in 2002 and 2003 for each sample station.

increased at higher temperatures and, on average, Greenwich Cove warmed past the 15°C and 20°C thresholds 42 d and 24 d earlier, respectively, than Dutch Island station (Fig. 5A). However, temperature averages only partially describe important differences between the thermal characteristics of the stations. Spring warming did not always occur at a uniform rate; instead, warming often occurred in a series of surges. The pulsed nature of spring warming was most evident in Greenwich Cove, and pulse amplitude decreased toward the mouth of the bay. Warming-event amplitudes at the Dutch Island station were highly damped between 12–20°C. One striking example of between-station differences in spring thermal pulses occurred during a surge centered in mid-April 2002. The surge was evident simultaneously at all three stations (Fig. 4); however, the rate of temperature increase at Greenwich Cove was twice that at the Dutch Island station (Fig. 5C). As a consequence primarily of the higher rate of increase, temperatures in Greenwich Cove surged well into optimal reproductive temperatures (pulse peak = 18°C) compared with marginal reproduction temperatures (pulse peak = 11.4°C) at the Dutch Island site.

Table 2. Dates when temperature thresholds were reached or surpassed during field sampling in Narragansett Bay.

Temperature (°C)	Year	Station		
		Dutch Island	Fox Island	Greenwich Cove
5	2002	30 Jan	27 Feb	30 Jan
	2003	02 Apr	26 Mar	26 Mar
10	2002	17 Apr	17 Apr	10 Apr
	2003	07 May	30 Apr	30 Apr
15	2002	12 Jun	29 May	17 Apr
	2003	11 Jun	11 Jun	14 May
20	2002	01 Jul	01 Jul	29 May
	2003	09 Jul	02 Jul	25 Jun

Between-year variations in spring warming also contributed substantially to the dates at which thermal thresholds were passed. The largest differences between the warm year of 2002 and the cold year of 2003 occurred in Greenwich Cove at the 5°C threshold (Fig. 5B). However, the 15°C and 20°C thresholds were reached approximately 27 d earlier in the warm year of 2002 than the cold year of 2003. The between-year differences were less at the Dutch Island and Fox Island stations (Table 2). Together, these data indicate that seasonal warming patterns are relatively conservative between years in the open bay, but that embayments such as Greenwich Cove can experience approximately a month's acceleration of spring warming in the temperature ranges of 10–20°C during a warm year.

Salinity variations were most pronounced at Greenwich Cove (Fig. 2B). Although these salinity variations were reflected across all the stations, their impact was less pronounced at the Dutch Island station near the mouth of Narragansett Bay.

Water column stratification, as indicated by the index E (Knauss 1997), was substantially higher at Greenwich Cove than at the open-bay stations (Fig. 2C). Frequent stratification at Greenwich Cove reflected both greater temperature variations and, particularly during 2003, the strong influence of freshwater input as indicated by the correspondence between E and salinity values. In contrast, the Dutch Island site was characterized by values of E that were below the threshold for stratification. These data indicate that the Dutch Island station was generally characterized by a well-mixed water column, whereas Greenwich Cove was frequently stratified and the Fox Island station was essentially intermediate between the other two stations.

Biological characteristics of the sample sites—Distinct differences were evident in the plankton communities characterizing the sample stations. Phytoplankton standing stocks, measured as Chl a , were generally highest at Greenwich Cove, sometimes exceeding those of the Dutch Island station by an order of magnitude (Fig. 6A). The Fox Island station chlorophyll standing stocks were of intermediate levels but frequently resembled those of the Dutch Island station.

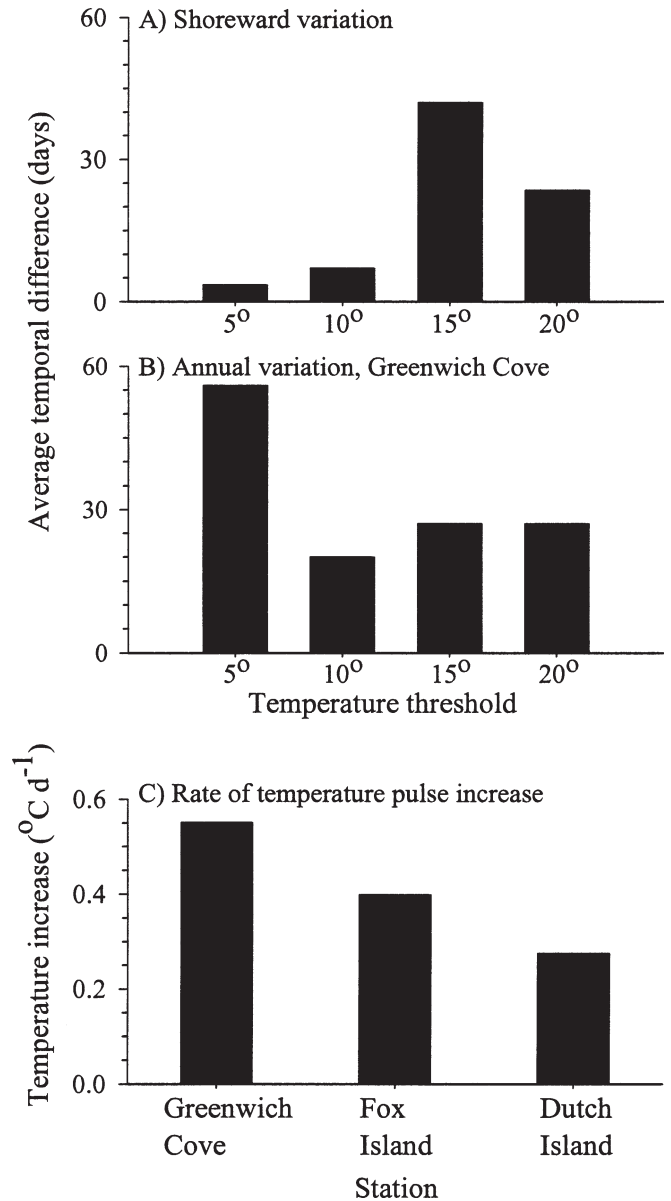


Fig. 5. Patterns of spring warming during 2002 and 2003 field seasons. (A) The increased rate of spring warming in a shoreward direction is demonstrated by the average difference, in days, between the dates at which the outermost site, the Dutch Island station, and the innermost site, the Greenwich Cove station, surpassed the same temperature thresholds. (B) Annual acceleration of spring warming, in days, between a warm year (2002) and a cold year (2003) at the innermost site, the Greenwich Cove station. (C) Differences in the rate of temperature increase during a pulsed warming event (26 March–01 May 2002) that was recorded simultaneously at all three stations.

Zooplankton assemblages were distinctly different between Greenwich Cove and both open-bay stations. Copepods dominated the zooplankton numerically at both Fox Island and Dutch Island stations and copepod concentrations were generally higher at these open-bay stations than in Greenwich Cove (Fig. 6B). In contrast, rotifers and meroplanktonic larvae of polychaetes, mollusks, and barnacles typically dominated the zooplankton

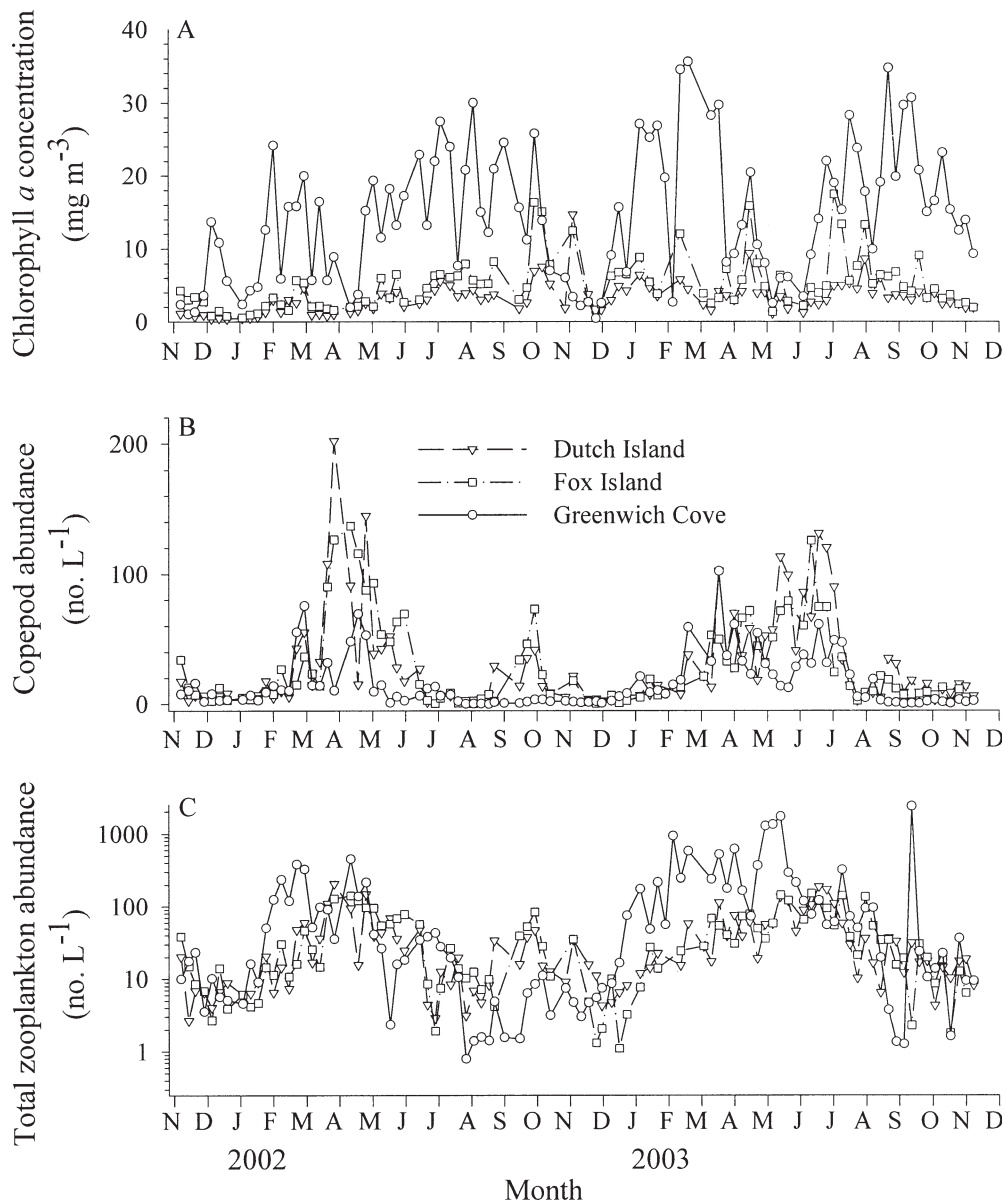


Fig. 6. Biological characteristics, (A) Chl *a* concentration, (B) copepod abundance (includes nauplii, copepodites, and adults), and (C) total zooplankton abundance at sample sites during field study. Note the logarithmic scale in (C).

of Greenwich Cove. Although the numerical abundance of zooplankton was highest in Greenwich Cove for much of the period we sampled, total zooplankton concentrations were often lower there during the summer months of June through September, compared with the open-bay stations (Fig. 6C).

Mnemiopsis leidyi distribution patterns—*M. leidyi* exhibited strongly seasonal distribution patterns at all sample stations. Maximum *M. leidyi* concentrations occurred between the months of June and August during both sample years at all stations (Fig. 7). Minimum population levels typically occurred during late winter or early spring (February–May) at all stations, and *M. leidyi* reached undetectable levels during these times at the Fox and Dutch

Island stations. Although rapid population declines were usually of this seasonal nature, local population declines could occur in the midst of typically high abundance periods. For example, during 28 August–18 September 2002, *M. leidyi* concentrations in Greenwich Cove dropped precipitously during an intense algal bloom (Fig. 7C). This event was not repeated in 2003.

Despite general seasonal similarities, there were important among-station differences in seasonal population demographics of *M. leidyi* in Narragansett Bay. The most striking of these was the persistence of *M. leidyi* throughout the winters of 2002 and, for all but two sample dates, 2003 at Greenwich Cove (Fig. 7C). This period included intervals with ice cover and temperatures below 1°C throughout the water column during which net tows through thin ice

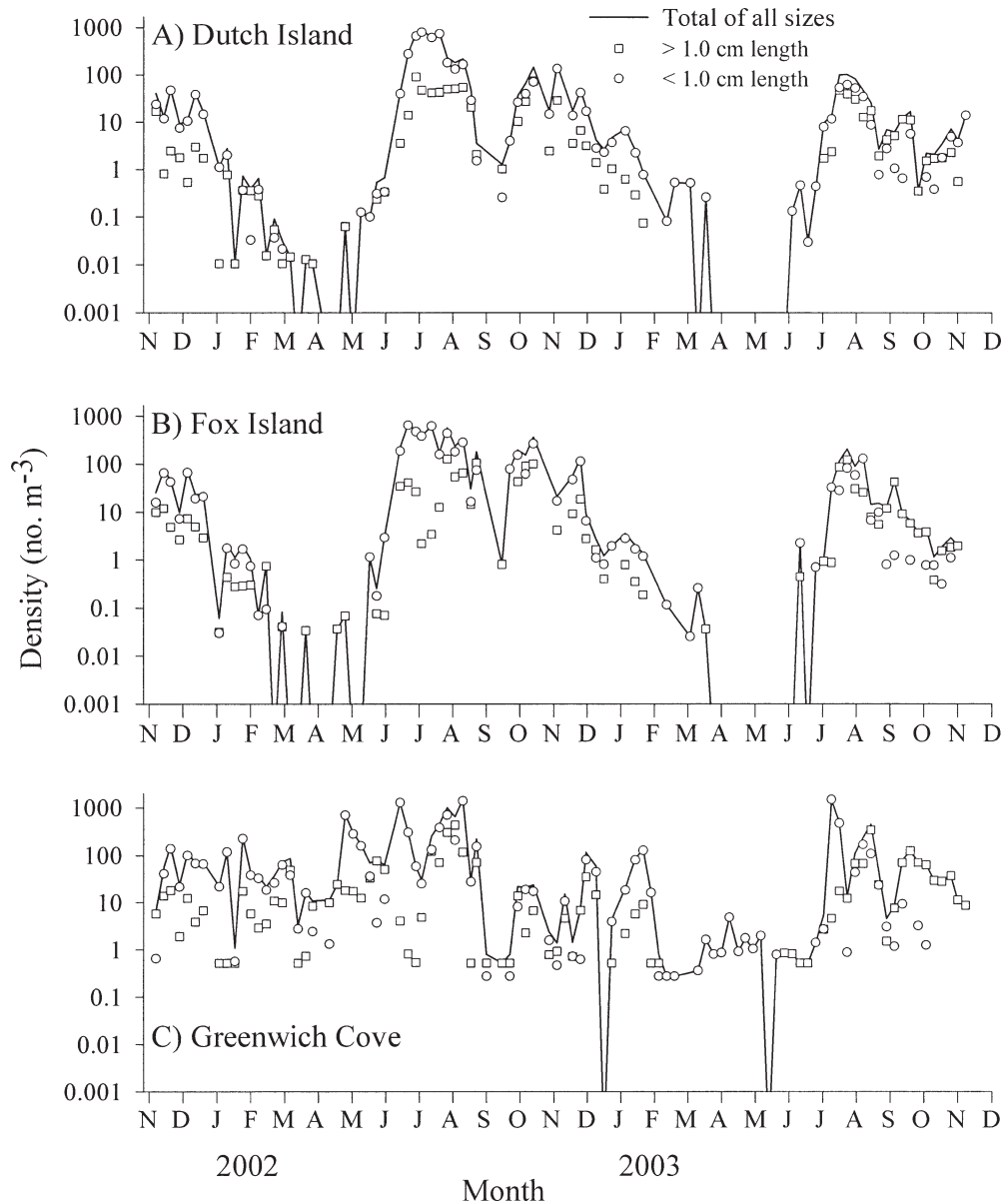


Fig. 7. Concentrations of ctenophores (<1.0 cm, >1.0 cm, and combined) at each of the sample stations throughout the field study. Note the logarithmic scale used for ctenophore concentrations.

captured *M. leidyi* at this station. In contrast to this persistence within Greenwich Cove, larval and adult concentrations of *M. leidyi* declined to undetectable levels at the open-bay stations of Fox and Dutch Islands during late winter and early spring (Fig. 7A,B). Adult (>1.0 cm total length) *M. leidyi* were irregularly present in Greenwich Cove during the late winter–spring of 2003, but reappeared more than a month earlier (14 May 2003) than at the Fox and Dutch Island stations (25 June 2003). Larval (<1.0 cm total length) *M. leidyi* were less predictable in their occurrence than adults and appeared regularly at a slightly earlier date (28 May) at the Dutch Island station in 2003 than at the Fox Island station.

Populations of *M. leidyi* differed among stations in several other important aspects. In addition to appearing earlier in the spring (Fig. 8A), adult populations typically peaked later at Greenwich Cove than at the Fox or Dutch Island stations (Fig. 8B). An apparent gradient in the date of peak abundance existed each year from the Greenwich Cove to the Dutch Island station, but among-year variability obscured any significant between-station differences (RM ANOVA, $p > 0.05$ for all comparisons). Adult populations of *M. leidyi* during peak summer months (01 July–30 September) were significantly higher in Greenwich Cove than at the Fox (RM ANOVA, $p = 0.04$) or Dutch (RM ANOVA, $p = 0.01$) Island stations. Average summer

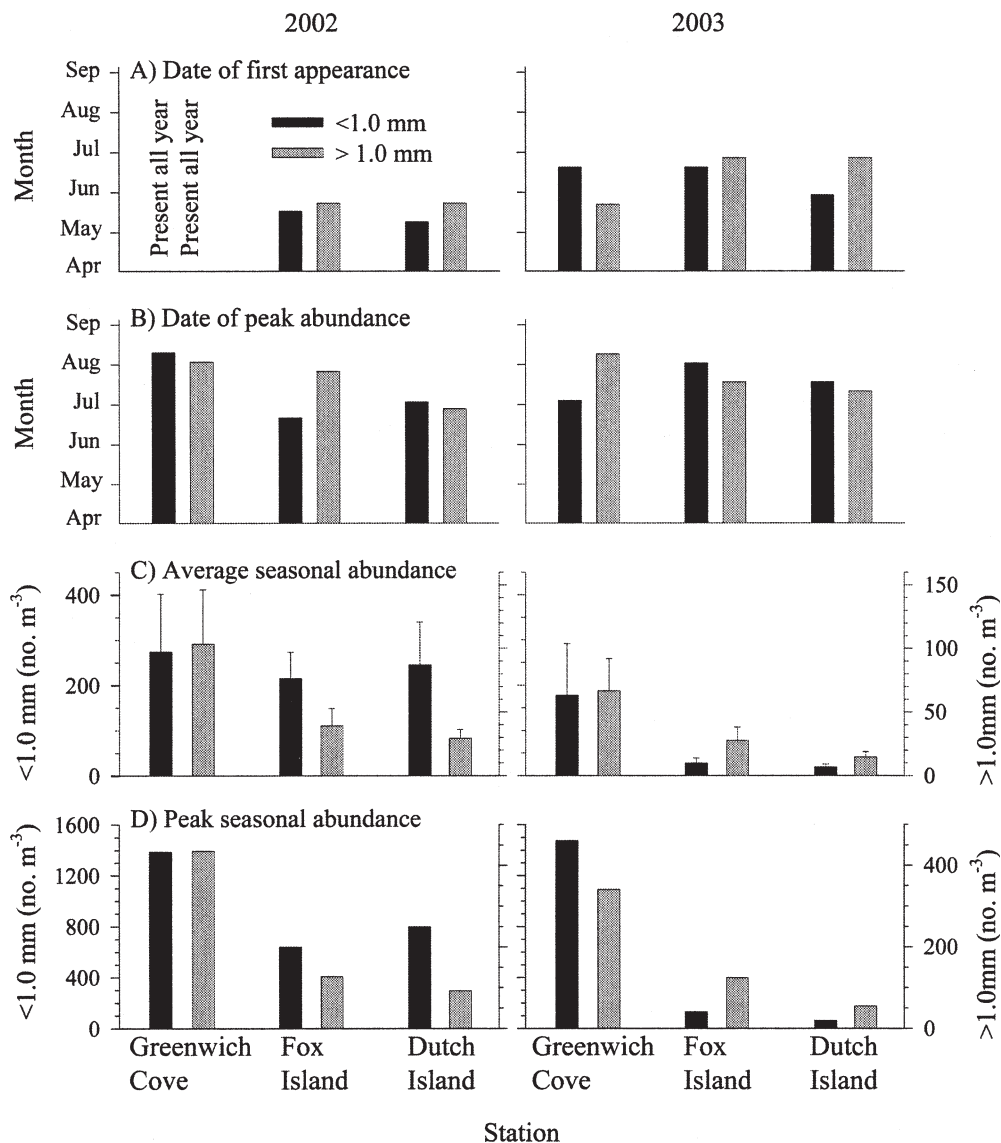


Fig. 8. Demographic traits of *M. leidy* populations at sample sites during both sample years. (A) Dates of first appearance. (B) Peak abundance. (C) Average seasonal abundance. (D) Peak seasonal abundance during the summer (June–September).

concentrations of large *M. leidy* were not significantly different between the Fox and Dutch Island stations (RM ANOVA, $p = 0.14$). Average summer concentrations of large *M. leidy* were higher in 2002 than 2003 at all stations, but the differences between years within any station were not significant (RM ANOVA, all comparisons, $p > 0.07$). Patterns of average summer larval abundance were less predictable than those of adult *M. leidy* because larval patterns differed between the two summers (Fig. 8C). Average summer concentrations were higher in 2002 than 2003 at the Fox (ANOVA, $p = 0.002$) and Dutch (ANOVA, $p = 0.016$) Island stations, but not in Greenwich Cove (ANOVA, $p = 0.578$). High among-year variation obscured any effect of among station differences (Wilks, $p = 0.441$) on average summer larval concentrations (Fig. 8C). Peak summer concentrations of large *M. leidy*

were significantly higher in Greenwich Cove than at the Fox (ANOVA, $p = 0.015$) or Dutch (ANOVA, $p = 0.011$) Island stations. Although there appeared to be a gradient in peak adult concentrations extending from Greenwich Cove maxima to Dutch Island station minima in both sample years (Fig. 8D), among-year variability obscured any significant differences in peak summer adult abundances between the Fox and Dutch Island stations (ANOVA, $p = 0.251$). Peak summer abundances of larval *M. leidy* paralleled average summer abundances. Consequently, peak summer concentrations of larval *M. leidy* were higher, but not significantly so, at Greenwich Cove compared with the Fox (ANOVA, $p = 0.074$) and Dutch (ANOVA, $p = 0.080$) Island stations.

Taken together, these results indicate that adult reproductive *M. leidy* appeared earlier in the spring,

persisted longer, and reached higher average and peak concentrations in Greenwich Cove than at the Fox or Dutch Island stations. Although inshore–offshore gradients were evident in summer abundance patterns (date of peak, average, and peak concentrations), interannual variation obscured differences between the two open-bay stations. Consequently, these open-bay stations were statistically indistinguishable for these variables. Larval summer abundance patterns were less clear with respect to station and more strongly variable between years, rendering conclusions about larval distribution patterns less clear-cut than those of adult *M. leidyi*.

Although Greenwich Cove was the only inshore embayment that we sampled regularly, opportunistic sampling during the winter of 2002 at a variety of other small embayments along the northern periphery of Narragansett Bay indicated that maintenance of overwintering *M. leidyi* populations was not unique to Greenwich Cove. On the basis of presence/absence visual surveys of surface waters, a number of small embayments were observed to contain lobate *M. leidyi* throughout the winter months (Fig. 1). These six sites were usually visited twice monthly during the winter of 2002, but heavy ice cover in these shallow regions prevented collection of similar visual survey data during 2003.

Reproductive patterns of M. leidyi—Egg production by field populations of *M. leidyi* was strongly temperature dependent (Fig. 9). Very low rates of egg production occurred on some occasions at temperatures as low as 6°C. However, substantial egg production characterized by rates of >10 eggs individual⁻¹ d⁻¹ did not occur below 10°C, and rates were highest between 10°C and 25°C. The 10°C temperature threshold was exceeded earliest in both years of sampling at Greenwich Cove (Fig. 2A), and egg production began earlier there each year than other stations. Although temperatures >10°C were generally necessary for high egg production, high temperature alone was not sufficient to generate egg production because food limitation occurred frequently during warm summer months (Sullivan et al. unpubl. data). As a result, even during warm periods, low egg production was common.

Migration between stations—Winter extinction periods at the midbay stations were interrupted by ephemeral pulses of adult, and in some cases larval, *M. leidyi* (Fig. 7). These unexpected occurrences were often followed by several weeks when no *M. leidyi* were detected and temperatures were below *M. leidyi*'s egg production threshold. The absence of adults at the open-bay stations during previous weeks and the low temperatures during the ephemeral population pulses eliminated the explanation of rapid population growth as the source of *M. leidyi* comprising these open-bay ephemeral pulses. Alternatively, advective transport from overwintering populations in embayments such as Greenwich Cove could provide the ctenophores comprising such ephemeral pulses. Demographic data are consistent with this alternative explanation. The overwintering population in Greenwich Cove possessed a similar size frequency profile (χ^2 , $p = 0.997$) to that of the

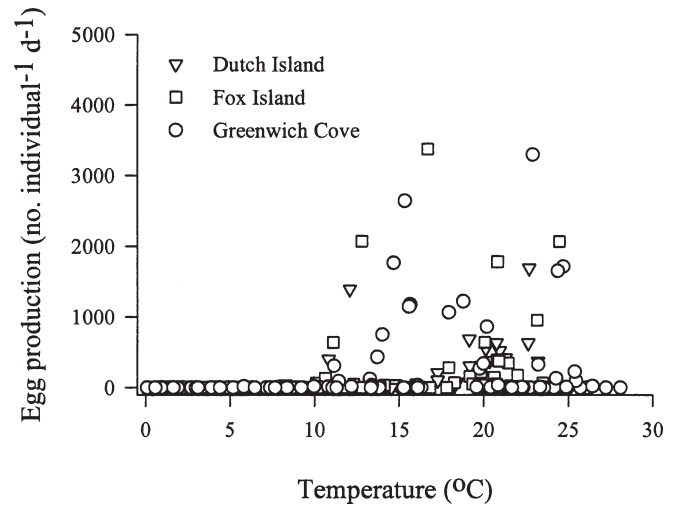


Fig. 9. Egg production of *M. leidyi* in relation to the temperature at which they were collected in the field.

ctenophores comprising an ephemeral pulse at the Dutch Island station the following week (24 April 2002 sample, Fig. 10).

Size frequency data indicate that the different stations were experiencing different population phenomena during the same time interval. The Dutch Island station lagged behind the overwintering Greenwich Cove population on 17 April, and by 24 April Greenwich Cove had experienced a rapid warming event (Fig. 4A), egg production, and larval recruitment (Fig. 10). Reproduction and recruitment continued from that time into the summer at Greenwich Cove but the Dutch Island station (and the Fox Island station as well, but not shown in Fig. 10) subsequently returned to undetectable *M. leidyi* concentrations and did not begin consistent population increase until 4 weeks later in late May 2002. These data indicate that open-bay ephemeral population pulses were characterized by size frequency distributions similar to those of overwintering embayment populations such as Greenwich Cove, and that spring population growth patterns at open-bay stations lagged several weeks behind that of the embayment population. The similarity in demographic traits between the populations comprising open-bay pulses and the overwintering population in Greenwich Cove suggests that Greenwich Cove might be a source population for such pulses; however, it is but one of a variety of overwintering populations (Fig. 1) with potentially similar size frequency patterns that occur in other sections of Narragansett Bay.

Discussion

Embayments as source population regions—Greenwich Cove served as a winter refuge for *M. leidyi* (Fig. 7), and preliminary evidence from other shallow embayments (Fig. 1) indicates that this phenomenon was common along the margins of Narragansett Bay. Even during a cold winter (2003) with widespread ice cover, *M. leidyi* were found in Greenwich Cove on all but two sample dates. Earlier spring warming enabled the Greenwich Cove

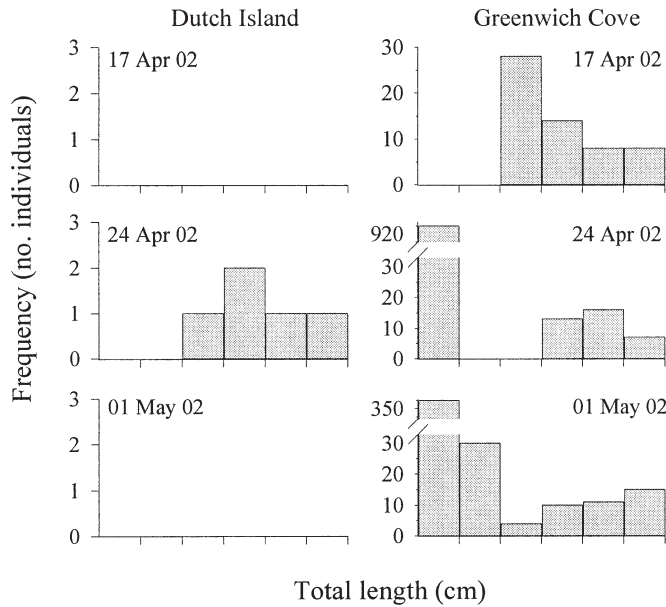


Fig. 10. Size frequency distributions of *M. leidy* during an episodic occurrence at Dutch Island (open-bay station) in contrast to Greenwich Cove (embayment station) during the same period.

population to grow and reproduce weeks earlier than open-bay stations (Figs. 10, 11). The sudden arrival of fully grown adults at the open-bay stations during winter and spring suggests that these embayment refugia serve as source populations from which advective transport provides inocula for the open regions of the bay. These advective transport events occurred irregularly throughout the winter of 2002, but successful establishment of persistent populations in the open bay occurred only after the latter regions warmed sufficiently to allow reproduction. Before reaching these temperatures, pulses likely were ephemeral because the thermal physiology of *M. leidy*

constrains reproductive potential and the ctenophores had no mechanism for population replacement to counter advective losses caused by high average flushing rates in Narragansett Bay (Pilson 1985). Once temperature limitation was relaxed by spring warming throughout the bay, the dramatic feeding (Reeve et al. 1978; Kremer 1979) and reproductive capacities (Kremer 1975; Sullivan unpubl. data) of *M. leidy* allowed rapid colonization and population expansion throughout the bay.

It is important to note that the relative advantages enjoyed by Greenwich Cove populations of *M. leidy* were not limited to winter and spring. Average and peak summer concentrations were significantly higher in Greenwich Cove than the open-bay stations. Reproduction began earlier, reached higher average and peak levels, and lasted longer in Greenwich Cove than the open-bay stations. During the 2 yr of this study, Greenwich Cove, and presumably other embayments, served as refugia from which *M. leidy* populations could expand during favorable summer periods and to which populations contracted during unfavorable winter periods. In contrast, open-bay stations were characterized by predictable seasonal extinctions (reductions to levels below detection) during each winter.

The different dynamics characterizing populations of *M. leidy* existing in different regions of the bay correspond to patterns described by metapopulation theory. A metapopulation is a population of populations linked by dispersal (Hanski 1999). The source-sink metapopulation model (Pulliam 1988) describes source regions as those occupied by populations with positive local recruitment which, via migration, supplement sink regions characterized by long-term net negative growth and frequent local extinction. The expansion from source regions during favorable environmental periods may encompass multiple sink regions and a large proportion of the total metapopulation range can exist in sink habitats if the source regions are sufficiently productive to subsidize the larger sink regions. Greenwich

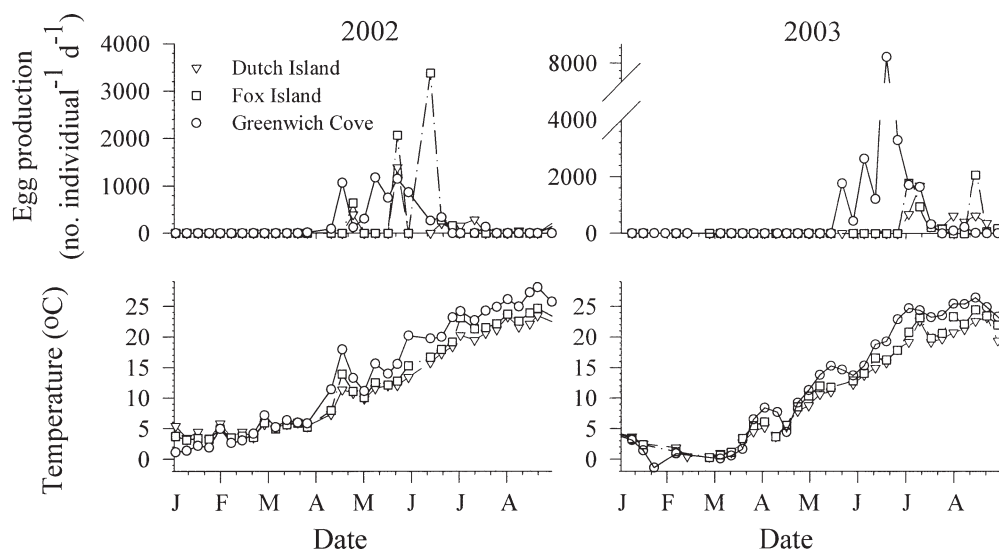


Fig. 11. Correspondence of *M. leidy* egg production with pulsed temperature events during the spring of years 2002 and 2003.

Table 3. Annual patterns of *Mnemiopsis leidyi* distributions sharing metapopulation traits with the current study.

Region	Seasonal variation pattern	Reference
Narragansett Bay, USA	Providence River regions characterized by longer seasonal presence and higher average abundances than the mouth of the bay bordering the Atlantic Ocean. Spring growth spread from inshore to offshore stations.	Kremer and Nixon (1976)
Black Sea	Spring population growth earliest at nearshore stations with subsequent seaward spread during 2-yr sampling period.	Shiganova et al. (2001)
Aral Sea	Annual reintroduction necessary from adjoining Black Sea due to yearly winter extinction in the Aral Sea.	Shiganova et al. (2001)
Sea of Marmosa	Persistent year-round population provides a source region for annual colonization of adjoining areas via advective transport	Shiganova et al. (2001)
Bahia Bay, Argentina	Winter persistence of <i>M. leidyi</i> in core region of bay occupied by a cluster of islands. Seasonal population expansion from this core region during summer months followed by contraction to core region during winter months over a 3-yr period.	Mianzan and Sabatini (1985)

Cove and other embayments along the bay's margin provide persistent winter refugia and, via advective transport, inocula for summer growth in open-bay areas such as the Fox and Dutch Island stations. Population growth can be rapid in these open-bay areas under favorable summer conditions, but is subsequently followed by seasonal extinction when temperature-limited reproduction and high winter flushing rates inevitably result in seasonal extinction in the open bay.

The source-sink perspective is consistent with seasonal distribution patterns described by previous studies in Narragansett Bay as well as in other regions of the world persistently occupied by *M. leidyi* (Table 3). Source regions, particularly in temperate regions with cold winters, are suggested by seasonal population expansion from nearshore regions in areas as diverse as New England (Kremer and Nixon 1976), Argentina (Mianzan and Sabatini 1985), and the Black Sea (Shiganova et al. 2001). Studies permitting delineation of *M. leidyi* source and sink regions are limited in number because this distinction requires multiyear sampling regimes of sufficient spatial variation to distinguish different types of habitat within a metapopulation region.

*What variables distinguish source from sink habitats?—*Hydrographic characteristics are probably the critical variables distinguishing source habitats within metapopulations of *M. leidyi* living in temperate regions characterized by cold (<10°C) winter sea temperatures. Documentation of most parameters integral to population dynamics, such as natality, mortality, immigration, and emigration, are difficult for a holoplanktonic species such as *M. leidyi* existing in a dynamic hydrographic environment such as Narragansett Bay. Instead, we delineate source habitats by seasonal persistence—population source habitats persist through annual seasonal cycles, while sink

regions experience local extinctions each winter. Refugia allowing overwintering are crucial to *M. leidyi* because, unlike many other neritic plankton, the entire life cycle is planktonic and does not include any overwintering cyst or benthic stages. Flushing and advective transport are important factors in population persistence because there are long winter periods (>90 d) when water temperatures are below the physiological threshold for reproduction and, therefore, replacement of individuals lost through advection is not possible. Flushing rates are strongly affected by winds, tidal variations, and freshwater input; but average estimates of residence times (duration of time that a parcel of water resides in a location) for Narragansett Bay are short (28 d—Pilson 1985; 43 d—Abdelrhman 2005) compared with the winter nonreproductive interval of *M. leidyi*. However, not all regions of the bay are hydrographically equivalent and some areas experience much longer local residence times than the baywide mean values (Abdelrhman 2005). Source regions may simply be those regions, such as Greenwich Cove, characterized by comparatively long local residence times that allow sufficient retention of *M. leidyi* to survive winter nonreproductive months. This characterization could include a variety of regions with comparatively long residence times, whether in shallow embayments with limited exchange to the open bay, such as Greenwich Cove, or retention features such as gyres within the open bay.

We envision source-sink interactions affecting local metapopulation dynamics and operating within temperature and feeding constraints that determine global patterns of *M. leidyi* seasonality and abundance. Kremer (1994) described the relationship between temperature and food availability patterns with large-scale patterns of *M. leidyi* seasonality. These physiologically based patterns apply to *M. leidyi* in both source and sink regions within Narragansett Bay. For example, only when temperatures rise

above the 10°C threshold for egg production do populations increase either at Greenwich Cove or the open-bay stations. Likewise, reproduction declines and overall population sizes decrease at all stations in midsummer when zooplankton availability diminishes (Sullivan unpubl. data). However, neither temperature nor food availability are likely to determine the role of Greenwich Cove and other embayments as source regions within the Narragansett Bay metapopulation of *M. leidy*. Minimum winter temperatures are less favorable for *M. leidy* at Greenwich Cove than the open-bay stations (Fig. 3B). Likewise, winter copepod concentrations are frequently lower in Greenwich Cove than the open-bay stations (Fig. 6B). Therefore, although temperature and food availability affect *M. leidy* throughout Narragansett Bay, just as they do in other regions (Kremer 1994), the relative roles of source and sink habitats within Narragansett Bay are most likely determined by hydrographic traits that determine retention durations. This is because retention durations most directly affect winter population persistence in a region and it is population persistence that primarily distinguishes the Greenwich Cove source habitat from open-bay sink habitats.

Metapopulation interactions with climate change—The source-sink perspective permits a mechanistic understanding of climatic effects upon *M. leidy* seasonality in Narragansett Bay. It does so by establishing a relationship between the local effects of warming and the population structure of *M. leidy*. The global process of climate warming is expressed locally in Narragansett Bay through spring warming surges whose amplitudes are magnified within shallow embayments (Figs. 4, 5). This shoreward thermal amplification is maximized within the source regions containing overwintering populations of *M. leidy*. Shoreward thermal amplification results in temperature spikes within source habitats that exceed temperature thresholds for reproduction and *M. leidy* responds to these pulsed warming events with pulsed reproductive events (Fig. 11). Once these spring reproductive events are initiated, reproduction continues into the summer and generates high population concentrations in source regions more than a month prior to sink regions (Fig. 7). Advective events likely transport ctenophores from source to sink regions (Fig. 10). Rapid population expansion throughout the bay can then occur when sink region temperatures exceed the thermal reproductive limits of *M. leidy*. This early expansion typically coincides with high zooplankton availability (Fig. 6) that provides the nutritional source fueling *M. leidy*'s high reproductive capabilities (Kremer 1975).

The synergistic interaction between source-sink population dynamics of *M. leidy* and shoreward thermal amplification is rooted in local-scale interactions that are not described well by global temperature averaging. Our original research approach sought to determine the mechanism whereby a 2°C increase in average annual temperature could produce a phenological shift by *M. leidy* of approximately 2 months. Our results suggest that both the location and time duration of the 2°C average

increase may underemphasize the importance of climate change on *M. leidy* in Narragansett Bay. The 2°C increase represents an average annual temperature increase at Newport, near the mouth of Narragansett Bay (Sullivan et al. 2001). However, shallow embayments are affected more dramatically by variations in air temperature than open-bay stations near the bay mouth (Fig. 5C). This is important for *M. leidy* seasonality because it is the temperatures in source embayments, such as Greenwich Cove, not sink regions of the open bay near the bay mouth, such as the Newport region, that determine the onset of seasonal reproduction for the Narragansett Bay metapopulation of *M. leidy*. A second factor influencing the utility of the 2°C Newport increase is the time duration of the average. Spring (March–June) is the relevant time period for examining between-year variation in the onset of *M. leidy* seasonal growth (Sullivan et al. 2001) and average temperatures for these spring months are the most useful indicators of the difference in *M. leidy* seasonality observed in Greenwich Cove between 2002 and 2003. In contrast, annual averages for 2002 and 2003 from the same station (Greenwich Cove) include many irrelevant dates causing important between-year patterns to be masked. Given these qualifications regarding location and duration of temperature averaging, it is not surprising that a 2°C annual increase in average temperature at Newport could result in major phenological shifts by *M. leidy*. Such an average annual temperature change near the bay mouth could result in dramatic alterations in spring temperature regimes that would be highly amplified in shallow embayments (Fig. 5) serving as *M. leidy* source habitats.

The effect of climatic changes on *M. leidy*'s seasonality is linked to the ctenophore's particular population dynamics. However, the same environmental changes might affect another species very differently if it possessed different population dynamics. For example, species with population centers located in open-bay regions would not be as strongly affected by shoreward thermal amplification and therefore might experience little phenological variation during the same period for which *M. leidy*'s phenology changed dramatically. The net result of different species-specific responses to environmental variation is expressed at the community level as trophic mismatching (Edwards and Richardson 2004) and can result in important community-level alterations (Sullivan et al. unpubl. data). Understanding, and ultimately predicting, community-level alterations will require identification of the critical interactions governing how individual species respond to environmental change.

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