Estuarine, Coastal and Shelf Science 133 (2013) 2–10

Contents lists available at SciVerse ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Invited feature

Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores

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ARTICLE INFO

Article history:
Received 25 January 2013
Accepted 17 April 2013
Available online 23 May 2013

Keywords:
trophic cascade
cydippid larvae
ciliates
population dynamics
in situ

ABSTRACT

The ctenophore *Mnemiopsis leidyi* is a gelatinous predator capable of exerting strong regulatory control on the zooplankton community. *Mnemiopsis* populations are comprised of lobate adults and cydippid larvae. Since the larvae depend on microplankton for prey, its availability may determine the magnitude of larval survivorship and growth, and their subsequent recruitment into mesozooplankton-feeding adults. Ctenophore population data were used alongside mesozooplankton and microplankton abundances to interpret predatory impacts of *M. leidyi* in a Long Island, New York estuary over two years. Field data suggested significant top-down control of mesozooplankton and microplankton during peak abundances of adult and larval ctenophores, respectively. Abundances of dinoflagellates and ciliates declined by 45–56% and 83–97%, respectively, during highest larval abundances in 2008 and 2009. Furthermore, the dramatic reduction of mesozooplankton by adult *M. leidyi* resulted in a cascading effect on microplankton. A relationship between high adult *M. leidyi*/low mesozooplankton with high microplankton abundances was identified, and preceded an increase in ctenophore larvae. These data suggest that blooms of *M. leidyi* result in a direct feedback system, wherein intense feeding activity by adults on mesozooplankton releases certain microplanktonic taxa from predation pressure, enhancing prey conditions for larval ctenophores.

Editor's note

McNamara and colleagues report on new experiments and field sampling that demonstrate the dynamics of two features of plankton dynamics that have recently received much attention and speculation. First, the results confirm in a concrete fashion multiple trophic level interactions that have been discussed in many papers on trophic dynamic theory. Second, their work also provide substantial information on the key, and complex, role of gelatinous predators in structuring plankton food webs. The novel combination of methods, and the compelling results should challenge pursuit of similar work in other coastal waters to assess how general the results of McNamara et al. might be.

1. Introduction

The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 is a planktonic predator capable of exerting significant mortality on the zooplankton community in temperate coastal environments (e.g., Kremer, 1979; Deason and Smayda, 1982; Purcell et al., 2001; Purcell and Decker, 2005; McNamara et al., 2010). *Mnemiopsis* blooms may consist of both adults and larvae, the latter of which must pass through distinct morphological stages. After hatching, *M. leidyi* undergo a tentaculate (cydippid) stage during which they possess two tentacles which are used to seize and capture microplanktonic (20–200 μm) prey (Sullivan and Gifford, 2007). As the larva grows, it develops lobes and the tentacles are resorbed. The transformation from a tentaculate to lobate body plan is marked by a transitional stage, in which both tentacles and lobes are used to capture microplanktonic and mesozooplanktonic prey (Reeve et al., 1978; Sullivan and Gifford, 2004). *Mnemiopsis leidyi* typically enter the transitional stage between 0.5 and 1.5 cm and the transformation to lobate form is usually complete when the ctenophore

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http://dx.doi.org/10.1016/j.ecss.2013.04.019

reaches lengths greater than 1.5 cm (Stoecker et al., 1987; Sullivan and Gifford, 2004; Rapoza et al., 2005; Sullivan and Gifford, 2007).

The survival of larval *M. leidyi* depends, in part, on the availability and composition of microplanktonic prey. In laboratory incubations, a diet consisting entirely of microplankton (diatoms, flagellates, autotrophic and heterotrophic dinoflagellates, naked and tintinnid ciliates, and rotifers) supported significant growth of larval ctenophores (Stoecker et al., 1987; Sullivan and Gifford, 2007). Larvae incubated in low concentrations of microplankton were smaller than larvae incubated in medium and high concentrations during long-term feeding experiments, and those fed a diet consisting predominantly of mixotrophic dinoflagellates exhibited significantly higher growth rates than those fed other microplanktonic taxa (Sullivan and Gifford, 2007). Larvae also experienced significant differences in growth and survival rates when fed ciliates and copepod nauplii compared to those fed high amounts of phytoplankton alone, which did not survive (Stoecker et al., 1987). Larval *M. leidyi* frequently dominate numerically during high ctenophore densities (Costello et al., 2006; Condon and Steinberg, 2008), and it has been suggested that the abundance and composition of microplankton may ultimately explain the timing and magnitude of ctenophore recruitment into mesozooplankton-feeding adults (Sullivan and Gifford, 2004; Rapoza et al., 2005).

While the abundance and composition of zooplankton communities are likely to influence the population dynamics of *M. leidyi* differently across life stages, the influence of *M. leidyi* on the plankton community will depend on the magnitude and size-distribution of the ctenophore population. Clearance rates of larval *M. leidyi* obtained experimentally indicated that larvae, when abundant, have the potential to exert significant predatory control over microzooplankton (Stoecker et al., 1987; Sullivan and Gifford, 2004, 2007). Larvae fed *in situ* concentrations of microplankton significantly reduced the abundance of aloricate ciliates, rotifers and copepod nauplii (Stoecker et al., 1987). Sullivan and Gifford (2004) estimated that high abundances of the larvae could potentially clear up to ~60% of the water column d^{-1} of microplankton. Further, the ingestion rates of larvae increased with increasing prey density, like those of adult *M. leidyi* on mesozooplankton (e.g., Kremer, 1979). For these reasons, it has been suggested that regions of high microplankton abundance may serve as “nurseries” for ctenophores during their earliest life-history stage (Sullivan and Gifford, 2007).

The larvae of *M. leidyi* may also benefit from the presence of adult ctenophores that feed on crustacean zooplankton. Firstly, high densities (100 L^{-1}) of copepod nauplii have been shown to damage the tentacles of developing ctenophores (Reeve et al., 1978) and newly-hatched *M. leidyi* suffered 84–100% mortality in the presence of copepods >200 μm (Stanlaw et al., 1981). Waggett and Sullivan (2006) observed that ctenophores <0.8 cm were frequently damaged by encounters with copepodites. Secondly, high densities of adult *M. leidyi* may increase microplankton abundance through reduction of the latter’s crustacean predators. Mesocosm experiments performed with a ctenophore (*Pleurobrachia pileus* Müller 1776; Granéli and Turner, 2002) or non-zooxanthellate jellyfish (*Catostylus mosaicus*, Scyphozoa; West et al., 2009; Pitt et al., 2007) documented significant increases in ciliate and dinoflagellate abundance, respectively, in the presence of the gelatinous species compared to control tanks or those with mesozooplankton additions. In contrast, ciliates decreased in the absence of ctenophores, presumably due to increased predation by copepods (Granéli and Turner, 2002).

Despite a preponderance of data on the predatory influence of adult *M. leidyi* on mesozooplankton, little is known about the changes in microplankton communities during blooms of *M. leidyi*. The aim of this study was to identify and interpret changes in microplankton abundance and composition in response to top-down control of mesozooplankton by adult *M. leidyi* and microplankton by larval *M. leidyi in situ*. We hypothesized that blooms of *M. leidyi* are involved in a direct feedback system in which intense feeding activity by adults on mesozooplankton enhances prey conditions for larval ctenophores by removing crustacean predators and increasing microplanktonic prey. To our knowledge, this is the first study to compare temporal changes in mesozooplankton and microplankton to *M. leidyi* abundance and size composition *in situ*.

2. Methods

2.1. Temporal and spatial distribution of M. leidyi

Collections for *Mnemiopsis leidyi* were made weekly from May through October in 2008 and 2009 in Great South Bay, New York, USA (Fig. 1). Sampling was conducted by boat and occurred weekly at site M and biweekly at site A (except during high *M. leidyi* abundance when weekly collections were made) using a 1.0-m diameter, 1-mm mesh net ($n = 2$) and a 0.5-m diameter, 250-μm mesh net ($n = 2$) equipped with flow meters. An exception to weekly sampling occurred in 2008 at site M when one potential sampling date (Aug 21) was canceled due to severe weather. To minimize damage to ctenophores during collection, both nets were equipped with soft, flexible cod ends and tow times restricted to short intervals (2–5 min). Tows were conducted obliquely to sample the entire water column (~1.5 m and 3 m at sites A and M, respectively). Collected ctenophores were rinsed of debris and any surface-attached zooplankton (e.g., crab zoea) with 20-μm filtered seawater and then poured through a 500-μm sieve to remove excess water (Purcell, 1988). Total live volume (biovolume) of ctenophores was then measured in graduated cylinders. Collected ctenophores were counted individually and measured (length, including lobes) to the nearest 0.5 cm (when smaller individuals dominated) or 1.0 cm (when larger individuals dominated) and divided into length-based size classes. Depending upon ctenophore abundance, either the entire sample or only a subsample was measured. All species of ctenophores and other gelatinous zooplankton were counted and recorded.

2.2. Mesozooplankton and microplankton sampling and enumeration

Sampling of mesozooplankton and micrometazoa (*i.e.*, copepod eggs and nauplii, rotifers) was conducted as described for ctenophores but using a 0.5-m diameter, 64-μm mesh net ($n = 2$) equipped with a flow meter. Samples were preserved immediately in 5% (final concentration) buffered formalin. In the laboratory, a minimum of 200 mesozooplankton were identified (Omori and Ikeda, 1992) to the lowest possible taxonomic group using a dissecting microscope.

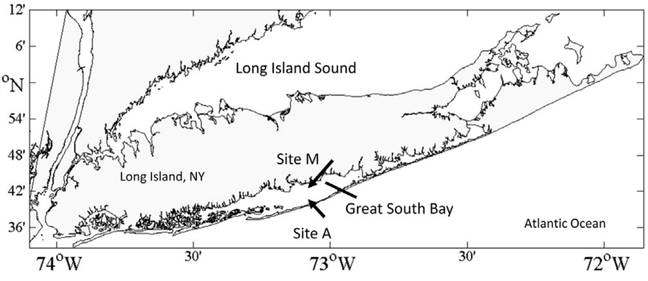

Fig. 1. Sampling locations (sites M and A) in Great South Bay, Long Island, NY, USA. Sampling designations correspond with previously-established sites maintained by The Nature Conservancy.