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Influence of top-down control in the plankton food web on vertical carbon flux: A case study in the Chesapeake Bay

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ABSTRACT

Carnivorous gelatinous zooplankton dominate the zooplankton community in Chesapeake Bay during summer months, exerting considerable top-down control on the planktonic food web. To examine the cascading effects of gelatinous zooplankton blooms on the plankton food web and particulate organic carbon (POC) flux, multiple 2-day mesocosm experiments were conducted in the York River tributary of Chesapeake Bay in July–August 2015. Mesocosms contained a natural assemblage of phytoplankton, microzooplankton, and copepods, and each treatment received additions of the ctenophore (*Mnemiopsis leidyi*), the scyphozoan medusae (*Chrysaora chesapeakei*), or both gelatinous zooplankton. There was no significant difference between treatments in total POC or PON flux. However, presence of *M. leidyi* reduced the abundance of copepods, in turn significantly decreasing copepod fecal pellet carbon flux compared to treatments without *M. leidyi* by 50% (from 36 to 18 μg C d^{-1} m^{-3}, or 6% to 3% of total POC flux). Total POC export fluxes were small in all treatments (< 1%) compared to previously measured sedimentation rates in the Chesapeake Bay. Top-down changes in copepod fecal pellet carbon flux are equivalent to a modest portion (~10%) of previously calculated *C. chesapeakei* carcass flux. Future experiments and models of zooplankton contributions to vertical carbon flux should include top-down processes and cascading effects.

1. Introduction

The relative importance of bottom-up vs. top-down control in food webs has been examined extensively in a wide variety of ecosystems, and trophic cascades initiated by top-down control have been demonstrated repeatedly throughout terrestrial, aquatic, and marine environments (Borer et al., 2005; Borer et al., 2006; Duffy et al., 2007; Micheli, 1999). The effects of top-down control and community composition on cycling of organic matter and nutrients have been examined in terrestrial and freshwater ecosystems (Brett and Goldman, 1996; Schmitz et al., 2010; Vanni, 2002). For example, presence of zooplanktivorous fish in freshwater systems reduce herbivorous crustacean zooplankton, increasing phytoplankton biomass and changing composition of sediment organic matter (SOM; Allard et al., 2011; Attayde and Hansson, 2001). However, the top-down effects on SOM deposition have only recently been examined in marine ecosystems. In a benthic marine system, the presence of the predator blue crab (*Callinectes sapidus*) reduced epiphyte grazers in seagrass beds, leading to increases in epiphytes, decreases in seagrass, and complex changes in sediment organic matter amount and composition (Canuel et al., 2007; Spivak et al., 2007; Spivak et al., 2009). However, there is a paucity of data on how top-down control affects cycling and export of carbon and nutrients in marine planktonic ecosystems.

Carnivorous gelatinous zooplankton (e.g., cnidarians, ctenophores) are conspicuous and effective marine planktonic predators that are known to initiate trophic cascades (Dinasquet et al., 2012; McNamara et al., 2014; Verity and Smetacek, 1996; West et al., 2009). Gelatinous zooplankton are taxonomically diverse, but share two key characteristics: rapid rates of reproduction and large, fast-growing, gelatinous bodies. These traits allow their population biomass to grow extremely rapidly under good environmental conditions (Purcell, 2005) and to be extremely efficient predators (Acuña et al., 2011; Pitt et al., 2013). These life history characteristics allow gelatinous zooplankton to exert top-down control during blooms that can extend several trophic levels down (Compte et al., 2010; Purcell and Decker, 2005).

In the Chesapeake Bay, phytoplankton biomass is highest during the spring, and primary production increases to a peak during the summer months (Malone et al., 1988). This mismatch between the peaks of phytoplankton biomass and production is caused by the high grazing of crustacean zooplankton, primarily calanoid copepods, which are more abundant in the late spring and summer than early spring (Steinberg and Condon, 2009; White and Roman, 1992). This spring progression of

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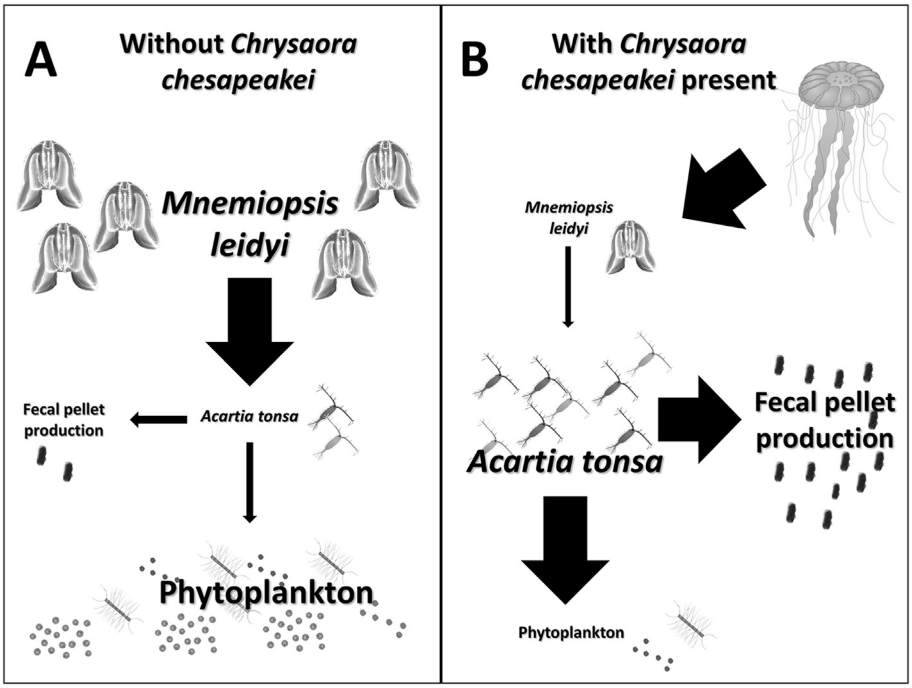

Fig. 1. Conceptual diagram of the top-down effects of *Chrysaora chesapeakei* on the relative abundances of taxa and strength of carbon transfer for the summer Chesapeake Bay ecosystem when A) *C. chesapeakei* medusae are absent and B) *C. chesapeakei* are present. Relative size of text and number of images represents the relative abundance of each category, and relative size of arrows represents strength of carbon transfer between categories. Illustrations courtesy of Tracey Saxby, Dieter Tracey, and Diana Kleine of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

blooms – phytoplankton followed by copepods – is followed by two species of carnivorous gelatinous zooplankton that exert wide-ranging top-down control throughout the zooplankton food web in summer in Chesapeake Bay: the lobate ctenophore *Mnemiopsis leidyi* and the scyphozoan medusa *Chrysaora chesapeakei* (Papenfuss, 1936) (note - previously *Chrysaora quinquecirrha*; Bayha et al., 2017) (Cargo and King, 1990; Feigenbaum and Kelly, 1984; Purcell et al., 1991). *M. leidyi* is present year-round throughout the mesohaline and polyhaline regions of Chesapeake Bay and its tributaries, but is most abundant from June through October (Purcell et al., 2001; Purcell and Decker, 2005; Steinberg and Condon, 2009). *M. leidyi* is a voracious predator of crustacean mesozooplankton and can exert high predation pressure on copepods, as well as icthyoplankton during *M. leidyi* blooms (Condon and Steinberg, 2008; Purcell et al., 1994; Purcell et al., 2001; Purcell and Roman, 1994).

In contrast to *M. leidyi*, *C. chesapeakei* medusae populations are greatly reduced in the winter as they often do not survive temperatures below 10 °C (Gatz et al., 1973). *C. chesapeakei* overwinter as benthic polyps and begin to produce planktonic medusae when water temperatures rise above 17 °C in the late spring (Purcell and Decker, 2005). These medusae are present from May to October, but the highest abundances are from July to September (Purcell, 1992).

C. chesapeakei feed on a wide variety of meso- and macrozooplankton, and are the primary predator of *M. leidyi* (Purcell and Cowan Jr, 1995; Suchman and Sullivan, 1998). When present, *C. chesapeakei* can exert strong top-down control of *M. leidyi* and significantly reduce their populations (Purcell and Cowan Jr, 1995). This reduction of *M. leidyi* in turn releases their prey (primarily copepods) from predation pressure, resulting in high summer copepod abundances (Purcell and Decker, 2005). This sets up a trophic cascade where years with higher abundance of *C. chesapeakei* have lower abundance of *M. leidyi* and therefore higher abundance of copepods, increasing grazing pressure on phytoplankton by copepods (Purcell and Decker, 2005). Populations of the top predator, *C. chesapeakei*, are regulated by the timing of spring warming and rainfall, with earlier warming and low rainfall (higher salinities) leading to years with higher medusae abundances (Cargo and King, 1990). Thus, changes in weather patterns (Purcell and Decker, 2005) from year to year may have significant top-down effects on the Chesapeake Bay food web, and consequently–as we hypothesize–on vertical carbon and nitrogen flux to the benthos.

Gelatinous zooplankton can affect vertical flux through a variety of mechanisms (Pitt et al., 2009). At the end of a bloom, sinking gelatinous zooplankton carcasses provide a large, episodic pulse of carbon to the benthos (Lebrato et al., 2013), but throughout the life of a bloom, gelatinous zooplankton produce mucus which may entrain phytoplankton and other particles, causing the mass to sink out of the water column as a loose, sticky aggregate (Deason and Smayda, 1982). Additionally, both *C. chesapeakei* and *M. leidyi* egest waste material as loose, poorly defined ‘fecal fluff’ which sinks more slowly and disintegrates more quickly than the compact fecal pellets produced by copepods (Alldredge and Gotschalk, 1988; Kremer, 1979). Because of the sinking speed and disintegration differences between the gelatinous zooplankton-produced fecal material and the copepod-produced fecal pellets, the quality and overall mass flux to the benthos may change depending on which species is dominant in the plankton. It is these interactions between top-down effects and vertical flux that we explore in this study.

We hypothesized that increases in *C. chesapeakei* medusae during the summer months will lead to top-down control and a resulting trophic cascade in which *M. leidyi* abundance decreases, releasing copepods from predation pressure and leading to an increase in POC and PON export in the form of copepod fecal pellets (Fig. 1). Conversely, absence of *C. chesapeakei* will allow *M. leidyi* to decrease the abundance of copepods, decreasing predation pressure on phytoplankton and increasing the export of particulate organic carbon and nitrogen (POC, PON) in the form of phytoplankton aggregates. To test this hypothesis, mesocosm experiments were conducted in the Chesapeake Bay with four treatments of zooplankton communities: 1) natural copepod assemblage with no gelatinous zooplankton, 2) natural assemblage plus *M. leidyi,* 3) natural assemblage plus *C. chesapeakei*, and 4) natural assemblage plus both *M. leidyi* and *C. chesapeakei*. By analyzing the changes in zooplankton abundance, total PON and POC flux, and flux from fecal pellets for each treatment, top-down controls on vertical particle flux could be examined.

2. Methods

2.1. Mesocosm design

Mesocosm experiments were conducted in July (Pilot), August (experiments 1, 2, and 3), and September (experiment 4), 2015 in a