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JELLYFISH BLOOMS

Response of *Chrysaora quinquecirrha* medusae to low temperature

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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 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. In order to test whether medusae sink upon cooling, we exposed *C. quinquecirrha* medusae to low temperatures in large static tanks and measured their depth and pulsation rates twice daily for at least 6 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.

Keywords *Chrysaora quinquecirrha* · Temperature · Depth · Seasonal disappearance

Introduction

The medusa stage of *Chrysaora quinquecirrha* (Desor, 1984) is seasonally abundant in the mesohaline Chesapeake Bay and its tributaries. It has been shown to affect populations of other gelatinous zooplankton, copepods, and ichthyoplankton (e.g., Feigenbaum & Kelly, 1984; Purcell, 1992; Cowan & Houde, 1993). Feigenbaum & Kelly (1984) suggest that *C. quinquecirrha* influences the trophic structure of the bay through its predation on *Mnemiopsis leidyi* (A. Agassiz, 1865). By means of a control over the population of the voraciously feeding ctenophore, high abundances of *C. quinquecirrha* can positively affect secondary production (Purcell et al., 1994b; Purcell & 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,

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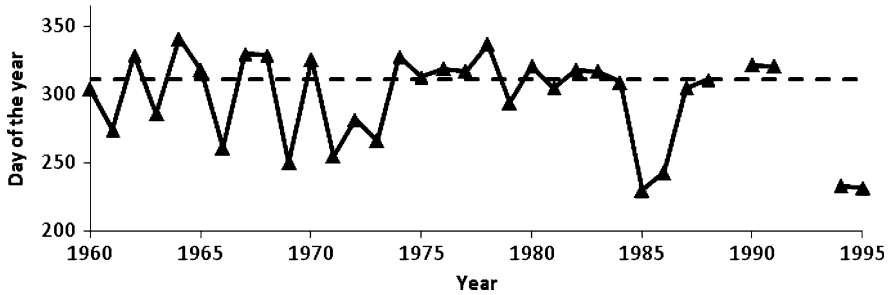

Fig. 1 Day of last occurrence of *Chrysaora quinquecirrha* medusae from visual counts made at the Chesapeake Biological Laboratory on the Patuxent River, Solomons Island, Maryland during1960–1995. Dashed line indicates the median day of last occurrence ($m = 311$, 7 November)

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 & King, 1990; Purcell & Decker, 2005; Breitburg & Fulford, 2006; Decker et al., 2007) and the conditions that cue strobiliation (e.g., Cargo & Schultz, 1967; Cargo & 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 et al. (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 & 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* (CQC) may play an important role in carbon cycling in the mesohaline Chesapeake Bay. The time at which *C. quinquecirrha* medusae disappear each year has implications to the timing and location of release of organic matter from gelatinous zooplankton.

We addressed temperature as one possible cause of the annual disappearance of medusae. Gatz et al. (1973) showed that the 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. We 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. We hypothesize that *C. quinquecirrha* exposed to temperatures between 10 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 h from June 6, 2005 to September 15, 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 × 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 to calculate volume sampled and density of medusae. On September 16, 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 June 1st 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* (CQC) for medusae 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 during the years 2005–2008, as described above, and the average July–August count on the Patuxent River from Cargo & King (1990). Patuxent River counts were assumed to have a visible depth of 1 m 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 & Decker (2005):

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

An average diameter of 33 mm was assumed based on average diameters in late August as 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 & 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 from there in the following years, i.e.,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 to 3 m depending on tide. We 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 & 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 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, 20 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 & 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 s was counted for each individual. Water temperature was also 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 according to 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 & Rohlf, 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. 2). Disappearance from

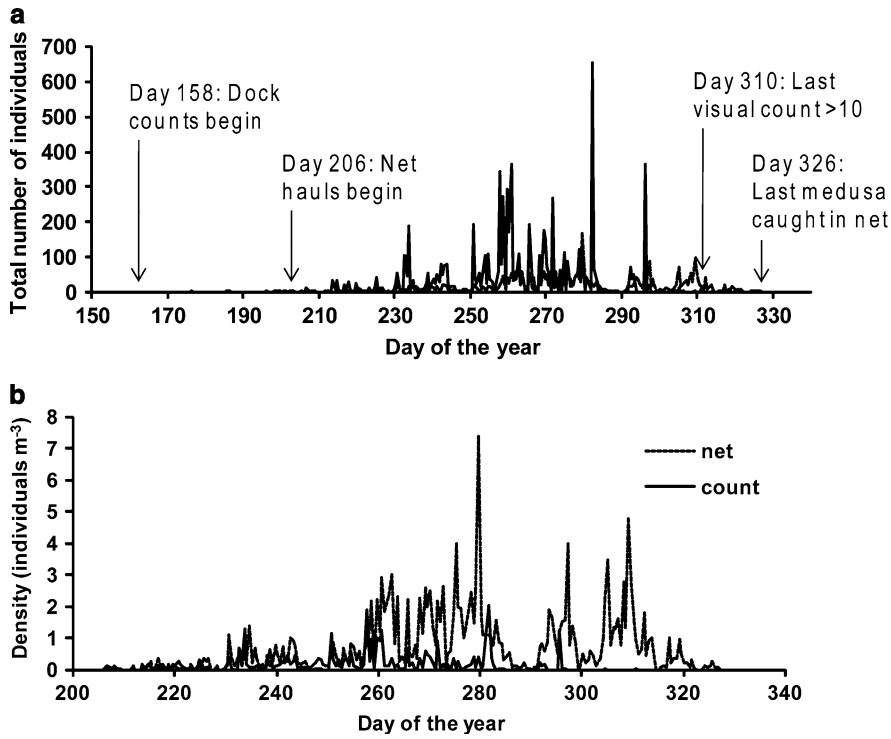

Fig. 2 Abundance (**a**) and density (**b**) of *Chrysaora quinquecirrha* medusae as measured by visual surface counts (*solid*) and vertical net hauls (*dashed*) in 2005 made from the Horn Point Laboratory dock, Cambridge, Maryland

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. 2 and 3).

In all the 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. 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). In the third trial, which lasted 3 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 ($r^2 = 0.501$, $P < 0.05$) and pulsation rate ($r^2 = 0.896$, $P < 0.05$) (Fig. 6).

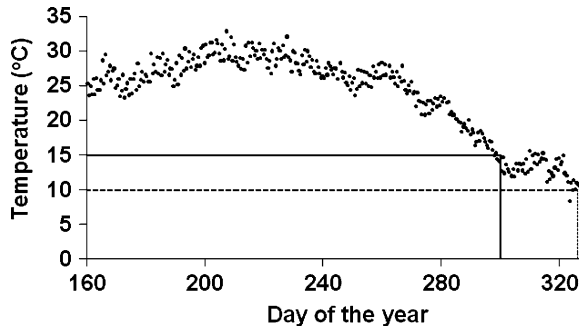

Fig. 3 Time series of water temperature measured at the Horn Point Laboratory dock, Cambridge, Maryland in 2005. Dashed lines indicate the temperatures on the dates of disappearance of *Chrysaora quinquecirrha* medusae from the surface (*solid*) and disappearance from the net hauls (*dashed*) shown in Fig. 2

Discussion

Because the last medusae have been observed most frequently near or after the beginning of November (Fig. 1) when water temperatures are decreasing (Fig. 3), low temperature is a likely cause of the seasonal disappearance of *C. quinquecirrha* in most years. In some years, disappearance occured long before the water temperature began to decrease toward the minimum tolerated by *C. quinquecirrha* medusae. In 7 years of the 35-year time series, the day of final occurrence was at least 50 days earlier than the median day of final occurrence (Fig. 1).

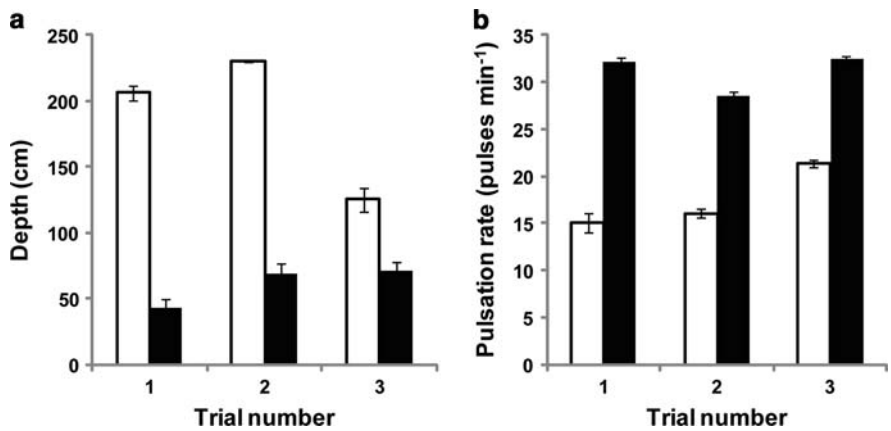

Fig. 4 Average depth (**a**) and pulsation rate (**b**) of *Chrysaora quinquecirrha* medusae for each trial. Average depths and pulsation rates were significantly different in the cold treatment tank (*open bars*) than in the control (*dark bars*) in all trials. Error bars represent standard error

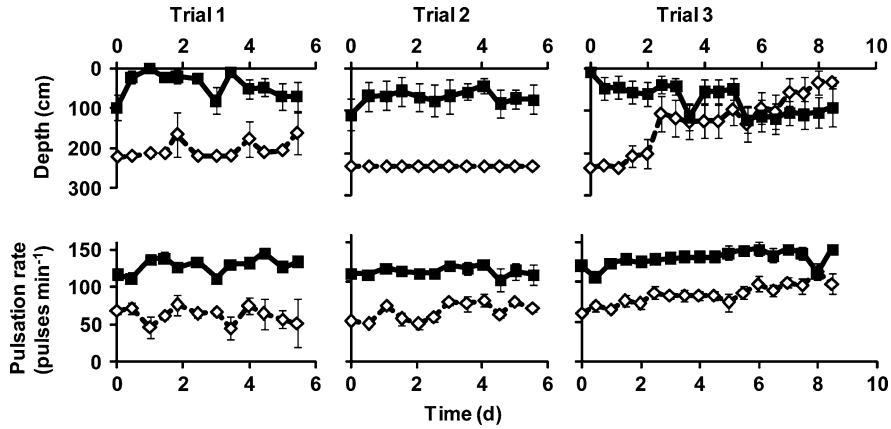

Fig. 5 Time series of average depth (*top row*) and pulsation rate (*bottom row*) of *Chrysaora quinquecirrha* medusae as measured twice daily in the cold treatment (*open symbols*) and the warmer control (*filled symbols*) tanks. Error bars represent standard error

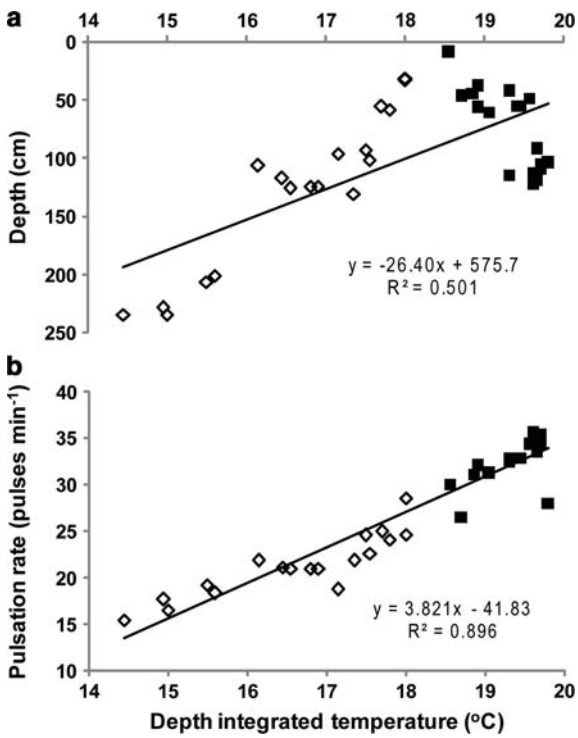

Fig. 6 Least squares linear regression lines calculated for average depth (**a**) and pulsation rate (**b**) of *Chrysaora quinquecirrha* medusae from Trial 3 with respect to depth-integrated temperature. Open points are from the cold treatment and filled points are from the control

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. In addition, 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's disappearance in most years. Throughout the season, densities found in the net were higher than those measured by the visual counts (Fig. 2b). We 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. 4, 5, 6), as was suggested by the field observations (Figs. 2 and 3). Thus, the living medusae would be deposited on the sediment surface, and the 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 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 1). Literature values of dissolved organic carbon (Fisher et al., 1998), total annual carbon flux (Kemp et al., 1997), and rate of

Table 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 during 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 CQC were based on relationships between bell diameter, dry weight, and carbon content from Purcell & Decker (2005) applied to abundance estimates from this study and Cargo & 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 to 10°C in the Choptank River

deposition from the spring bloom (Hagy et al., 2005) from the mesohaline portion of Chesapeake Bay were compared with the calculated values (Table 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. We have assumed that CQCremains in the tributaries; however, further study is needed to understand the fate of this carbon once it reaches the sediment surface.

West et al. (2009) 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 of 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 (e.g., Cowan & Houde, 1993; Behrends & 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 (e.g., Feigenbaum & 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 activites negatively affect the health of most marine and estuarine systems; therefore, it is likely that some of these factors may cause the death of jellyfish, and their subsequent role in carbon cycling may be affected. 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. Because fishermen cut up the jellyfish caught in their nets, they may alter the timing, rate, and location of jellyfish carcasses deposited on the sea floor. Understanding how such factors 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.

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References

Behrends, G. & G. Schneider, 1995. Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). Marine Ecology Progress Series 127: 39–45.

Billet, D. S. M., B. J. Bett, C. L. Jacobs, I. P. Rouse & B. D. Wigham, 2006. Mass deposition of jellyfish in the deep Arabian Sea. Limnology and Oceanography 51: 2077–2083.

Breitburg, D. L. & R. S. Fulford, 2006. Oyster-sea nettle interdependence and altered control within the Chesapeake Bay ecosystem. Estuaries and Coasts 29: 776–784.

Cargo, D. G., 1976. Some effects of tropical storm Agnes on the sea nettle population in the Chesapeake Bay. In Davis, J. & B. Laird (eds), The Effects of Tropical Storm Agnes on the Chesapeake Bay Estuarine System. Chesapeake Bay Consortium, Inc. Publ. No. 54: 417–424.

Cargo, D. G. & D. R. King, 1990. Forecasting the abundance of the sea nettle, *Chrysaora quinquecirrha*, in the Chesapeake Bay. Estuaries 13: 486–491.

Cargo, D. G. & G. E. Rabenold, 1980. Observations on the asexual reproductive activities of the sessile stages of the sea nettle *Chrysaora quinquecirrha* (Scyphozoa). Estuaries 3: 20–27.

Cargo, D. G. & L. P. Schultz, 1967. Further observations on the biology of the sea nettle and jellyfishes in Chesapeake Bay. Chesapeake Science 8: 209–220.

Condon, R. H. & D. K. Steinberg, 2008. Development, biological regulation, and fate of ctenophore blooms in the York River Estuary, Chesapeake Bay. Marine Ecology Progress Series 369: 153–168.

Cowan, J. H. & E. D. Houde, 1993. Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Marine Ecology Progress Series 95: 55–65.

Decker, M. B., C. W. Brown, R. R. Hood, J. E. Purcell, T. F. Gross, J. C. Matanoski, R. O. Bannon & E. M. Setzler-Hammilton, 2007. Predicting the distribution of the scyphozomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. Marine Ecology Progress Series 329: 99–113.

Feigenbaum, D. & M. Kelly, 1984. Changes in the lower Chesapeake Bay food chain in presence of the sea nettle *Chrysaora quinquecirrha* (Schyphomedusa). Marine Ecology Progress Series 19: 39–47.

Fisher, T. R., J. D. Hagy & E. Rochelle-Newall, 1998. Dissolved and particulate organic carbon in Chesapeake Bay. Estuaries 21: 215–229.

Fisher, T. R., J. D. Hagy, W. R. Boynton & M. R. Williams, 2006. Cultural eutrophication in the Choptank and Patuxent estuaries of Chesapeake Bay. Limnology and Oceanography 51: 435–447.

Gatz, A. J., V. S. Kennedy & J. A. Mihurski, 1973. Effects of temperature on activity and mortality of the scyphozoan medusa, *Chrysaora quinquecirrha*. Chesapeake Science 14: 171–180.

Hagy III, J. D., W. R. Boynton & D. A. Jasinski, 2005. Modelling phytoplankton deposition to Chesapeake Bay sediments during winter-spring: interannual variability in relation to river flow. Estuarine, Coastal and Shelf Science 62: 25–40.

Kemp, W. M., E. M. Smith, M. Marvin-DiPasquale & W. R. Boynton, 1997. Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. Marine Ecology Progress Series 150: 229–248.

Kemp, W. M., W. R. Boynton, J. E. Adolf, D. F. Boesch, W. C. Boicourt, G. Brush, J. C. Cornwell, T. R. Fisher, P. M. Glibert, J. D. Hagy, L. W. Harding, E. D. Houde, D. G. Kimmel, W. D. Miller, R. E. I. Newell, M. R. Roman, E. M. Smith & J. C. Stevenson, 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Marine Ecology Progress Series 303: 1–29.

Matanoski, J. C., R. R. Hood & J. E. Purcell, 2001. Characterizing the effect of prey on swimming and feeding efficiency of the scyphomedusa *Chrysaora quinquecirrha*. Marine Biology 139: 191–200.

Mills, C. E., 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES Journal of Marine Science 52: 575–581.

Mills, C. E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451: 55–68.

Nemazie, D. A., J. E. Purcell & P. M. Glibert, 1993. Ammonium excretion by gelatinous zooplankton and their contribution to the ammonium requirements of microplankton in Chesapeake Bay. Marine Biology 116: 451–458.

Pitt, K. A., D. T. Welsh & R. H. Condon, 2009. Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. Hydrobiologia 616: 133–149.

Purcell, J. E., 1992. Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay. Marine Ecology Progress Series 87: 65–76.

Purcell, J. E. & M. B. Decker, 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. Limnology and Oceanography 50: 376–387.

Purcell, J. E., D. A. Nemazie, S. E. Dorsey, E. D. Houde & J. C. Gamble, 1994a. Predation mortality of bay anchovy *Anchoa mitchelli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Marine Ecology Progress Series 114: 47–58.

Purcell, J. E., J. R. White & M. R. Roman, 1994b. Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. Limnology and Oceanography 39: 263–278.

Purcell, J. E., J. R. White, D. A. Nemazie & D. A. Wright, 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. Marine Ecology Progress Series 180: 187–196.

Riemann, L., J. Titelman & U. Bamstedt, 2006. Links between jellyfish and microbes in a jellyfish dominated fjord. Marine Ecology Progress Series 325: 29–42.

Schuyler, Q. & B. K. Sullivan, 1997. Light responses and diel migration of the scyphomedusa *Chrysaora quinquecirrha* in mesocosms. Journal of Plankton Research 19: 1417–1427.

Sokal, R. R. & F. J. Rohlf, 1995. Biometry. W. H. Freeman and Co., New York.

Tinta, T., A. Malej, M. Kos & V. Turk, 2010. Degradation of the Adriatic medusa *Aurelia* sp. by ambient bacteria. Hydrobiologia. doi:10.1007/s10750-010-0223-x.

Titelman, J., L. Riemann, T. A. Sornes, T. Nilsen, P. Griekspoor & U. Bamstedt, 2006. Turnover of dead jellyfish: stimulation and retardation of microbial activity. Marine Ecology Progress Series 325: 43–58.

West, E. J., D. T. Welch & K. A. Pitt, 2009. Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics. Hydrobiologia 616: 151–160.

Yamamoto, J., M. Hirose, T. Ohtani, K. Sugimoto, K. Hirase, N. Shimamoto, T. Shimura, N. Honda, Y. Fujimori & T. Mukai, 2008. Transportation of organic matter to the sea floor by carrion falls of the giant jellyfish *Nemopilema nomurai* in the Sea of Japan. Marine Biology 153: 311–317.