Vol. 510: 151–165, 2014
doi: 10.3354/meps10900

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 9

Contribution to the Theme Section 'Jellyfish blooms and ecological interactions'

Role of eutrophication in structuring planktonic communities in the presence of the ctenophore *Mnemiopsis leidyi*

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ABSTRACT: Increasing evidence implicates anthropogenic activities with recently documented shifts in the abundance and seasonal distribution of gelatinous zooplankton in coastal waters. The ctenophore *Mnemiopsis leidyi* occurs in mid-Atlantic estuaries in the USA where seasonal blooms occur earlier and in greater magnitude than those studied decades ago. Large densities of adult *M. leidyi* exert significant predation pressure on mesozooplankton, potentially influencing microplankton abundance and composition. Field-based mesocosm experiments were conducted to examine the individual and interactive roles of ctenophore predation and nutrient loading on the microplankton community using historic and recent abundances of *M. leidyi* in Great South Bay, New York, USA. High (recent) abundances of *M. leidyi* exposed to eutrophic conditions influenced plankton community structure in a way that was distinctly different from when the processes occurred separately or under low (historic) abundances. Microplanktonic ciliates exhibited an order of magnitude increase in tanks receiving either nutrient or ctenophore amendments, but increased by 2 orders of magnitude in treatments receiving both ctenophore and nutrient additions. Furthermore, ctenophores recovered from nutrient treatments produced nearly 3 times as many eggs than those reclaimed from ctenophore-only treatments, suggesting that nutrient enrichment enhances fecundity of *M. leidyi*. Since ciliates are an important prey item for developing *M. leidyi,* the combined bottom-up and top-down influences of eutrophication and ctenophore predation, respectively, on microplankton may help explain recently documented shifts in the population dynamics of *M. leidyi* in mid-Atlantic estuaries.

KEY WORDS: Mesocosm · Ciliates · Trophic cascade · Mesozooplankton · Nutrient enrichment · Great South Bay

INTRODUCTION

Although global increases in gelatinous zooplankton are subject to debate (Mills 1995, 2001, Purcell et al. 2007, Condon et al. 2013), some regions have experienced shifts in the abundance and seasonal distribution of their gelatinous predators (e.g. scyphomedusae, siphonophores, and ctenophores), which may be taking advantage of localized regime shifts brought about by overfishing, pollution, and/or global climate change (Mills 1995, 2001, Sullivan et al. 2001, Purcell 2005, Purcell et al. 2007). Increasing evidence suggests that anthropogenic eutrophication can promote increased abundances and earlier seasonal appearances of gelatinous zooplankton in coastal waters. The increased hypoxia and turbidity associated with nutrient enrichment can benefit non-visual, oxytolerant gelatinous zooplankton (i.e. ctenophores) over many fish and squid species (Arai 2001, Parsons & Lalli 2002, Grove & Breitburg 2005, Kemp et al. 2005, Thuesen et al. 2005, Purcell et al. 2007, Kimmel et al. 2012). Further, by preferentially elevating levels of ni-

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trogen and phosphorus, but not silica, anthropogenic eutrophication can shift phytoplankton communities from diatoms towards flagellates and other small autotrophs (Daskalov 2002, Parsons & Lalli 2002, Purcell et al. 2007), increasing the abundance of small zooplankton which ctenophores and small scyphomedusae favor (Uye 1994, Daskalov 2002). Although eutrophication has been implicated in the proliferation of small gelatinous zooplankton (e.g. *Aurelia aurita*) in disturbed habitats, it is difficult to attribute these observed increases to nutrient enrichment alone and not to other co-occurring environmental changes (Arai 2001, Purcell et al. 2007, Purcell 2012). This is further complicated by the success of non-native gelatinous species in exotic habitats already suffering from severe anthropogenic influences (e.g. Shiganova 1998).

The ctenophore *Mnemiopsis leidyi* Agassiz 1865 is a gelatinous zooplankton predator, occurring in coastal, temperate waters. Once limited in distribution to the Atlantic coasts of North and South America, this species has successfully invaded the Black, Caspian, Mediterranean, Aegean, North, and Baltic Seas, and has recently been identified along the Australian coast in the South Pacific Ocean (Costello et al. 2012). In their native mid-Atlantic estuaries in the USA, populations of *M. leidyi* have increased in abundance and shifted towards an earlier seasonal maximum (Narragansett Bay: Sullivan et al. 2001, Costello et al. 2006; Chesapeake Bay: Condon & Steinberg 2008; Long Island estuaries: McNamara et al. 2010). Seasonal blooms of *M. leidyi* can exert strong predation pressure on the surrounding mesozooplankton community as adults (e.g. Kremer 1979, Deason & Smayda 1982, Purcell et al. 2001, Purcell & Decker 2005, McNamara et al. 2010) and on microzooplankton as larvae (Stoecker et al. 1987, Sullivan & Gifford 2004, 2007, Rapoza et al. 2005, McNamara et al. 2013). Moreover, removal of mesozooplankton and microplankton by large densities of adult and larval *M. leidyi*, respectively, can cascade down the food web, influencing lower trophic levels. Correlations between high adult *M. leidyi*/low mesozooplankton with high microzooplankton abundances and high larval *M. leidyi*/low microzooplankton with high nanoplankton abundances have recently been identified in Great South Bay, New York, USA (McNamara et al. 2013). Such cascading influences on lower trophic levels can feedback to ctenophore population dynamics by enhancing the abundance of certain taxa (i.e. dinoflagellates and ciliates), which serve as prey for developing ctenophores (Stoecker et al. 1987, Sullivan & Gifford 2007, McNamara et al. 2013).

The ecological role of gelatinous zooplankton in disturbed habitats, however, is likely to differ from that in natural, undisturbed environments. When the scyphomedusa *Catostylus mosaicus* was added to mesocosms receiving nutrient additions, the result on the plankton community was distinctly different from that in mesocosms receiving *C. mosaicus* or nutrient additions alone (Pitt et al. 2007). While mesozooplankton abundance was reduced in tanks containing *C. mosaicus*, abundances of the toxic heterotrophic dinoflagellate *Nocticula scintillans* increased by a factor of 20 in tanks containing *C. mosaicus* and receiving nutrient additions. Pitt et al. (2007) hypothesized that nutrient enrichment increased the diatom prey of *N. scintillans*, while the addition of *C. mosaicus* removed mesozooplankton grazers, enabling the red tide-forming dinoflagellate to increase in abundance. Thus, responses of the plankton community to ctenophore predation under eutrophic conditions may differ from when the 2 processes occur independently.

In this study, we examined the individual and interactive roles of *M. leidyi* predation and nutrient loading on the microplankton community in Great South Bay, New York, in experimental mesocosms. Great South Bay is a shallow, lagoonal embayment located on the south shore of Long Island where seasonal population blooms of *M. leidyi* have increased by a factor of 2 to 5 and occur 2 to 3 mo earlier than populations studied 2 to 3 decades ago (McNamara et al. 2010, 2013). The relative impacts of eutrophication and ctenophore predation on the zooplankton community were further compared using historic (low) and recent (high) abundances of *M. leidyi* documented in the bay. We hypothesized that ctenophore predation and eutrophication exert significant top-down and bottom-up influences on the microplankton community, respectively; and that nutrient enrichment during large blooms of *M. leidyi* favors substantial increases in certain microplanktonic taxa (i.e. Pitt et al. 2007) such as ciliates, which may feed back to *M. leidyi* population dynamics by enhancing prey conditions for their larvae. To our knowledge, this is the first study to experimentally determine the contrasting influences of nutrients with varying densities of *M. leidyi* on the microplanktonic community and may help explain the recently documented shifts in the abundance of *M. leidyi* in coastal estuaries.

MATERIALS AND METHODS

Experimental design and set-up

Field-based mesocosm experiments were conducted to examine the individual and interactive impacts of

Mnemiopsis leidyi predation and nutrient loading on the abundance and composition of the plankton community in a coastal marine environment. During 2008 and 2009, 2 mesocosm experiments (1 in each year) were performed at the West Sayville Boat Basin located on Great South Bay (40° 48′ N, 72° 36′ W). Mesocosms consisted of 400 l translucent plexiglass cylinders (n = 12) filled with ~300 l of ambient bay water. Cylinders were enclosed within a large floating platform in the bay, with each cylinder secured by line to each other and/or to the platform. Cylinders were somewhat flexible and were mixed by ambient wave activity within the bay. The experimental set-up consisted of 4 treatments, each with 3 replicates: control (C), nutrient enrichment (Nt), ctenophore addition (Ct), and combined ctenophore addition and nutrient enrichment (Ct+Nt). Three cylinders were randomly assigned to each treatment.

Control treatments (C) consisted of bay water only and received neither nutrient enrichment nor ctenophore addition. To simulate eutrophic conditions, nutrient enrichment treatments (Nt and Ct+Nt) received daily additions of ammonium (10 µM final concentration) and orthophosphate (0.625 µM final concentration) as per Wall et al. (2008). In order to achieve final target concentrations of nutrients, the height of the water in each tank was regularly measured to calculate total water volume and determine the appropriate nutrient dosages for each tank. Ctenophore addition treatments (Ct and Ct+Nt) were supplemented with adult (>1.5 cm) *M. leidyi* in quantities reflecting maximum seasonal abundances observed historically and recently in Great South Bay (e.g. McNamara et al. 2010). Five adult *M. leidyi* (~15 ind. m^{-3}, ~25 ml m^{-3}) were added to Ct and Ct+Nt treatments in 2008 (mesocosm experiment 1, M1: 28 July to 2 August), whereas Ct and Ct+Nt treatments received 20 adult *M. leidyi* (~60 ind. m^{-3}, ~100 ml m^{-3}) in 2009 (M2: 13 to 18 July). Ctenophores were added at T_0, marking the beginning of the timed experiment. Ctenophores were collected approximately 12 to 24 h prior to the start of the experiment by dip net and held in 4 l glass jars containing 0.45 µm filtered seawater within an incubator set to ambient temperature. Mesocosm experiments ran for 5 full days, ending 120 h after their initiation (T_0 to T_{120}).

Environmental parameters and chl *a* content

Temperature, salinity, and dissolved oxygen concentration were sampled daily in each tank and the surrounding bay water using a YSI 85 sonde at 0.5 m below the surface. Measurements were also taken 0.5 m above the bottom of each tank to determine whether differences existed within cylinders. Chl *a* content was determined from whole (n = 2) and <5 µm fractioned samples (n = 2) collected from all cylinders at T_0, T_{48}, T_{96}, and T_{120}. Whole seawater (20 l) was gently collected from ~0.5 m beneath the surface of each cylinder, from which 250 ml samples were immediately stored in amber bottles inside a cool, dark cooler for chl *a* analysis. The remainder of the collected water was then returned to the cylinder. In the laboratory, size fractionation was accomplished by filtering samples through a 5 µm polycarbonate membrane filter. Whole and size-fractionated samples (30 ml) were concentrated onto Whatman GF/F filters and stored in acetone for 24 h at −20°C. After thawing for 1 h, samples were analyzed using a Turner Designs (model 10-AU) fluorometer following the method of Arar & Collins (1997).

Mesozooplankton abundance and composition

Mesozooplankton and micrometazoa (collectively referred to as mesozooplankton) were collected only at the beginning (T_0) and end (T_{120}) of each experiment due to the large volume of water required for accurate enumeration. At T_0, mesozooplankton samples (n = 3) were collected from surrounding bay water immediately before, after, and during the filling of experimental cylinders. At T_{120}, samples were collected individually from each experimental cylinder. To collect mesozooplankton, 20 l of seawater was filtered through a 64 µm sieve, and the contents on the mesh were preserved in 5% (final concentration) buffered formalin. In the laboratory, all mesozooplankton were enumerated to the lowest possible taxonomic group.

Microplankton abundance and composition

Microplankton (20–200 µm) samples were also collected at T_0, T_{48}, T_{96}, and T_{120}. A 90 ml sample was carefully removed from the 20 l of whole seawater previously collected for chl *a* analyses (as above), preserved in 10% acidic Lugol's solution (100 ml final sample volume) in amber glass jars, and stored immediately in the dark. Microplanktonic organisms were isolated following standard settling techniques (Stoecker et al. 1994) in 10 ml Utermöhl chambers, and identified to the lowest possible taxonomic level using an Olympus CK2 inverted light microscope.

For data analyses, taxa were characterized into one of the following categories: centric or pennate diatoms, flagellates, dinoflagellates, loricate ciliates, aloricate ciliates (e.g. oligotrichs), and others (e.g. heliozoans, acantharians). Individual length and width measurements of the first 25 representatives of each group were used to convert sizes into biovolume using calculations established by Sun & Liu (2003). In turn, biovolume and abundance values of each taxonomic category were converted into biomass estimates (µg C l^{-1}) using conversion factors published by Strathmann (1967; centric and pennate diatoms), Børsheim & Bratbak (1987; flagellates), Putt & Stoecker (1989; ciliates), and Menden-Deuer & Lessard (2000; dinoflagellates). Chains of small centric diatoms were counted as single microorganisms when chain lengths exceeded 20 µm.

M. leidyi abundance, size structure, and fecundity

Transplanted ctenophores were individually counted and measured (length, including lobes) to the nearest millimeter prior to their addition to the tanks. Ctenophores were recovered at T_{120} by gently stirring and dip-netting the cylinders after the aforementioned samples were collected, and measured. Attempts to recover ctenophores from tanks not having received ctenophore amendments were also made to determine the natural presence of *M. leidyi* from ambient seawater.

In 2009 (M2), a subset of collected ctenophores from Ct (n = 9) and Ct+Nt (n = 9) treatments was transferred back to the laboratory and examined for egg production. Recovered ctenophores were placed into individual watch glasses containing 0.45 µm filtered seawater and held in an incubator set at ambient temperature and light conditions. After 24 h, the ctenophores were removed and rinsed with 0.45 µm filtered seawater over the watch glass to allow enumeration of total eggs using a dissecting scope.

Statistical analyses

Microplankton abundance and biomass data at T_{48}, T_{96}, and T_{120} were analyzed using a repeated measures 2-way ANOVA (Statistica 9.0, StatSoft). Post hoc analyses were conducted using Tukey's HSD test. Mesozooplankton abundance data at T_{120} were analyzed by 2-way ANOVA with nutrients and ctenophores as fixed factors using BIOMstat (Statistical Software for Biologists, Ver. 3.30; Applied Biostatistics). Homogeneity of variance was tested prior to ANOVAs using F_{max}, Scheffé-Box (log-ANOVA), and Levene tests for homogeneity of variance (BIOMstat). Where necessary, data were log-transformed [ln(x + 1)] prior to the ANOVAs. No appropriate transformation could be identified to perform a repeated-measures ANOVA on chl *a* data. Instead, chl *a* data were analyzed by individual 2-way ANOVAs with nutrients and ctenophores as fixed factors for T_{48}, T_{96}, and T_{120} using BIOMstat.

RESULTS

Environmental parameters

Daily dissolved oxygen (DO) concentration, temperature, and salinity measurements taken within the experimental cylinders suggested adequate mixing of cylinder water throughout the experiments. Subsurface and bottom measurements did not differ within cylinders during either experiment. DO concentration within the cylinders consistently measured >50% saturation and was on average 25% higher than concentrations measured simultaneously in ambient water (data not shown). Temperatures within the cylinders ranged from 25.9 to 27.3°C in 2008 and 23.5 to 25.0°C in 2009, but for each experiment varied by less than 0.2°C within and among the cylinders and remained within 0.5°C of ambient temperatures. Cylinder salinity values ranged from 26.0 to 26.5 in 2008 and 22.1 to 22.5 in 2009, varied by ≤0.2 within and among cylinders, and never exceeded more than 1 unit of the salinity of ambient water.

Chl *a*

Whole and size-fractionated chl *a* levels were significantly elevated in Nt and Ct+Nt treatments compared to C and Ct treatments during both experiments (Fig. 1, Table 1). While chl *a* levels increased with time in Nt and Ct+Nt treatments, they exhibited a general trend of decline in C and Ct treatments during the duration of the 2 experiments. At T_{96} and T_{120}, differences in chl *a* content between Nt and Ct+Nt or between C and Ct treatments were indiscernible (Fig. 1), and post hoc analyses found no significant differences between Nt and Ct+Nt or C and Ct treatments during these times. A significant ctenophore (Ct and Ct+Nt) effect was detected at T_{48} for both whole and size-fractionated chl *a* during M2

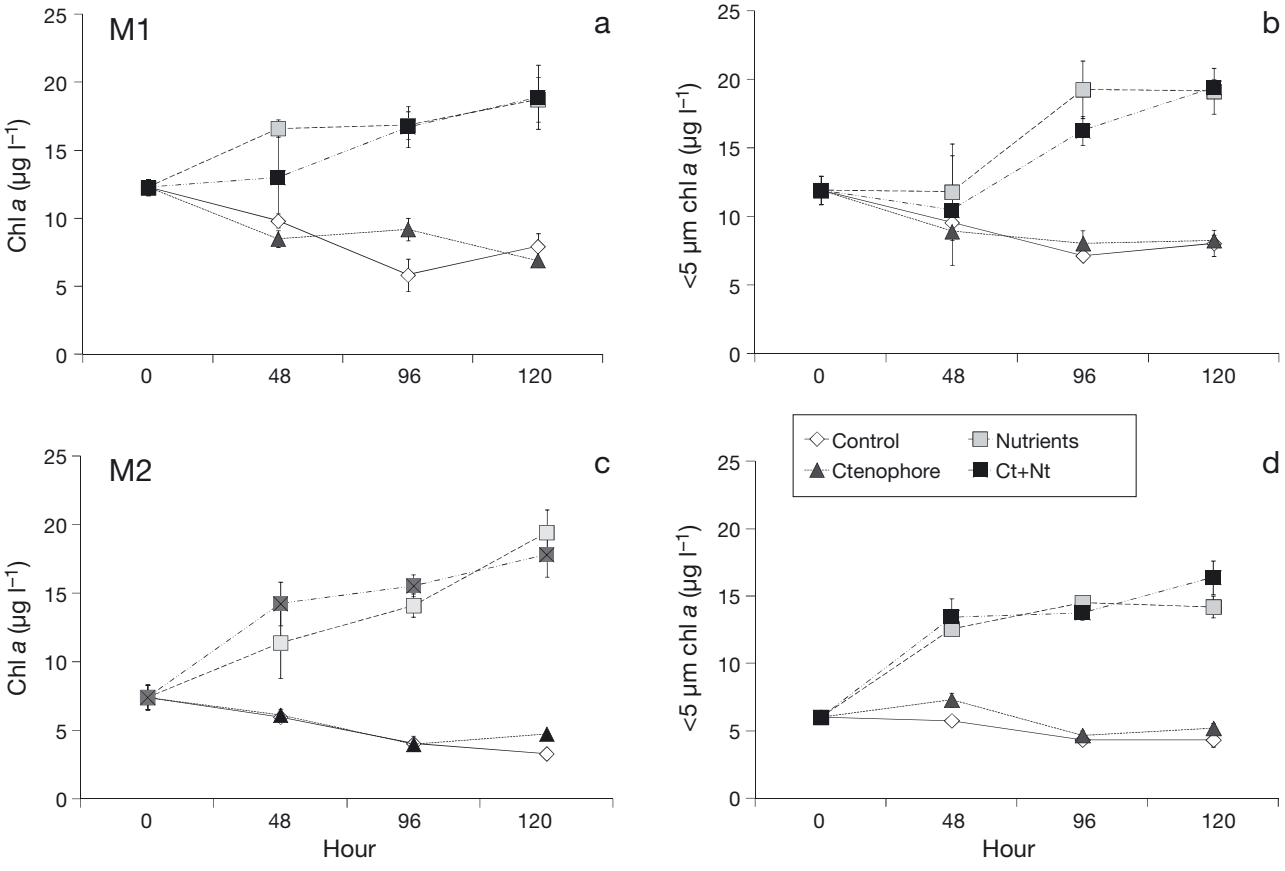

Fig. 1. Whole and size-fractionated chl *a* content (µg l^{-1}) by treatment and time interval during mesocosm experiments (a,b) M1 (2008) and (c,d) M2 (2009). Ct+Nt: ctenophores and nutrients. Error bars (SD) may be smaller than the symbols

(Table 1), but the influence was transitory and did not persist throughout the experiment. Chl *a* <5 µm comprised 97% and 81% of total chl *a* content at T_0 during M1 and M2, respectively, and occasionally matched or exceeded whole chlorophyll values throughout both mesocosms (Fig. 1a–d).

Mesozooplankton abundance and composition

Mean ± SD mesozooplankton densities at T_0 were 174 ± 56 l^{-1} and 81 ± 12 l^{-1} during M1 and M2, respectively, and increased substantially in all treatments during the experiments. Copepod nauplii (principally *Acartia tonsa*, and to a lesser extent *Oithona similis*) consistently dominated the mesozooplankton in all treatments during both experiments, comprising 84 to 95% of total mesozooplankton abundance at T_{120} (Table 2). Meroplankton, consisting primarily of polychaete larvae, barnacle cyprids, and bivalve veligers, comprised ~20% of the mesozooplankton assemblage during both experiments at T_0, but made up less than 4% at T_{120} (Table 2), possibly due to growth and settlement within and on cylinders, respectively, as the experiment progressed. Ctenophores significantly reduced mesozooplankton abundance in Ct and Ct+Nt treatments in both experiments, relative to the control (Fig. 2, Tables 2 & 3). In contrast, nutrients increased mesozooplankton abundance in both experiments; however, the differences were only significant in M2 (Fig. 2, Tables 2 & 3).

Microplankton abundance and composition

During both experiments, microplanktonic assemblages were dominated numerically (cells ml^{-1}) by pennate diatoms (e.g. *Nitzschia longissima, Pleurosigma directum*, and *P. elongatum*), which initially made up >93% of the microplanktonic community, but ranged from 80 to 90% and from 35 to 93% at the end of M1 and M2, respectively. However, diatoms contributed less than 26% to total microplanktonic biomass (µg C l^{-1}), which was dominated in both experiments by ciliates (aloricate and loricate). Dino-

Table 1. Results of 2-way ANOVA testing for differences in whole and <5 µm chl *a* content among treatments (with nutrients and ctenophores as fixed factors) at 48, 96, and 120 h after the onset of the experiment (T_{48}, T_{96}, and T_{120}) during mesocosm experiments M1 (2008) and M2 (2009). Ct×Nt: Interaction between ctenophore and nutrients. Significant values ($p < 0.05$) are highlighted in **bold**

M1 (whole chl *a*)	Factor	df	MS	*F*	p	M2 (whole chl *a*)	Factor	df	MS	*F*	p
T_{48}	Nutrients	1	192	26.7	**<0.001**	T_{48}	Nutrients	1	699	124	**<0.001**
	Ctenophore	1	36	5	**0.036**		Ctenophore	1	41.7	7.41	**0.013**
	Ct×Nt	1	7.8	1.1	0.310		Ct×Nt	1	37.4	6.64	**0.018**
Error		20	7.2			Error		20	5.6		
T_{96}	Nutrients	1	514	69.2	**<0.001**	T_{96}	Nutrients	1	700	405	**<0.001**
	Ctenophore	1	15.8	2.1	0.160		Ctenophore	1	2.84	1.65	0.214
	Ct×Nt		18.2	2.4	0.133		Ct×Nt	1	3.26	1.88	0.185
Error		20	7.4			Error		20	1.7		
T_{120}	Nutrients	1	588	71.9	**<0.001**	T_{120}	Nutrients	1	1280	7150	**<0.001**
	Ctenophore	1	10.1	1.23	0.160		Ctenophore	1	0.04	0.005	0.945
	Ct×Nt		17.7	2.16	0.157		Ct×Nt	1	14	1.65	0.213
Error		20	8.2			Error		20	8.5		
M1 (<5 µm chl *a*)	Factor	df	MS	*F*	p	M2 (<5 µm chl *a*)	Factor	df	MS	*F*	p
T_{48}	Nutrients	1	21.2	1.2	0.296	T_{48}	Nutrients	1	706	133	**<0.001**
	Ctenophore	1	6	0.33	0.574		Ctenophore	1	43.5	8.19	**0.010**
	Ct×Nt	1	0.72	0.04	0.845		Ct×Nt	1	35.7	6.72	**0.017**
Error		20	18.4			Error		20	5.3		
T_{96}	Nutrients	1	617	78.1	**<0.001**	T_{96}	Nutrients	1	560	350	**<0.001**
	Ctenophore	1	6.7	0.85	0.368		Ctenophore	1	0.256	0.16	0.693
	Ct×Nt	1	1.73	1.08	0.311		Ct×Nt	1	1.73	1.08	0.311
Error		20	7.9			Error		20	1.6		
T_{120}	Nutrients	1	739	122	**<0.001**	T_{120}	Nutrients	1	1190	4140	**<0.001**
	Ctenophore	1	0.36	0.06	0.810		Ctenophore	1	2.01	0.23	0.635
	Ct×Nt	1	0.004	0.001	0.979		Ct×Nt	1	6.38	0.74	0.401
Error		20	6.1			Error		20	8.7		

flagellates and flagellates comprised less than 3% of total microplanktonic abundance at T_0, but ranged from 0.2 to 5.8% and 0.3 to 57% throughout M1 and M2, respectively. Centric diatoms, while generally low in abundance during M2, were largely absent in M1. Uncategorized (other) microplankton (e.g. *Pterosperma*, heliozoans, and unidentified amoeboids) contributed little to total microplanktonic abundance in M2, but made up ≤14% of microplanktonic abundance in M1 (data not shown). Biomass conversions for these other microplanktonic taxa were not made.

Nutrients significantly increased densities of all microplanktonic taxa in M2, but only pennate diatoms, flagellates, and aloricate ciliates in M1 (Tables 4 & 5, Figs. 3 & 4). Increases of microplankton in Nt treatments were generally limited to between T_0 and T_{48} during both experiments, after which abundances remained relatively constant. Nutrients had no discernible influence on dinoflagellates (ml^{-1} or µg C l^{-1}) during M1, although increases in these taxa were identified during M2 (Tables 4 & 5). In M2 (2009), the dinoflagellate community was largely autotrophic and dominated by *Protoperidinium crassipes, Scrippsiella trochoidea, Prorocentrum minimum* and *Prorocentrum micans*, and *Pyrophacus* sp., whereas in M1 (2008), heterotrophic dinoflagellates (e.g. *Gyrodinium spirale*, *G. dominans*, *G. aureolum*, and *Akashiwo sanguinea*) dominated the assemblage. Thus, differences in species composition and trophic structure of the dinoflagellate community between the 2 years likely explain the contradiction. The scarcity of centric diatoms and loricate ciliates during M1 (each taxon averaged <0.6% of total microplankton throughout the experiment) may have precluded a statistically significant relationship between the influence of nutrients and these taxa.

The presence of *Mnemiopsis leidyi* in recent (M2), but not historic (M1), abundances altered microplanktonic abundance and composition over the 5 d experiments. High abundances of *M. leidyi* significantly influenced ciliate densities (cells ml^{-1} and µg C l^{-1}) during M2 (Table 5). There was also a trend of increased flagellate abundance (cells ml^{-1}) in the presence of *M. leidyi*; however, these increases were not significant ($p = 0.058$; Table 5). At T_{96} and T_{120}, loricate (e.g. *Tintinnopsis* sp. and *Favella* sp.) and

Table 2. Abundances (ind. l^{-1}; SD in parentheses) of mesozooplankton among treatments at 0 and 120 h after the onset of the experiment (T_0 and T_{120}) during mesocosm experiments M1 (2008) and M2 (2009). Ct+Nt: ctenophores and nutrients

M1	T_0	Control T_{120}	Nutrients T_{120}	Ctenophore T_{120}	Ct+Nt T_{120}
Acartia tonsa adults	3.5 (3.5)	33.1 (20.2)	30.9 (23)	17.5 (10.5)	10.4 (5.3)
A. tonsa copepodites	6.0 (3.5)	134.6 (177.6)	52.6 (32.2)	19.4 (14.8)	19.9 (13.1)
A. tonsa nauplii	46.7 (16)	737.2 (88.2)	989.2 (275.2)	423.5 (162.4)	608.9 (106.2)
Oithona similis adults	0.7 (0.7)	12 (4)	8.7 (1.6)	2.1 (0.8)	7.5 (5.9)
O. similis copepodites	11.4 (4)	2.4 (4.2)	0	1.3 (1.4)	1.6 (1.4)
O. similis nauplii	42.4 (4.6)	251.9 (170)	214.3 (31.4)	75.5 (46.4)	73.6 (44.6)
Other adult copepods	0	0	0	0	0
Other copepodites	0	0	0	0	0
Meroplankton	35.2 (0.9)	13.9 (10.3)	13.5 (9)	6.4 (1.8)	8.6 (4.2)
Tintinnids	0	3.0 (5.2)	3.7 (5)	0.9 (0.8)	2.4 (2.4)
M2	T_0	Control T_{120}	Nutrients T_{120}	Ctenophore T_{120}	Ct+Nt T_{120}
A. tonsa adults	15.6 (13.8)	45.8 (45.9)	25.1 (17.5)	0.8 (0.9)	0.8 (1.5)
A. tonsa copepodites	10.3 (2.2)	59.4 (31.7)	125.7 (155)	4.9 (2.4)	10.2 (4.7)
A. tonsa nauplii	13.2 (11.3)	454.2 (116.8)	1231 (161.2)	121.9 (17)	344.7 (88.8)
O. similis adults	9.5 (3.1)	2.2 (1.5)	17.1 (17.6)	1.9 (1.7)	0.4 (0.7)
O. similis copepodites	0	17.2 (2.4)	32.4 (36.3)	1.2 (1.2)	3.3 (2.7)
O. similis nauplii	16.4 (3.9)	153.7 (57.3)	473.4 (191.5)	42.7 (11.6)	88.8 (39.1)
Other adult copepods	2.3 (2.2)	1.7 (1)	7 (6.7)	0.2 (0.3)	0
Other copepodites	0	11 (13.5)	5.2 (8.9)	0.4 (0.3)	0
Meroplankton	13.4 (5.2)	4.3 (1.5)	6 (2.9)	6.6 (3.9)	5.9 (4.4)
Tintinnids	0.3 (0.5)	0	0	0	0

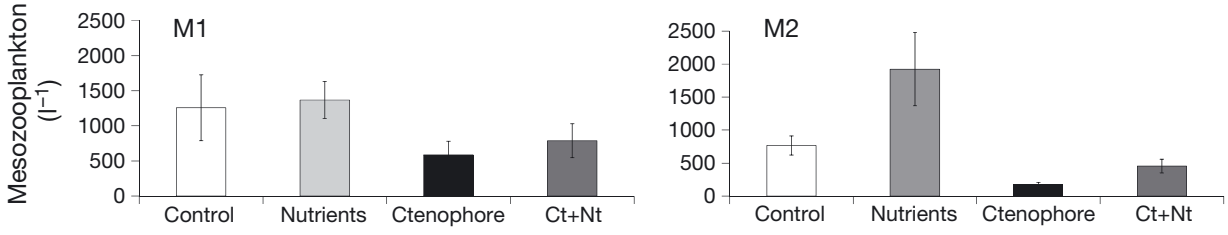

Fig. 2. Mean ± SD mesozooplankton densities (ind. l^{-1}) at 120 h after the onset of the experiment (T_{120}) for each treatment during mesocosm experiments M1 (2008) and M2 (2009). Ct+Nt: ctenophores and nutrients

aloricate ciliates (e.g. *Strombidinium* sp. and *Strobilidium* sp.) were more numerous in ctenophore treatments, relative to the control (Fig. 5a,b). Further, increases in aloricate ciliates were substantially greater in ctenophore treatments than in nutrient-amended cylinders. Aloricate ciliates, relative to the control, experienced a 3-fold increase in Nt treatments, but a 14-fold increase in Ct treatments at the end of M2 (Fig. 5a). Whereas ciliates increased immediately in Nt treatments, their increases in cylinders containing *M. leidyi* were not detected until T_{96} (Fig. 4). Flagellates also increased in the presence of *M. leidyi,* but these increases were not detected until T_{120}. Ctenophores significantly influenced densities of pennate diatoms in M2 (Table 5),

Table 3. Results of 2-way ANOVA testing for differences in mesozooplankton abundance (with nutrients and ctenophores as fixed factors) among treatments at 120 h after the onset of mesocosm experiments M1 (2008) and M2 (2009). Significant values are highlighted in **bold**. Ct×Nt: interaction between ctenophores and nutrients

Factor	df	MS	*F*	p	Error df	MSE
M1						
Nutrients	1	52100	0.741	0.407	8	95982
Ctenophore	1	23000	0.327	**0.008**	8	95982
Ct×Nt	1	362	0.005	0.817	8	95982
M2						
Nutrients	1	0.563	32.19	**0.005**	8	0.02
Ctenophore	1	1.2	68.8	**<0.001**	8	0.02
Ct×Nt	1	0.003	0.19	0.674	8	0.02

Table 4. Results of repeated measures ANOVA testing for differences in microplankton abundance and biomass among treatments during mesocosm experiment M1 (2008; at 48, 96, and 120 h after the onset of the experiment). Nt: nutrients, Ct: ctenophores. Significant values ($p < 0.05$) are highlighted in **bold**

Variable (abundance):		Centric diatoms		Pennate diatoms		Dinoflagellates		Flagellates		Aloricate ciliates		Loricate ciliates	
Transformation:		(none)		ln(x + 1)		(none)		(none)		(none)		(none)	
Factor	df	MS	p	MS	p	MS	p	MS	p	MS	p	MS	p
Nutrients	1	1910	0.219	9.81	**<0.001**	2030	0.295	3006	**0.003**	60067	**0.048**	727	0.154
Ctenophore	1	865	0.396	0.486	0.126	4670	0.128	27.9	0.698	7480	0.435	15.2	0.825
Ct×Nt	1	1120	0.337	0.005	0.869	149	0.770	4.39	0.877	600	0.822	1620	**0.046**
Error	8	1075		0.17		1622		172.8		11060		292.4	
Time	2	10133	**0.001**	2.32	**<0.001**	5.6	0.995	896	0.198	27530	**0.045**	1492	**0.008**
Time Nutrients	2	2570	0.095	0.035	0.567	1400	0.381	171	0.715	4850	0.528	54.3	0.786
Time Ctenophore	2	693	0.493	0.104	0.205	670	0.622	956	0.180	10240	0.274	159	0.504
Time Ct×Nt	2	906	0.401	0.007	0.897	497	0.701	207	0.668	7902	0.362	1098	**0.021**
Error	16	937.4		0.06		1370		499.5		7293		222.4	
Variable (biomass):		Centric diatoms		Pennate diatoms		Dinoflagellates		Flagellates		Aloricate ciliates		Loricate ciliates	
Transformation:		ln(x + 1)		ln(x + 1)		(none)		ln(x + 1)		(none)		ln(x + 1)	
Factor	df	MS	p	MS	p	MS	p	MS	p	MS	p	MS	p
Nutrients	1	2.78	0.069	6.37	**<0.001**	306	0.156	1.09	0.503	145000	**0.014**	17.8	0.341
Ctenophore	1	0.04	0.807	0.527	0.099	121	0.354	0.589	0.620	8670	0.464	6.26	0.565
Ct×Nt	1	1.21	0.204	0.063	0.538	129	0.339	2.27	0.342	192	0.912	19.3	0.323
Error	8	0.63		0.15		124.6		2.22		14650		17.4	
Time	2	3.36	**0.007**	2.25	**<<0.001**	169	0.410	2.17	0.286	9710	0.154	14.5	0.136
Time Nutrients	2	0.71	0.263	0.018	0.703	82.1	0.640	1.83	0.343	677	0.865	0.524	0.922
Time Ctenophore	2	0.47	0.405	0.218	**0.030**	247	0.279	0.734	0.640	10800	0.128	29.1	**0.028**
Time Ct×Nt	2	1.05	0.149	0.034	0.522	126	0.509	0.415	0.775	11100	0.123	4.02	0.548
Error	16	0.49		0.05		178.9		1.6		4613		6.43	

which were slightly elevated in ctenophore treatments at T_{120}, relative to the control (Fig. 4). No significant increases in centric diatoms or dinoflagellates were identified in ctenophore treatments during either experiment.

Moreover, *M. leidyi* predation and nutrient enrichment had a combined and interactive effect on the microplankton community. At T_{120}, ciliate and flagellate densities were higher in Ct+Nt tanks than any other treatment during both experiments, although the differences were only significant in M2 (Figs. 3 & 4, Tables 4 & 5). Aloricate ciliates, which had increased by an order of magnitude in Nt and Ct treatments, were 120× greater in abundance in Ct+Nt tanks, relative to the control, at T_{120} during M2 (Fig. 5a). The combined effect of eutrophication and ctenophore predation on pennate diatoms was conflicting; Ct+Nt treatments contained significantly more pennates than C and Ct treatments, but fewer than Nt treatments, suggesting that *M. leidyi* may have a reducing influence on this taxon in the presence of nutrient enhancement. The same was observed for centric diatoms, although their low abundance, especially during M1, likely precluded a statistically significant relationship.

M. leidyi abundance, size structure, and fecundity

Mnemiopsis specimens were seen actively swimming in ctenophore-amended tanks throughout the experiments. The ctenophores were recovered at the end of both experiments, and appeared in good health with no sign of bodily damage. The mean ± SD size of *M. leidyi* added to ctenophore treatments was 3.2 ± 0.1 cm in M1 and 2.4 ± 0.1 cm in M2. Ctenophores recovered from M1 did not vary greatly in size (<10%) between T_0 and T_{120}; however, ctenophores recovered at the end of M2 grew 83% over the course of the 5 d experiment. At T_{120}, the average size of ctenophores recovered from Ct and Ct+Nt treatment cylinders was 4.4 ± 0.4 cm and 4.3 ± 0.2 cm, respectively. No ctenophores were identified in non-ctenophore-amended cylinders at T_{120} during either experiment.

Ctenophores recovered from M2 were transported back to the laboratory for egg production studies. All recaptured *M. leidyi* produced eggs overnight. Ctenophores recovered from Ct cylinders averaged 3.5 ± 1.1 cm, whereas ctenophores recovered from Ct+Nt cylinders averaged 3.8 ± 0.8 cm. The size of collected ctenophores did not differ significantly

Table 5. Results of repeated measures ANOVA testing for differences in microplankton abundance and biomass among treatments during mesocosm experiment M2 (2009; at 48, 96, and 120 h after the onset of the experiment). Nt: nutrients, Ct: ctenophores. Significant values ($p < 0.05$) are highlighted in **bold**

Variable (abundance):		Centric diatoms		Pennate diatoms		Dinoflagellates		Flagellates		Aloricate ciliates		Loricate ciliates	
Transformation:		ln(*x* + 1)		ln(*x* + 1)		ln(*x* + 1)		(none)		ln(*x* + 1)		ln(*x* + 1)	
Factor	df	MS	p	MS	p	MS	p	MS	p	MS	p	MS	p
Nutrients	1	49.7	**0.005**	41.1	**<0.001**	1.8	**0.003**	81500	**0.035**	9.19	**0.003**	22.4	**<0.001**
Ctenophore	1	0.566	0.697	0.175	0.390	**0.003**	0.877	62100	0.058	23.8	**<0.001**	22.2	**<0.001**
Ct×Nt	1	0.101	0.868	1.2	**0.045**	0.237	0.170	51000	0.080	3.52	**0.033**	6.86	**0.006**
Error	8	3.46		0.21		0.1		12670		0.53		0.51	
Time	2	24.9	**<0.001**	0.14	0.443	1.91	**0.002**	73200	**0.002**	3.98	**0.004**	9.28	**<<0.001**
Time Nutrients	2	2.48	0.305	6.87	**<0.001**	1.09	**0.014**	61200	**0.004**	3.43	**0.007**	6.07	**<0.001**
Time Ctenophore	2	0.714	0.697	0.247	0.252	0.378	0.175	61000	**0.004**	10.4	**<0.001**	5.58	**<0.001**
Time Ct×Nt	2	0.25	0.880	0.372	0.136	0.284	0.261	40800	**0.016**	0.624	0.306	0.16	**<0.001**
Error	16	1.94		0.16		0.19		7500		0.49		0.16	
Variable (biomass):		Centric diatoms		Pennate diatoms		Dinoflagellates		Flagellates		Aloricate ciliates		Loricate ciliates	
Transformation:		(none)		ln(*x* + 1)		ln(*x* + 1)		ln(*x* + 1)		ln(*x* + 1)		ln(*x* + 1)	
Factor	df	MS	p	MS	p	MS	p	MS	p	MS	p	MS	p
Nutrients	1	51400	**0.002**	36.5	**<0.001**	2.08	**0.003**	2.76	0.263	9.68	**<0.001**	31.9	**<0.001**
Ctenophore	1	3261	0.292	0.706	0.178	0.004	0.868	2.3	0.303	18.7	**<0.001**	16.3	**0.005**
Ct×Nt	1	2160	0.386	1.8	**0.046**	0.235	0.206	0.079	0.844	1.89	**0.045**	3.77	0.106
Error	8	2566		0.32		0.12		1.9		0.34		1.14	
Time	2	7910	**0.011**	1.3	**0.023**	2.45	**0.001**	3.39	0.471	5.7	**0.002**	8.79	**0.012**
Time Nutrients	2	1350	0.375	6.88	**<0.001**	1.49	**0.007**	8.49	0.171	3.23	**0.015**	7.32	**0.022**
Time Ctenophore	2	599	0.637	0.347	0.305	0.421	0.175	0.439	0.903	8.49	**<0.001**	4.13	0.095
Time Ct×Nt	2	1450	0.350	0.295	0.361	0.208	0.403	2.48	0.573	0.505	0.439	4.62	0.075
Error	16	1292		0.27		0.22		4.3		0.58		1.51	

between treatments (df = 1, 16; $F = 0.408$; $p = 0.532$), however, the number of eggs produced by *M. leidyi* from Ct treatments differed significantly from the number produced by *M. leidyi* from Ct+Nt treatments (df = 1, 16; $F = 7.48$; $p = 0.015$). Ctenophores from Ct+Nt treatments produced nearly 3 times as many eggs as those reclaimed from Ct treatments; recovered *M. leidyi* produced an average of 466 ± 339 and 1324 ± 879 eggs ind.$^{-1}$ d^{-1} in Ct and Ct+Nt treatments, respectively.

DISCUSSION

Influence of *Mnemiopsis leidyi* on the plankton community

Nutrient enhancement in the presence of adult *M. leidyi* altered plankton community structure in a way that was distinctly different than when nutrient and predatory processes occurred separately. Certain microplanktonic taxa benefited under the combined influence of ctenophore predation and eutrophication. Moreover, these changes appeared to be dependent on ctenophore abundance; recent (high) densities of *M. leidyi* produced dramatic cascading changes in microzooplankton abundance and composition, whereas historic (low) abundances failed to elicit a significant response in the lower trophic assemblage. Aloricate ciliates increased by more than 12 000 % in Ct+Nt treatments containing high densities of *M. leidyi* at the end of M2, relative to control treatments.

The combination of top-down and bottom-up influences of nutrients and ctenophore predation, respectively, revealed an interactive, non-additive influence on the plankton community when *M. leidyi* abundances were high. The response of ciliates to simultaneous nutrient enrichment and ctenophore predation in M2 was significantly greater than the individual influence of nutrients or *M. leidyi*, and exceeded what would be expected if the 2 effects were purely additive. Cylinders containing recent abundances of *M. leidyi* or those receiving daily nutrient amendments experienced an order of magnitude increase in ciliates whereas the combination of nutrient enrichment in the presence of *M. leidyi* increased the abundance of ciliates by 2 orders of magnitude, relative to control treatments (Fig. 5).

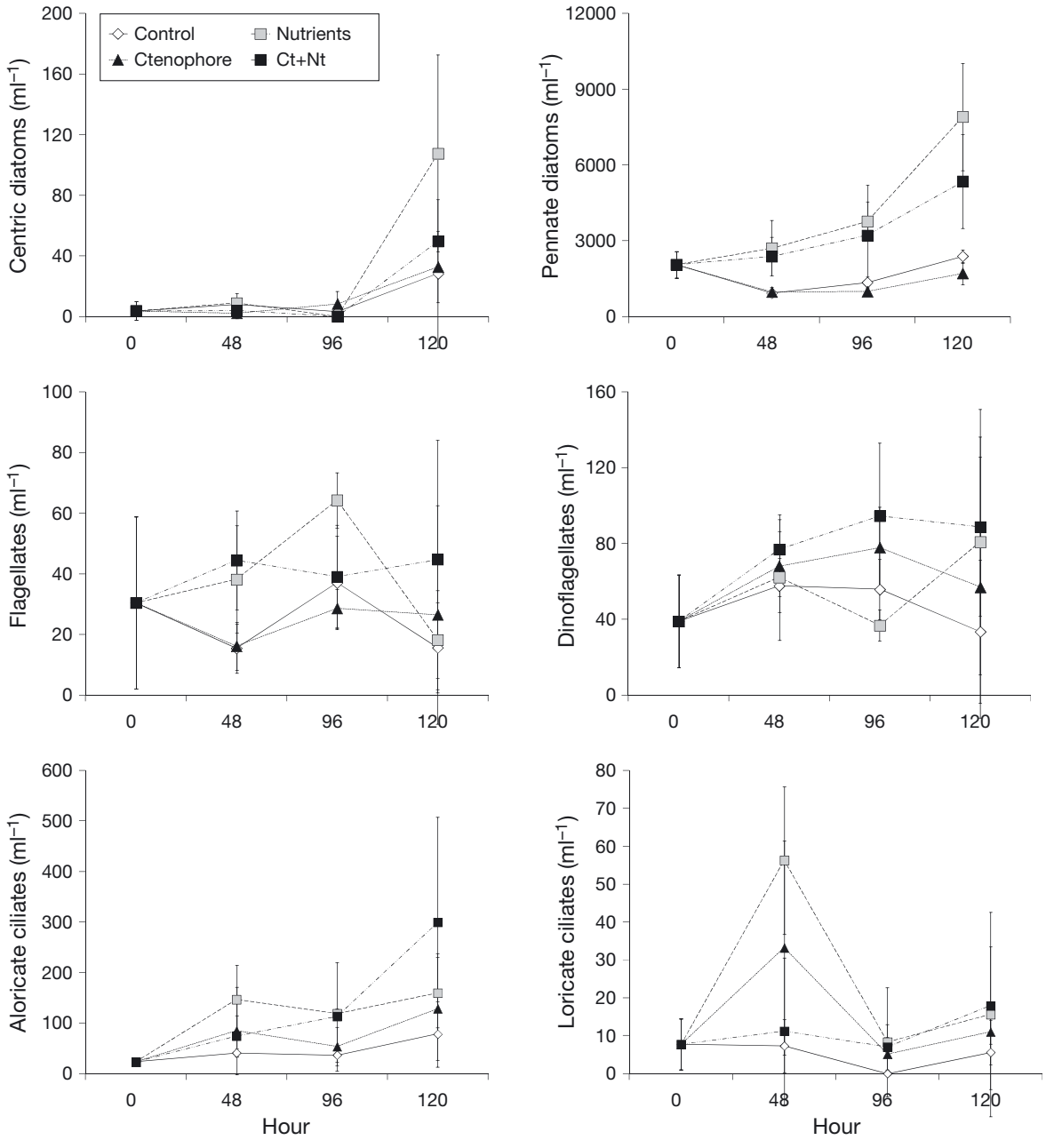

Fig. 3. Abundance (cells ml^{-1}) of centric and pennate diatoms, dinoflagellates, flagellates, and aloricate and loricate ciliates during mesocosm experiment M1 (2008). Ct+Nt: ctenophores and nutrients. Error bars: SD

The dominance of small (<5 µm) phytoplankton, as determined by similarities between whole and size-fractionated chlorophyll, suggests that eutrophication enhanced ciliate abundance by increasing their prey availability. In Great South Bay, autotrophic (and heterotrophic) nanoflagellates provide the greatest contribution to plankton productivity and biomass (Lonsdale et al. 1996, 2006), and 2 trophic levels separate nanoplanktonic phytoplankton from *M. leidyi* (microzooplankton and mesozooplankton; Deonarine et al. 2006, McNamara et al. 2013). These data demonstrate that predation by recent abundances of *M. leidyi* under eutrophic conditions can have significant impacts on the microplanktonic community, which may feedback to ctenophore population dynamics by enhancing prey for larval *M. leidyi*.

Note that because experiments M1 and M2 were conducted in separate years, differences in starting conditions (e.g. plankton assemblage), rather than in ctenophore abundance, may account for some of the

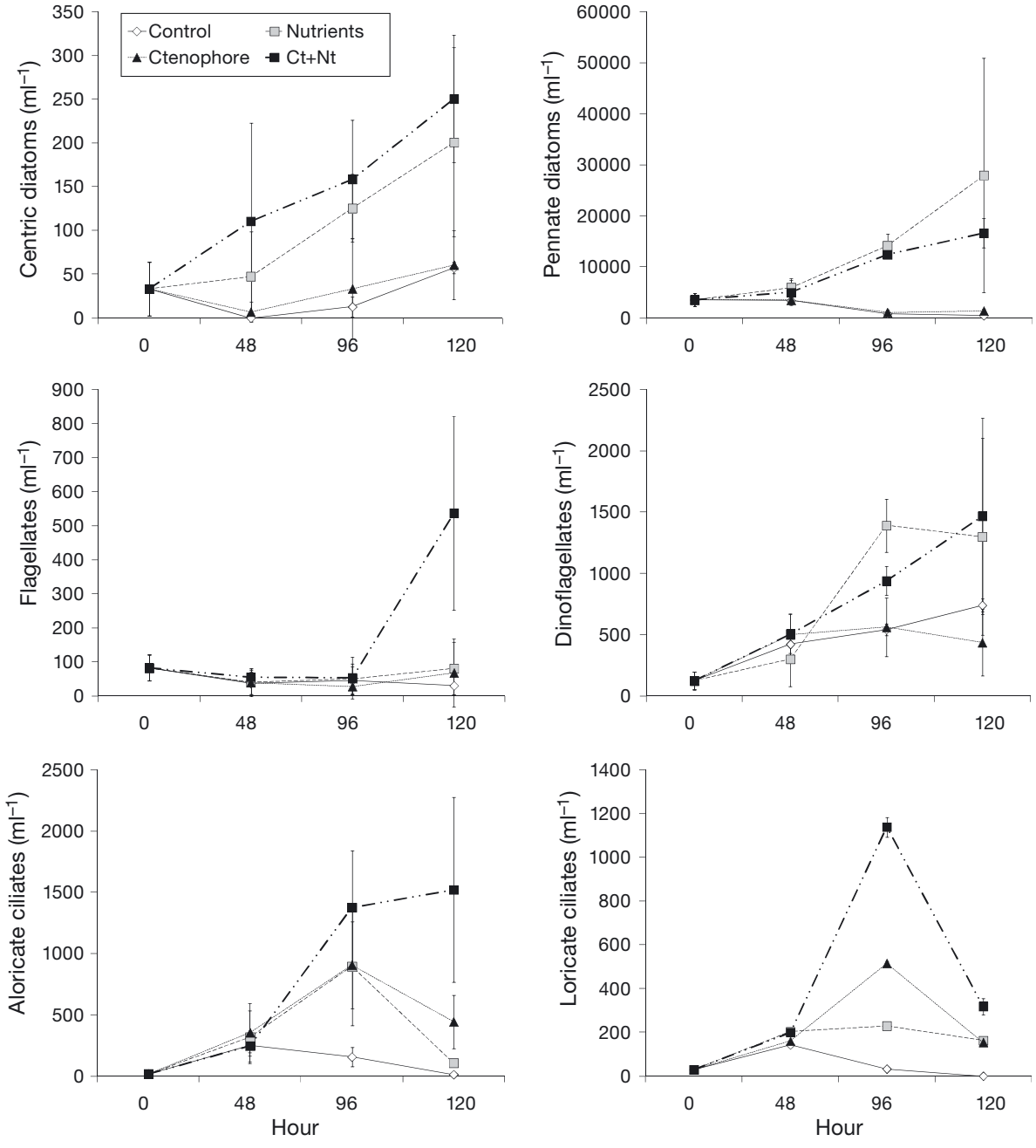

Fig. 4. Abundance (cells ml^{-1}) of centric and pennate diatoms, dinoflagellates, flagellates, and aloricate and loricate ciliates during mesocosm experiment M2 (2009). Ct+Nt: ctenophores and nutrients. Error bars: SD

observed increases in ciliates under high, but not low, *M. leidyi* abundance. Whole chl *a* values at T_0 were significantly higher ($p < 0.001$) during M1 relative to M2, which may have influenced (reduced) the response of ciliates to combined nutrient enrichment and ctenophore predation, particularly since removal of crustacean grazers by *M. leidyi* was found to be significant in both experiments. However, total microplankton and mesozooplankton abundance at T_0 did not differ significantly between the 2 years ($p = 0.11$ and 0.24, respectively), nor did the initial abundances of aloricate ciliates ($p = 0.67$). The interactive effect of ctenophore predation and eutrophication on microzooplankton is likely to be complex; differences in plankton community structure may be as influential as the magnitude of nutrient loading and predator abundance in driving cascading changes within the food web.

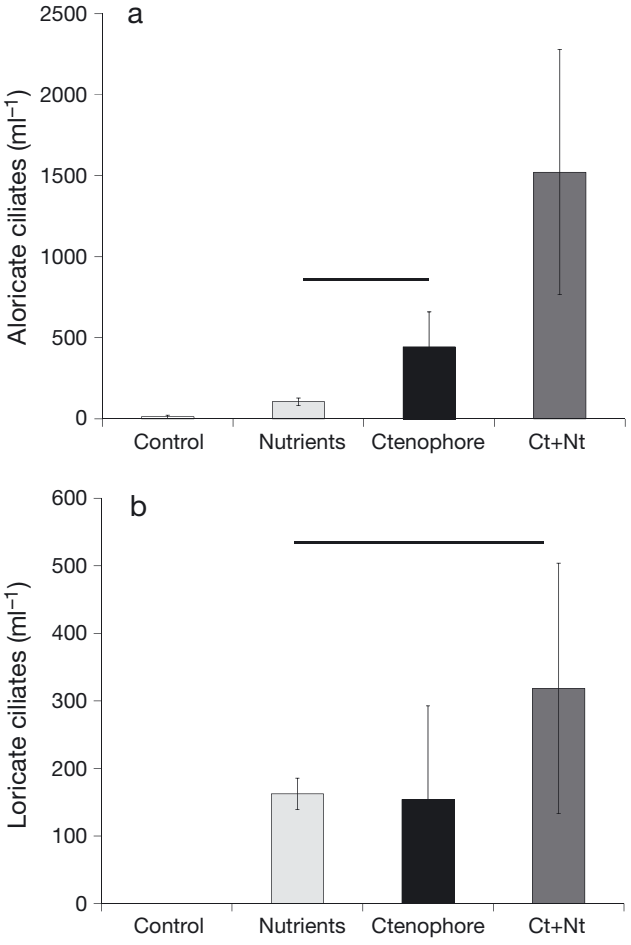

Fig. 5. Abundance (cells ml^{-1}) of (a) aloricate and (b) loricate ciliates at 120 h after the onset of the experiment (T_{120}) for mesocosm experiment M2 (2009). Note the different *y*-axis scales. Horizontal lines indicate where no difference exists among treatments (as determined from post hoc analyses). Ct+Nt: ctenophores and nutrients. Error bars: SD

Influence of nutrient enrichment on *M. leidyi*

Increases of certain microzooplanktonic taxa during population blooms of adult *M. leidyi* can influence the survival and recruitment of larval ctenophores into mesozooplankton-feeding adults. Ciliates, an important prey item for developing ctenophores (Stoecker et al. 1987, Sullivan & Gifford 2007), increased substantially in treatments containing high densities of *M. leidyi*. For example, aloricate ciliates experienced a 750% increase in nutrient treatments, but a 3500% increase in treatments containing *M. leidyi*. Significant increases in ciliate abundance alongside reduced mesozooplankton densities in the presence of the cydippid ctenophore *Pleurobrachia pileus* Müller 1776 have also been documented in experimental mesocosms (Granéli & Turner 2002). These results agree well with recent observations made in Great South Bay, where seasonal blooms of adult *M. leidyi* corresponded with subsequent and substantial increases in aloricate ciliates and dinoflagellates in 2008 and 2009 (McNamara et al. 2013). Increases in larval *M. leidyi* followed the microplanktonic surge, during which time dinoflagellate and ciliate abundance subsequently and dramatically declined (McNamara et al. 2013).

No significant increases in dinoflagellates associated with *M. leidyi* were detected in this study. However, large densities of adult *M. leidyi* drastically increased dinoflagellate abundance after reducing mesozooplankton abundance in mesocosms contained within the Baltic Sea (Dinasquet et al. 2012). The region in which Dinasquet et al. (2012) conducted their experiments is considered to be nutrient-limited, and the authors noted that the predatory influence of *M. leidyi* on lower trophic levels is likely to be dependent on local nutrient conditions. Moreover, their experiments differed from ours in that Cladocera, not copepods, dominated planktonic biomass, and no ciliate increases were detected within the *M. leidyi* treatments. The link between selective grazing by copepods and ciliate abundance is well established (e.g. Stoecker & Egloff 1987, Zöllner et al. 2003, Calbet & Saiz 2005), but ciliates also respond very rapidly to increasing nutrient concentrations (e.g. Gismervik et al. 2002). Accompanied by blooms of the indigenous *Aurelia aurita*, the invasion of *M. leidyi* in the heavily eutrophic Limfjorden (Denmark) corresponded with substantial declines in copepods (and cladocerans), at which time ciliates dominated the zooplankton assemblage (Riisgård et al. 2012). Low retention rates of ciliates by adult *M. leidyi* may also explain the observed increases of these taxa during high densities of the ctenophore. Adult *M. leidyi* and other lobate ctenophores (i.e. *Bolinopsis infundibulum*), however, are known to consume both loricate and aloricate ciliates, although they contribute little to the nutritional needs of the ctenophore (Costello & Coverdale 1998, Sullivan & Gifford 2004, Rapoza et al. 2005). While some studies have examined the retention rate of microplanktonic ciliates by larval *M. leidyi* and of large (tintinnid) ciliates by adult *M. leidyi,* the retention of microzooplankton by adult, lobate ctenophores warrants further study.

Eutrophication also appears to enhance the fecundity of *M. leidyi* by increasing mesozooplanktonic prey for adult ctenophores. Ctenophores taken from nutrient-enriched treatments produced significantly more eggs than those from treatments not receiving

nutrient amendments. *Mnemiopsis* from Ct+Nt treatments produced 3 times as many eggs as those from Ct treatments. These values agree well with differences in mesozooplankton abundance between the 2 *M. leidyi* treatments; at T_{120}, mean mesozooplankton abundance in Ct+Nt cylinders was nearly 3-fold greater than in Ct treatments (Fig. 2). The composition of the mesozooplankton assemblage at T_{120} was dominated by *Acartia tonsa* nauplii, which increased substantially from T_0 in all treatments (Table 2). This naupliar effect has been previously documented in other experimental studies (Granéli & Turner 2002, Lonsdale et al. 2007, West et al. 2009) and is likely the consequence of egg retention (from ambient water at T_0) and reproducing adults within the mesocosm cylinders. However, nutrient-amended treatments (Nt and Ct+Nt) contained nearly 3 times as many *A. tonsa* and *Oithona similis* nauplii at T_{120} than those not receiving nutrient additions (C and Ct; Table 2), suggesting that enhanced reproduction of copepods improved the fecundity of *M. leidyi*.

When (or where) seasonal population blooms of *M. leidyi* coincide with periods of nutrient enrichment, the combined influence of (top-down) ctenophore predation and (bottom-up) eutrophication processes could result in unique consequences for the plankton community, which can feedback to ctenophore population dynamics by increasing microplanktonic prey for their larvae and enhancing fecundity of the adults. In Great South Bay, major losses of eastern oysters, hard clams, and Atlantic menhaden (via salinity changes and overexploitation) has led to a decline in ecosystem maturity and increasing dominance of lower trophic level organisms (Nuttall et al. 2011). Warmer winter temperatures and increased nutrient enrichment have also been implicated in the decline of ecosystem structure in the bay (Nuttall et al. 2011) where increases in *M. leidyi* abundance and shifts to an earlier seasonal maximum have occurred over the past 2 decades (McNamara et al. 2010, McNamara et al. 2013). Great South Bay contains relatively high levels of inorganic nutrients, which are spatially and temporally influenced by freshwater discharge (groundwater seepage, fluvial discharge, storm drainage, and sewage effluents), anthropogenic influences, and physical, biological, and benthic processes (Clark et al. 2006). Higher concentrations of NH_4^+, NO_3^-, and PO_4^{3-} have been observed in rivers and groundwater, and at stations located near river mouths during high flow periods (April and September; Clark et al. 2006). The release of nutrients and subsequent increases in certain mesozooplanktonic and microplanktonic taxa may help explain the increased abundance and earlier population blooms of *M. leidyi* in coastal estuaries, and offer insight into the successful proliferation of this ctenophore in eutrophic regions where it has been introduced.

CONCLUSIONS

This is the first study to document interactive effects of nutrient enrichment and *Mnemiopsis leidyi* predation on the microplanktonic community using recent (high) and historic (low) ctenophore abundances. Our results agree well with previously conducted mesocosm experiments wherein nutrient enrichment and gelatinous zooplankton predation resulted in cascading, positive impacts on microplankton (Granéli & Turner 2002, Pitt et al. 2007). The role of gelatinous zooplankton in disturbed habitats is likely to differ from that in natural, undisturbed environments; large blooms of *M. leidyi* occurring during periods or in regions of nutrient enrichment may elicit unique responses within the microplanktonic community, as top-down predatory influences coincide with bottom-up nutrient processes. Since microplankton are important prey for developing *M. leidyi,* the combined bottom-up and top-down influences of eutrophication and predation, respectively, may help explain recently documented shifts in the population dynamics of *M. leidyi* in native and exotic habitats.

Acknowledgements. We thank J. Aspell, J. Collier, M. Deangelis, L. Holt, C. Hui, J. Lin, Y. Liu, L. Mars, M. Murray, J. Pan, A. Podlaska, and L. Schnal for their assistance in the field and laboratory. This is contribution no. 1425 of the School of Marine and Atmospheric Sciences, Stony Brook University. Support for this study was provided by the New York Department of State Division of Coastal Resources and the National Science Foundation (9ANT-0542111 to D.J.L.).

LITERATURE CITED

Arai MN (2001) Pelagic coelenterates and eutrophication: a review. Hydrobiologia 451:69–87

Arar EJ, Collins GB (1997) *In vitro* determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence. USEPA, Cincinnati, OH

Børsheim KY, Bratbak G (1987) Cell volume to cell carbon conversion factors for a bacterivorous *Monas* sp. enriched from seawater. Mar Ecol Prog Ser 36:171–175

Calbet A, Saiz E (2005) The ciliate-copepod link in marine ecosystems. Aquat Microb Ecol 38:157–167

Clark LB, Gobler CJ, Sanudo-Wilhelmy SA (2006) Spatial and temporal dynamics of dissolved trace metals, organic carbon, mineral nutrients, and phytoplankton in a coastal

lagoon: Great South Bay, New York. Estuaries Coasts 29: 841–854

Condon RH, Steinberg DK (2008) Development, biological regulation, and fate of ctenophore blooms in the York River estuary, Chesapeake Bay. Mar Ecol Prog Ser 369: 153–168

Condon RH, Duarte CM, Pitt KA, Robinson KL and others (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Natl Acad Sci USA 110:1000–1005

Costello JH, Coverdale R (1998) Planktonic feeding and evolutionary significance of the lobate body plan within the Ctenophora. Biol Bull 195:247–248

Costello JH, Sullivan BK, Gifford DJ, Van Keuren D, Sullivan LJ (2006) Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Limnol Oceanogr 51:1819–1831

Costello JH, Bayha KM, Mianzan HW, Shiganova TA, Purcell JE (2012) Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. Hydrobiologia 690:21–46

Daskalov GM (2002) Overfishing drives a trophic cascade in the Black Sea. Mar Ecol Prog Ser 225:53–63

Deason E, Smayda T (1982) Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972-1977. J Plankton Res 4:203–217

Deonarine SN, Gobler CJ, Lonsdale DJ, Caron DA (2006) Role of zooplankton in the onset and demise of harmful brown tide blooms (*Aureococcus anophagefferens*) in US mid-Atlantic estuaries. Aquat Microb Ecol 44:181–195

Dinasquet J, Titelman J, Møller LF, Setälä O and others (2012) Cascading effects of the ctenophore *Mnemiopsis leidyi* on the planktonic food web in a nutrient-limited estuarine system. Mar Ecol Prog Ser 460:49–61

Gismervik I, Olsen Y, Vadstein O (2002) Micro- and mesozooplankton response to enhanced nutrient input—a mesocosm study. Hydrobiologia 484:75–87

Granéli E, Turner JT (2002) Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. Mar Ecol Prog Ser 239:57–68

Grove M, Breitburg DL (2005) Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. Mar Ecol Prog Ser 301:185–198

Kemp WM, Boynton WR, Adolf JE, Boesch DF and others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Mar Ecol Prog Ser 303:1–29

Kimmel DG, Boynton WR, Roman MR (2012) Long-term decline in the calanoid copepod *Acartia tonsa* in central Chesapeake Bay, USA: an indirect effect of eutrophication? Estuar Coast Shelf Sci 101:76–85

Kremer P (1979) Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Estuaries 2: 97–105

Lonsdale DJ, Cosper EM, Kim WS, Doall M, Divadeenam A, Jonasdottir SH (1996) Food web interactions in the plankton of Long Island bays, with preliminary observations on brown tide effects. Mar Ecol Prog Ser 134: 247–263

Lonsdale DJ, Greenfield DI, Hillebrand EM, Nuzzi R, Taylor GT (2006) Contrasting microplanktonic composition and food web structure in two coastal embayments (Long Island, NY, USA). J Plankton Res 28:891–905

Lonsdale DJ, Cerrato RM, Caron DA (2007) Zooplankton changes associated with grazing pressure of northern quahogs (*Mercenaria mercenaria* L.) in experimental mesocosms. Estuar Coast Shelf Sci 73:101–110

McNamara ME, Lonsdale DJ, Cerrato RM (2010) Shifting ctenophore abundance and its implications for bivalve mortality. Mar Biol 157:401–412

McNamara ME, Lonsdale DJ, Cerrato RM (2013) Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores. Estuar Coast Shelf Sci 133:2–10

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol Oceanogr 45:569–579

Mills C (1995) Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. J Mar Sci 52:575–581

Mills C (2001) Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451:55–68

Nuttall MA, Jordaan A, Cerrato RM, Frisk MG (2011) Identifying 120 years of decline in ecosystem structure and maturity of Great South Bay, New York using the Ecopath modeling approach. Ecol Model 222:3335–3345

Parsons TR, Lalli CM (2002) Jellyfish population explosions: re-visiting a hypothesis of possible causes. Mer (Paris) 40:111–121

Pitt KA, Kingsford MJ, Rissik D, Koop K (2007) Jellyfish modify the response of planktonic assemblages to nutrient pulses. Mar Ecol Prog Ser 351:1–13

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. J Mar Biol Assoc UK 85:461–476

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annu Rev Mar Sci 4:209–235

Purcell JE, Decker MB (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987-2000. Limnol Oceanogr 50:376–387

Purcell JE, Shiganova T, Decker MB, Houde E (2001) The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries *versus* the Black Sea Basin. Hydrobiologia 451:145–176

Purcell JE, Uye S, Lo WT (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174

Putt M, Stoecker DK (1989) An experimentally determined carbon:volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. Limnol Oceanogr 34: 1097–1103

Rapoza R, Novak D, Costello JH (2005) Life-stage dependent, *in situ* dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* Agassiz 1865. J Plankton Res 27: 951–956

Riisgård HU, Madsen CV, Barth-Jensen C, Purcell JE (2012) Population dynamics and zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark). Aquat Invasions 7:147–162

Shiganova TA (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fish Oceanogr 7:305–310

Stoecker DK, Egloff DA (1987) Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. J Exp Mar Biol

Ecol 110:53–68

Stoecker DK, Verity PG, Michael AE, Davis LH (1987) Feeding by larval and postlarval ctenophores on microzooplankton. J Plankton Res 9:667–683

Stoecker DK, Gifford DJ, Putt M (1994) Preservation of marine planktonic ciliates: losses and cell shrinkage during fixation. Mar Ecol Prog Ser 110:293–299

Strathmann RR (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol Oceanogr 12:411–418

Sullivan BK, Van Keuren D, Clancy M (2001) Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. Hydrobiologia 451:113–120

Sullivan LJ, Gifford DJ (2004) Diet of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophore, Lobata). J Plankton Res 26:417–431

Sullivan LJ, Gifford DJ (2007) Growth and feeding rates of the newly hatched larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). J Plankton Res 29:949–965

Sun J, Liu D (2003) Geometric models for calculating cell biovolume and surface area for phytoplankton. J Plankton Res 25:1331–1346

Thuesen EV, Rutherford LD Jr, Brommer PL (2005) The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei, Bolinopsis infundibulum*, and *Mnemiopsis leidyi.* J Mar Biol Assoc UK 85:627–633

Uye S (1994) Replacement of large copepods by small ones with eutrophication of embayments: cause and consequence. Hydrobiologia 292-293:513–519

Wall CC, Peterson BJ, Gobler CJ (2008) Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. Mar Ecol Prog Ser 357:165–174

West EJ, Pitt KA, Welsh DT, Koop K, Rissik D (2009) Top-down and bottom-up influences of jellyfish on primary productivity and planktonic assemblages. Limnol Oceanogr 54:2058–2071

Zöllner E, Santer B, Boersma M, Hoppe H, Jürgens K (2003) Cascading predation effects of *Daphnia* and copepods on microbial food web components. Freshw Biol 48: 2174–2193

Submitted: August 30, 2013; Accepted: June 3, 2014

Proofs received from author(s): July 14, 2014