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MODELING PLANKTON IN A HUMAN-IMPACTED ESTUARY:
COPEPOD- vs. JELLYFISH-DOMINATED COMMUNITIES

by

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ABSTRACT OF THE THESIS

Modeling plankton in a human-impacted estuary:

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Taxonomic shifts can alter predator feeding preference and modify ecosystem function through top-down biological control. In Barnegat Bay-Little Egg Harbor Estuary, sea nettle (*Chrysaora quinquecirrha*) abundances have increased in the northern portions of the estuary, where salinity and density of anthropogenically hardened surfaces are favorable. Here I evaluate the geographical variation in top-down influence of *C. quinquecirrha* on marine plankton communities. I simulated a range of jellyfish- to copepod-dominated ecosystems using a highly size-resolved nutrient-phytoplankton-zooplankton (NPZ) model. Zooplankton feeding is parameterized as a community-averaged value based on predator-prey size ratios and breadth of prey sizes. I compared model output to observational data collected in the estuary during two months of high *C. quinquecirrha* abundance (July and August 2012).

I predicted that observational data from the northern region would be more similar to the jellyfish-dominated model outputs, because *C. quinquecirrha* abundance is higher in the north. Contrary to expectations, increased *C. quinquecirrha* abundance in the northern regions of the estuary did not lead to better agreement between observational

data from northern sites and *C. quinquecirrha* feeding based model simulations. All northern sites had observational data more similar to the copepod-dominated model. In fact, the site that was most similar to the jellyfish-dominated model was in the southern region, where *C. quinquecirrha* are excluded. I suspect that these results indicate complex interactions between *C. quinquecirrha* and ctenophore *Mnemiopsis leidyi*. The abundance of *M. leidyi*, a voracious copepod predator, is greatly reduced in the northern region despite having wide environmental tolerances. Predation by *C. quinquecirrha* may limit the distribution of *M. leidyi* and indirectly cause copepod-dominance in the northern region of the estuary. The results of this study suggest that the impact of jellyfish on marine plankton community functioning is site- and taxa-specific. Feeding preferences are shown to be important top-down control on marine phytoplankton communities.

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1. INTRODUCTION

1.1 Top-down Forcing in NPZ Models

Top-down forcing has been included in nutrient-phytoplankton-zooplankton (NPZ) models since their inception. In the first NPZ models, grazing was parameterized as a linear function based on zooplankton abundance alone (Riley, 1946). This parameterization was sufficient to describe phytoplankton blooms in Georges Bank (Riley, 1946), but more realistic parameterizations have since been developed. Zooplankton grazing rate varies with prey concentration because of handling times and capture rates involved in predation (Gentleman et al., 2003). Numerous functional responses of saturating or linear forms have been used to describe the dependence of grazing on prey concentrations (Franks, 2002, Gentleman et al., 2003). However, the presence of multiple prey taxa complicates the functional responses derived from single resource grazing studies (Gentleman et al., 2003). Parameterizations where zooplankton feeding is adjusted based on relative abundances of different prey (ie. switching functions) have been used in complex ecosystem models, but the application of these methods can be arbitrary (Visser and Fiksen, 2013). The choice of zooplankton feeding parameterization can have large impacts of model outcomes (Anderson et al., 2010, Fuchs and Franks, 2010, Banas, 2011, Prowe et al., 2012). Recent models have sought to improve on the zooplankton feeding parameterization even further.

New versions of zooplankton feeding parameterization involve optimal foraging theory or morphometric ratios (Fuchs and Franks, 2010, Wirtz, 2012, Visser and Fiksen, 2013). Optimal foraging methods base grazing to optimize energy intake for zooplankton, while accounting for diet breadth and feeding mode (Visser and Fiksen,

2013). Morphometric ratio methods use predator-prey size relationships and feeding modes (or taxonomic groups) to parameterize zooplankton grazing. These parameterizations are better able to handle the mixed prey assemblages found in real ecosystems (Visser and Fiksen, 2013).

The NPZ model by Fuchs and Franks (2010) was used for this study. The model uses community-averaged values for the mean predator-prey size ratio and predator diet breadth to parameterize zooplankton feeding. This zooplankton feeding parameterization is flexible for many plankton community types, but determining the community-averaged feeding parameters for a real ecosystem is non-trivial. Many zooplankton taxa with different feeding preferences interact to form the zooplankton community. Fortunately, the study area used for this study has been researched extensively over the last 30 years (Kennish, 2001a, Kennish and Lutz, eds, 1984). Therefore, data is available to help constrain the possible zooplankton community in Barnegat Bay-Little Egg Harbor Estuary.

1.2 Barnegat Bay-Little Egg Harbor Background

The Barnegat Bay-Little Egg Harbor Estuary is a shallow coastal lagoon system consisting of three bays (from north to south): Barnegat Bay, Manahawkin Bay, and Little Egg Harbor. The system spans ~70 km along the New Jersey coastline and varies in width from ~2 to 6 m. Long Beach Island and Island Beach separate the bays from the Atlantic Ocean, and allow exchange via Barnegat and Little Egg Inlets and Point Pleasant Canal (Figure 1). Water depth ranges <1-6 m, ~1-2 m, and <1-7 m in Barnegat Bay, Manahawkin Bay, and Little Egg Harbor, respectively (Kennish, 2001b). Average depth

increases from ~1.5 m in Barnegat Bay to ≥ 2 m in Little Egg Harbor (Olsen and Mahoney, 2001, Kennish, 2001b). Flushing time in Barnegat Bay averages 49 days, but varies seasonally (Guo et al., 2004) and latitudinally (Ganju, per. comm.).

Salinity increases in the Barnegat Bay-Little Egg Harbor Estuary from north to south, driven by the locations of major freshwater and saltwater inputs (Figure 1). Barnegat Bay receives greater surface freshwater input than Manahawkin Bay or Little Egg Harbor (Kennish, 2001b), with Toms River providing the greatest inflow (Hunchak-Kariouk et al., 2001, Seitzinger et al., 2001). Direct groundwater discharge is relatively limited compared to surface input to Barnegat Bay (Guo et al., 2004). Ocean exchange occurs predominantly at Barnegat Inlet and Little Egg Inlet, along the central and southeastern estuary boundary (Kennish, 2001b). Low freshwater input and high ocean exchange generate high salinity in the southern regions of the estuary, with the reverse occurring in the north, except for localized elevated salinity near the Point Pleasant Canal. In Barnegat Bay, mean salinities range from ~18ppt in the north to ~25ppt in the south (Moser, 1997), although salinity can be <15ppt at the mouth of the Toms River and >30ppt near the inlets (Kennish, 2001b). Salinities in the shallows of Manahawkin Bay and Little Egg Harbor tend to be higher than Barnegat Bay, and often surpass 30ppt in summer (Kennish, 2001b).

The Barnegat Bay-Little Egg Harbor Estuary is currently classified as a highly eutrophic system based on the National Oceanic and Atmospheric Administration's National Estuarine Eutrophication Assessment (NEEA) model, largely due to low freshwater input, slow flushing, and a highly developed watershed (Kennish et al., 2007). However, anthropogenic forcing is spatially variable. Human population growth and

land development have been concentrated around the northern sections of the estuary (Carter, 1997, Lathrop Jr and Bognar, 2001, Kauffman and Cruz-Ortiz, 2012). Nitrogen loading to the estuary is dominated by surface runoff (66%), and nutrient concentrations appear correlated with upstream development intensity for streams in the New Jersey Coastal Plains (Hunchak-Kariouk and Nicholson, 2001, Wieben and Baker, 2009). The Metedeconk and Toms Rivers alone provide over 60% of the surface water nitrogen loading to the estuary, both of which are located in the north (Wieben and Baker, 2009). This generates a decreasing gradient in nutrient loading from north to south in the estuary (Moser, 1997). Sediment core records confirm that spatial gradients in nitrogen and phosphorus have become more prominent since the 1950s (Velinsky et al., 2011).

Surveys of Barnegat Bay prior to the 1990s have developed a baseline understanding of plankton community functioning. Phytoplankton abundance and primary production in Barnegat Bay peak in the summer and trough in the winter (Mountford, 1984). Throughout the year, nanoplankton (1-3 μ m) are numerically dominant, but diatoms (winter-spring) and dinoflagellates (summer-fall) bloom seasonally and may dominate the biomass/chlorophyll-a content (Mountford, 1984). Copepods are the bay's primary herbivore, and the most common species shift from *Acartia hudsonica* in the winter-spring to *A. tonsa* and *Oithona colcarva* in the summer-fall (Sandine, 1984). Microzooplankton abundance is dominated by copepods and peaks following the winter-spring phytoplankton bloom and in the summer (Sandine, 1984). Macrozooplankton are dominated by mysids (*Neomysis Americana*), sand shrimp zoeae (*Crangon septemspinosa*), and hydromedusae (*Sarsia* spp., *Rathkea octopunctata*) when water temperature is below 18°C (late fall to early spring) and by brachiuran zoeae and

amphipods when water is warmer (late spring to early fall) (Kennish and Loveland, 1984). Ctenophores (*Mnemiopsis leidyi*) may be important grazers of microzooplankton in spring and summer, but their mean and peak density is highly variable inter-annually (Mountford, 1980, Sandine, 1984). These studies devoted little analysis to spatial variability, and preceded the USEPA declaring Barnegat Bay-Little Egg Harbor a National Estuary Program site by over a decade.

More recently, ecological differences have been reported between the northern and southern portions of Barnegat Bay. Southern extremes of the bay support mostly picoplankton, while northern extremes sustain greater abundances of larger phytoplankton taxa (Olsen and Mahoney, 2001). Larger cell size leads to greater chlorophyll-a concentrations in the north, despite typically having lower cell densities than the south (Olsen and Mahoney, 2001). Picoplankton blooms start earlier in the year and sustain high cell concentrations for longer in southern regions relative to northern regions (Olsen, 1989, Olsen and Mahoney, 2001). Spatial variability in the phytoplankton community likely drives similar variability in the zooplankton community. Zooplankton abundance in Barnegat Bay is closely linked to phytoplankton abundance, as peak zooplankton abundances occur shortly after phytoplankton blooms (Loveland et al., 1969, Kennish, 2001c).

A notable zooplankton group whose abundance is spatial variable is gelatinous zooplankton. The northern extremes of the Barnegat Bay-Little Egg Harbor Estuary likely provide favorable growing habitat for these taxa relative to the rest of the estuary. A rapidly expanding human population has led to urbanization and shoreline conversion (Carter, 1997, Lathrop Jr and Bognar, 2001). Hardened surfaces (e.g. docks, bulkhead,

marine litter) provide substrate for the asexually reproducing polyp stage of Scyphozoa, such as sea nettle (*Chrysaora quinquecirrha*) (Cargo and Schultz, 1966, Holst and Jarms, 2007, Hoover and Purcell, 2009). The low salinity in the north estuary favors the mesohaline-tolerant *C. quinquecirrha*, which may be excluded from the higher salinity portions of the estuary (Decker et al., 2007). Initial reports suggest that *C. quinquecirrha* medusa are concentrated in the northern estuary (Bologna and Gaynor, unpub. data), and overwintering *C. quinquecirrha* podocysts have only been observed at Cattus Island (in the northern estuary) (Bologna, 2011). Expansion of the northern *C. quinquecirrha* population may be further aided by removal of competitors or predators through fishing (Purcell and Arai, 2001). Ctenophores (e.g. *Mnemiopsis*) do not have a sedentary polyp stage and are cosmopolitan in salinity and temperature tolerances (Purcell et al., 2001). However, high primary productivity in the north may support more productive *Mnemiopsis* prey populations.

2. MODELING PLANKTON IN A HUMAN-IMPACTED ESTUARY:

COPEPOD- vs. JELLYFISH-DOMINATED COMMUNITIES

2.1 Introduction

Top-down biological control is a process where organisms influence the trophic structure and abundance of organisms in lower trophic levels through predation.

Although top-down control is strong enough in some systems to produce trophic cascades (Estes et al., 1998, Frank et al., 2005), such dramatic effects are uncommon in mid- to low-latitude marine plankton communities (Sommer, 2008). Copepods are the main herbivores in these communities, preying heavily on large phytoplankton cells. Blooms of copepods can initially decrease phytoplankton abundance overall, but growth of less-grazed phytoplankton size classes will eventually compensate (Sommer, 2008).

Therefore, marine planktonic perturbations often lead to shifts in abundance rather than trophic cascades. Top-down control in marine plankton communities is strongly related to feeding selectivity of predators.

Predator feeding selectivity is determined by many factors, ranging from predator anatomy and behavior to prey density and biochemical composition. Feeding apparatus sets the absolute limits on the prey sizes a predator is able to consume (Hansen et al., 1994). Within that range, clearance and uptake rates of prey are influenced by prey motility (Gonzalez et al., 1993), concentration (Bogdan and Gilbert, 1982), and biochemical composition (Poulet and Marsot, 1978). The feeding mode employed by a predator (e.g. filter feeder or raptorial feeder) further refines feeding selectivity (Hansen et al., 1994).

Size can be used to generalize many of the complexities in predator feeding selectivity. Predators tend to feed optimally on a predictable prey size that is smaller than the predator's size (Hansen et al., 1994). Ingestion rate of prey decreases when prey size is further from optimal. The optimal prey size scales with predator size, leading to consistent predator-prey size ratios within taxonomic groups (Hansen et al., 1994). However, the optimal predator-prey size ratio can vary greatly among taxonomic groups (Hansen et al., 1994). Dinoflagellates tend to have the lowest predator-prey size ratios (~ 1.5) and salps tend to have the highest (~ 940), while other marine zooplankton (e.g. copepods, rotifers, ciliates, etc) are intermediate (Fuchs and Franks, 2010). In a general size-structured sense, the feeding preference of a predator of a given size is defined by the predator-prey size ratio and the range of the prey sizes on which it can feed, with generalists feeding on a wide range of prey sizes and specialists feeding on a narrower range of prey sizes.

In modeling studies, feeding parameterization influences marine community structure and functioning through top-down control. Altering the zooplankton functional response causes shifts in phytoplankton distributions in a spatially resolved ecosystem model (Anderson et al., 2010) and changes phytoplankton diversity in a global ecosystem model (Prowse et al., 2012). In size-resolved nutrient-phytoplankton-zooplankton (NPZ) models, ecosystem biomass (Banas, 2011) and phytoplankton biomass (Fuchs and Franks, 2010) respond less predictably to nutrient forcing in communities with more generalist feeding than in communities with more specialist feeding. In a highly size-resolved NPZ model, simulated plankton communities tend to have higher connectance and steeper size spectra when zooplankton feeding preference uses higher predator-prey

size ratios (Fuchs and Franks, 2010). Due to the importance of zooplankton top-down forcing, several recent studies have sought to improve parameterizations for zooplankton feeding selectivity using morphometric ratios (Wirtz, 2012) and optimal foraging (Visser and Fiksen, 2013). Ecosystem functioning is influenced by zooplankton feeding parameterization and may be sensitive to shifts in zooplankton feeding preference.

Zooplankton prey selectivity may be altered at the community level through taxonomic shifts. Copepods can make up 80% of the total abundance of zooplankton in some locations, and small pelagic copepods (<1mm) may be the most abundant metazoans on earth (Turner, 2004). Since copepods tend to be specialist feeders (Fuchs and Franks, 2010), a majority of the predator-prey interactions in temperate marine plankton communities are likely specialist in nature. Therefore, increases in taxa with dissimilar feeding preferences, like jellyfish (Fuchs and Franks, 2010), could alter community dynamics. In Narragansett Bay, ctenophore blooms (*Mnemiopsis leidyi*) blooms are associated with rapid declines in zooplankton abundance and initiation of a summer phytoplankton bloom (Deason and Smayda, 1982). In western Baltic Sea, scyphomedusa abundance (*Aurelia aurita*) regulates mesozooplankton and ultraplankton abundance (Schneider and Behrends, 1998). In Chesapeake Bay tributaries, the scyphomedusa *Chrysaora quinquecirrha* may consume 10-78% of daily copepod production during July and August (Purcell, 1992). Water bodies with greater human impacts may be more susceptible to jellyfish invasions (Richardson et al. 2009) and the associated shifts in zooplankton feeding preference.

Barnegat Bay-Little Egg Harbor Estuary in New Jersey, USA is a potential hotspot of seasonal shifts in zooplankton feeding preferences. During the summer

months, abundances of the *C. quinquecirrha* have increased in the northern portion of the estuary over the last two decades (Kennish, 2007, Bologna, 2011). The main factors restricting *C. quinquecirrha* to the northern estuary are availability of anthropogenically hardened substrate for asexual reproduction (Bologna, 2011) and salinity preference (Decker et al., 2007). The limited range of *C. quinquecirrha* enables comparison of plankton community metrics between sites in the estuary with and without the influence of an invading generalist feeding zooplankton.

For the purposes of this study, the Barnegat Bay-Little Egg Harbor Estuary was divided into 2 regions. The dividing line between the north and south regions was set just south of the Toms River mouth (Figure 2). Sites 1-5 are in the northern region and sites 6-14 are in the southern region. This delineation is supported by spatial variability in human population and salinity throughout the estuary, and is similar to zonation previously used for the estuary (Kennish, per. comm.). A higher human population in the north leads to higher nutrient loading (Carter, 1997, Lathrop Jr and Bogner, 2001, Wieben and Baker, 2009). Consequently, chlorophyll-a concentrations and phytoplankton cell sizes tend to be larger in the north (Olsen and Mahoney, 2001). Although copepods are the dominant phytoplankton grazer throughout the estuary (Sandine, 1984), gelatinous zooplankton may be favored in the north region due to greater human impacts (Richardson et al., 2009) and the aforementioned low salinity that favors *C. quinquecirrha* growth in the north. *Mnemiopsis leidyi* is also abundant in the estuary but has no physiological restraints that would exclude it from the southern region (Purcell et al., 2001). Both scyphomedusae (e.g. *C. quinquecirrha*) and ctenophores (e.g.

M. leidy) have smaller average predator-prey size ratios than copepods (Fuchs and Franks, 2010).

The present study examined plankton community dynamics at various sites throughout Barnegat Bay-Little Egg Harbor Estuary using the highly resolved nutrient-phytoplankton-zooplankton (NPZ) model from Fuchs and Franks (2010). The model assumes that zooplankton predation can be described as a community average that will change if zooplankton taxonomic shifts occur. The objectives of the study were (1) to simulate copepod-like and jellyfish-like hypothetical plankton communities, (2) to compare model results to observational data from Barnegat Bay-Little Egg Harbor Estuary, and (3) to model the effects of reducing nutrient loading to the estuary. I predicted that observational data from the southern region would be most similar to the copepod-like model simulations, that the northern region would be more jellyfish-like due to higher *C. quinquecirrha* abundance, and that copepod-like and jellyfish-like model simulations would respond differently to nutrient reductions. For the remainder of this paper, Barnegat Bay-Little Egg Harbor Estuary will be referred to as BBLEH.

2.2 Methods

2.2.1 NPZ Model

I simulated hypothetical plankton communities using the Fuchs and Franks (2010) model of nutrient, phytoplankton, and zooplankton:

$$N(t) = N_T - \int P(x, t)dx - \int Z(x, t)dx \quad (1)$$

$$\frac{\partial P(x, t)}{\partial t} = P(x, t) \left(-\lambda + \mu_{max}(x) \frac{N(t)}{N(t) + k_s} - g \int F^-(x, y) Z(y, t) dy \right) \quad (2)$$

$$\frac{\partial Z(x, t)}{\partial t} = Z(x, t) \left(-\delta - g \int F^-(x, y) Z(y, t) dy + \gamma g \int F^+(y, x) [P(y, t) + Z(y, t)] dy \right) \quad (3)$$

For this model, N is free nutrients, P is phytoplankton biomass, Z is zooplankton biomass, N_T is total nutrients, x and y are cell size (equivalent spherical diameter on a \log_{10} scale), t is time, λ is phytoplankton death rate, μ_{max} is maximum phytoplankton growth rate, k_s is the half-saturation constant for nutrient uptake by phytoplankton, g is zooplankton grazing rate, δ is zooplankton death rate, γ is zooplankton assimilation efficiency, F^- is the feeding kernel, and F^+ is the redistribution kernel. The kernels (F^- and F^+) are community-averaged probability distributions that control size-dependent predation (nutrient loss from prey and nutrient gain to predators, respectively) along the size spectrum. F^- is a Laplace distribution defined by the community-averaged mean \log_{10} prey-predator size ratio ($-m$) and the standard deviation of the community-averaged \log_{10} prey size distribution (s). F^+ is a Laplace distribution defined by m and s . All model parameters were held constant among simulations, except N_T , m and s (see Section 2.2.2).

Some numerical details were changed from the Fuchs and Franks (2010) version to provide greater flexibility in simulations. The time step (dt) was decreased to 0.2 d^{-1} to ensure convergence in high nutrient simulations ($N_T \geq 40$). The model was considered to be at quasi-equilibrium when the change in both ΣP and ΣZ between two consecutive time steps were less than $N_T^* 10^{-10}$. However, the quasi-equilibrium threshold was loosened by 1-4 orders of magnitude for 12 simulations that were slow to converge. Quasi-equilibrium values will be denoted with asterisks for the remainder of this paper (e.g. N^* is quasi-equilibrium free nutrient). Table 1 summarizes all symbols used in this paper.

2.2.2 Parameter Selection: N_T , m , and s

Model simulations covered a range of nutrient statuses and zooplankton community types by varying N_T , m , and s . In all, 120 simulations were run using 20 N_T values and 6 m - s pairs (hereafter referred to as feeding regimes) in all possible combinations. Feeding regime and N_T were held constant within each separate simulation.

Values of N_T were selected to encompass nutrient statuses ranging from oligotrophic to eutrophic. Observed total nitrogen values in BBLEH were used to set the maximum N_T used in model simulations, because the estuary is highly eutrophic (Kennish et al., 2007). The highest mean total nitrogen at any site in the estuary for July-August 2012 was 51.9 μmol of nitrogen per liter (see Section 2.2.3 for observational data details). Model simulations used N_T values ranging from 2.5 to 50 $\mu\text{mol-N L}^{-1}$.

Feeding regimes were selected to encompass a broad range of zooplankton feeding preferences that may be present in BBLEH. One regime (Regime 1) was based on copepod feeding preferences, because copepods are numerically dominant in the estuary's mesozooplankton (Sandine, 1984). Size-structured feeding data are lacking for the common copepod species in Barnegat Bay (ie. *Acartia hudsonica*, *A. tonsa*, and *Oithona colcarva*) (Sandine, 1984), so the copepod-dominated regime was defined using the mean copepod feeding preference calculated by Fuchs and Franks (2010) ($m = 2$, $s = 0.15$). One regime (Regime 5) was based on *Chrysaora quinquecirrha* feeding preferences, because *C. quinquecirrha* may be ecologically important zooplankton and are increasing in abundance in the estuary (Kennish, 2007). *C. quinquecirrha* feeding preference ($m = 0.638$, $s = 0.162$; Cowan Jr and Houde, 1993, Purcell and Cowan Jr,

1995, Suchman and Sullivan, 1998) is similar to another abundant jellyfish in the estuary (*Mnemiopsis leidyi*). Regime 5 will be referred to as jellyfish-dominated. Three intermediate regimes (Regimes 2-4) were defined assuming a linear transition from copepod-dominated to jellyfish-dominated communities. The regimes defined to this point differ in m , but have similar s . I also included the generalist regime (Regime 6) from Fuchs and Franks (2010) for comparison purposes ($m = 1.2$, $s = 0.3$). The generalist regime has a higher s than the other regimes, but an intermediate m .

2.2.3 Available Observational Data

I compared model results to publicly available data from water-quality monitoring by the New Jersey Department of Environmental Protection (NJDEP) (accessible at <http://www.state.nj.us/dep/barnegatbay/bbmapviewer.htm>). Data were collected at 14 sites in BBLEH from June 2011 to December 2012. Sampling frequency was ~1-4 samples per month, except for an intense sampling effort in July and August 2012 when frequency was ~26-27 samples per month. Unless otherwise noted, analyses were performed with July-August 2012 data, which coincided with the usual *C. quinquecirrha* bloom period (Decker et al., 2007). Measurements used here include surface and bottom total nitrogen (mg per L), surface and bottom chlorophyll-a (μg per L), surface dissolved nitrate plus nitrite (mg per L), surface dissolved ammonia (mg per L), and surface particulate organic carbon (mg per L). Field-sampled total nitrogen, nitrate plus nitrite and ammonia, and chlorophyll-a are similar to the NPZ model input total nitrogen (N_T), output free nitrogen (N^*), and phytoplankton biomass (ΣP^*), respectively. For comparisons to model outputs, field-sampled variables were converted to units of

nitrogen concentration (methods detailed below). For clarity in the rest of this section, NPZ model values will be referred to by the appropriate abbreviation (e.g. N_T) and observational data will be preceded by “Barnegat” (e.g. Barnegat total nitrogen).

Barnegat total nitrogen was measured with EPA Method 351.4, which measures all nitrogen species except N_2 gas. The measurement includes particulate nitrogen, such as cells (Pang, per. comm.). Therefore, Barnegat total nitrogen is analogous to NPZ model input N_T (ie. the sum of all biologically relevant nitrogen in the model). For comparison to N_T , Barnegat total nitrogen was converted from mg of nitrogen per liter to μmol of nitrogen per liter.

Barnegat dissolved nitrate plus nitrite and dissolved ammonia were measured with EPA Method 353.4 and Standard Method 4500-NH3: G, respectively. Barnegat dissolved nitrate plus nitrite was reported in mg of nitrogen per liter, while Barnegat dissolved ammonia was reported in mg of ammonia per liter. Barnegat dissolved ammonia was multiplied by 0.822 to convert it to mg of nitrogen per liter. Then the two measurements were summed to generate Barnegat dissolved inorganic nitrogen (excluding N_2 gas). Barnegat dissolved inorganic nitrogen is analogous to NPZ model output N^* . For comparison to N^* , calculated Barnegat dissolved inorganic nitrogen was converted from mg of nitrogen per liter to μmol of nitrogen per liter.

Barnegat chlorophyll-a was measured with Standard Method 10200-H, reported as mg of chlorophyll-a per liter. For comparison to NPZ model units, measurements of chlorophyll-a were converted to concentration of nitrogen using cellular mass ratios for carbon to chlorophyll-a (C:Chl) and carbon to nitrogen (C:N). The C:Chl and C:N were either calculated empirically from Barnegat field data or obtained from the literature, as

detailed below. After the mass ratios were applied, Barnegat chlorophyll-a was similar to NPZ model output $\sum P^*$. However, in order to be directly comparable, Barnegat chlorophyll-a was converted from mg of nitrogen per liter to μmol of nitrogen per liter.

Several options were selected for the mass ratios, because each can vary spatially and temporally based on the abiotic conditions and the taxonomic makeup of the phytoplankton community. Estimates of C:Chl were derived from the available Barnegat data and a previous study in a nearby estuary. An estimate of C:Chl may be calculated with a linear regression of particulate organic carbon against chlorophyll-a from the same sample (Strickland, 1960), where the slope of the regression is C:Chl. The slope can be biased by co-variation between phytoplankton, zooplankton, and detrital carbon (Menzel and Ryther, 1964, Riley, 1965, Banse, 1977), and additional error is caused by intra-annual variability in C:Chl (Cerc0 and Noel, 2004). These errors can be limited by using data from narrow time spans. Therefore, a regression was performed on Barnegat particulate organic carbon and chlorophyll-a data from July and August 2011 (no particulate organic carbon data were available for 2012). After removal of one outlier, the regression yielded a C:Chl near 150 (Figure 3). Nearby Chesapeake Bay has a C:Chl of ~50 during July and August (Cerc0 and Noel, 2004), but differs from BBLEH in size, morphology, and salinity range. Both C:Chl ratios were used in analysis to encompass uncertainty associated with the value. However, the Barnegat C:Chl is considered more appropriate, because it was derived in the estuary of interest.

Estimates of C:N could only be obtained from previous studies on plankton chemical composition. The C:N ratios vary among taxa and range from 3.44 to 6.45 for dinoflagellates (Menden-Deuer and Lessard, 2000), 4.5 to 8.8 for pico- and nanoplankton

(Verity et al., 1992), and 3.5 to 25.4 for diatoms (Brzezinski, 1985). To encompass the uncertainty associated with community-averaged C:N, three values were selected: low (3.5), high (12), and Redfield (5.67; Redfield et al., 1963). All three C:N ratios were used in analysis to encompass the uncertainty associated with the value. However, the Redfield C:N is considered most appropriate, because it is an often-cited community-averaged value.

2.2.4 Processing of Observational Data

Several NPZ model variables were selected for comparison to Barnegat data. Model variables with comparable observational data include N_T , N^* , and $\sum P^*$ (see Section 2.2.3). Ratios of these variables, N^*/N_T , $\sum P^*/N_T$, and $\sum P^*/N^*$ were also used for comparison. Ratios were calculated sample-wise from the observational data, and if either value required was missing or “below detection limit”, the ratio for that sample was excluded.

Excluding samples below the detection limit may have biased direct estimates of mean values, so I used a statistical procedure to generate expected values, 95% confidence intervals, and ad-hoc estimates of the bias introduced by the detection limit (Figure 4). I estimated the expected value for measurements at each site assuming all sites and measurements were drawn from the same distribution class. The distribution of samples was examined estuary-wide, because there were not enough samples at each site to reliably determine a distribution. Histograms of all measurement variables were non-normal (skewed left) and resembled lognormal distributions. Concentration data cannot be negative and often fit the lognormal distribution when the mean is low and variance is

high (Limpert et al., 2001). Lognormal distributions are self-replicating by division, so the derived ratios should still be lognormally distributed. Despite the fact that the sum of lognormal distributions has no explicit solution (Dufresne, 2008), Barnegat dissolved inorganic nitrogen appeared to be reasonably lognormally distributed. I used Lilliefors tests to confirm that most measurement data could be treated as lognormal. A lognormal distribution was fit to each measurement variable at each site, excluding all samples that were below detection limit. Lognormal distributions have a mean of $e^{\mu+\sigma^2/2}$, where μ and σ are the mean and standard deviation of the natural logarithm of the data. The accuracy of the fit is limited by the measurement's detection limit and the total number of samples taken. The mean of the lognormal fit was considered the expected value for the site measurement.

For each expected value, I calculated a preliminary 95% confidence interval using a Monte-Carlo approach. The fitted lognormal distribution was randomly re-sampled for the same number of samples as in the original data set. A new lognormal fit was done on the re-sampled data, and a re-sampled mean was calculated. This was repeated 100,000 times. The spread in the re-sampled means represents the uncertainty associated with the given sample size. Since the expected values appeared normally distributed, 1.96 standard deviations above and below the mean of the expected values gives an initial estimate of the preliminary 95% confidence interval. For variables that require more than one measurement to calculate (ie. N^* , N^*/N_T , $\sum P^*/N_T$, and $\sum P^*/N^*$), values were re-sampled from each measurement distribution, then added/divided appropriately and fit to a new lognormal distribution.

We accounted for the effect of the detection limit by repeating the Monte Carlo approach and excluding re-sampled values that were “below detection limit.” The difference between the average re-sampled means from the Monte-Carlo approaches (including and excluding “below detection limit” samples) gives an estimate of the bias introduced by the detection limit. The preliminary 95% confidence interval was extended to account for this bias (e.g. if the detection limit biases the re-sampled mean to increase by 2, then the lower bound of the 95% confidence interval for that variable would be decreased by 2). This gave the 95% confidence intervals shown in the results. Expected values were not adjusted to account for this bias, because the bias estimates an uncertainty involved in fitting the data. Hereafter, all mentions of observational Barnegat data refer to the estimated expected values.

2.2.5 Model-Data Comparisons

I quantified the degree of similarity between model outputs and Barnegat data using sums of squared error. The Barnegat-derived C:Chl ratio and Redfield C:N ratio were used for all applicable calculations, because they are the most appropriate mass ratios (see Section 2.2.3). Model outputs for N^* , N^*/N_T , $\sum P^*$, $\sum P^*/N_T$, and $\sum P^*/N^*$ were plotted against N_T and N^* with site observational data overlaid. Often site N_T values did not match those simulated in the model, so model outputs were interpolated to the appropriate N_T . Data from each site was compared to six model interpolations (one for each feeding parameterization).

The overall differences between the northern and southern region of BBLEH was also examined. I summed the squared error for all sites within both regions. The feeding

regime with the smallest sum of squared error was considered best for describing that region. This calculation was performed for N^* , N^*/N_T , ΣP^* , $\Sigma P^*/N_T$, and $\Sigma P^*/N^*$. This analysis was repeated using all C:Chl and C:N ratios to assess the uncertainty in these ratios could affect the comparisons.

2.2.6 Nutrient Reductions

For nutrient reduction scenarios, I used previously described quasi-equilibrium solutions as initial conditions. Two methods for nutrient reduction were evaluated: small sequential decreases in nutrients and singular large decreases in nutrients. In the small reductions, 2.5% of N_T was removed from N^* and the simulation continued until a new quasi-equilibrium was reached. This was repeated 15 times for 4 model parameterizations (feeding regime 1 and 5 with $N_T=12.5$ and 50). In the large nutrient reductions 50% of N^* was removed, and the simulation continued until a new quasi-equilibrium was reached. This was performed on 6 model parameterizations (all combinations of feeding regime 1 and 5 with $N_T=35$, 4.5, and 50). The effect of nutrient reductions was evaluated by examining the magnitude and direction of $\Delta N^*/\Delta N_T$, $\Delta \Sigma P^*/\Delta N_T$, and $\Delta \Sigma Z^*/\Delta N_T$.

2.3 Results

In general, model outputs clustered into 3 groups: regimes 1-2, regimes 3-4, and regimes 5-6. Therefore, BBLEH sites/regions that are most similar to regimes 1-2 will be considered copepod-dominated, sites/regions most similar to regimes 3-4 will be

considered intermediate, and sites/regions that are most similar to regimes 5-6 will be generalized as jellyfish-dominated.

2.3.1 Site Comparisons (Barnegat C:Chl and Redfield C:N only)

There was a clear separation in total nitrogen and phytoplankton biomass between sites in the northern and southern regions of BBLEH. All northern sites had greater total nitrogen and phytoplankton biomass than any southern site (Figure 5). Despite separation in observational variables, most sites in the north and south were most similar to the copepod-dominated model outputs for both the ΣP^* vs. N_T and ΣP^* vs. N^* plots. The only exceptions were sites 2,9,10, and 13 for ΣP^* vs. N_T and sites 9 and 11 for ΣP^* vs. N^* . Site 4 was not similar to any model outputs in either plot (Figure 5).

With a few exceptions, northern and southern sites had relatively similar ratios of free nitrogen to total nitrogen and phytoplankton biomass to free nitrogen. In general, the northern sites had lower free nitrogen to total nitrogen ratios than the southern sites (Figure 6). However, this was not true for site 4 (a northern site with a high N^*/N_T) and sites 6 and 7 (southern sites with a low N^*/N_T) (Figure 6). Conversely, the northern sites had higher phytoplankton biomass to free nitrogen ratios than southern sites (Figure 7). The notable exceptions to this pattern were sites 4 and 7. For all related plots (N^*/N_T vs. N_T , N^*/N_T vs. N^* , $\Sigma P^*/N^*$ vs. N_T , and $\Sigma P^*/N^*$ vs. N^*), most sites in the north and south were similar to the copepod-dominated model outputs (Figures 6-7). The only exceptions were sites 4 and 11 for both N^*/N_T plots and site 9 for both $\Sigma P^*/N^*$ plots. Despite being most similar to the copepod-dominated model outputs, sites 1-5 and 7 were poorly matched by any regime for both $\Sigma P^*/N^*$ plots (Figures 6-7). The large 95% confidence

intervals for free nitrogen to total nitrogen ratio and phytoplankton biomass to free nitrogen ratio were caused by a low sample size for the measurements that make up free nitrogen. Dissolved nitrate plus nitrite had the greatest percentage of samples below detection limit, and dissolved ammonia had the second greatest (data not shown).

There is no clear north-south gradient on the other parameters analyzed. Free nitrogen was similar for all sites except 4 and 11 (Figure 8). The phytoplankton biomass to total nitrogen ratio at many of the northern sites fell in the middle of the range observed for southern sites (Figure 9). For both variables, the spread in values was greater for southern sites than northern sites. Free nitrogen values for northern sites were clustered near the bottom of the range of southern sites, except site 4 (Figure 8). The phytoplankton biomass to total nitrogen ratio for northern sites was clustered in the center of the range for southern sites, except site 4 (Figure 9). Most sites in the north and south were most similar to the copepod-dominated model outputs for both N^* vs. N_T and $\Sigma P^*/N_T$ vs. N_T plots (Figures 8-9). The only exceptions were sites 4 and 11 for N^* vs. N_T and sites 2, 9, and 13 for $\Sigma P^*/N_T$ vs. N_T . Site 4 was not similar to any model outputs in the $\Sigma P^*/N_T$ vs. N_T plot. There was not enough separation between copepod- and jellyfish-dominated model outputs in the $\Sigma P^*/N_T$ vs. N^* to determine difference among BBLEH sites (Figure 9B).

For the majority of comparisons, BBLEH sites were copepod-dominated. The sites that were most often similar to jellyfish-dominated model outputs were sites 9, 11, and 4. However, sites 4 and 11 may not be representative of typical BBLEH summertime plankton communities. Site 4 is located at the Toms River mouth and was dissimilar from other northern sites for all observational data. Sampling at site 11 was halted

midway through the summer, so the dataset there was incomplete. It should also be noted that sites 8 and 14 had extremely similar observational data, and had lower total nitrogen than the other southern sites. These sites were both located at ocean inlets, and therefore, may not be representative of typical BBLEH summertime plankton communities.

2.3.2 Regional Comparisons (all C:Chl and C:N)

Similar to site-specific comparisons, regional data most resembled the copepod-dominated model results when Barnegat C:Chl and Redfield C:N were used. As a region, the north was best described by feeding regime 1 (Tables 2-3). The southern region was similar, except feeding regime 2 best described phytoplankton biomass (Table 2-3). Since free nitrogen and the free nitrogen to total nitrogen ratio don't require a C:Chl or C:N to calculate, those variables won't be repeated later in this section.

However, phytoplankton biomass, phytoplankton biomass to total nitrogen ratio, and phytoplankton biomass to free nitrogen ratio varied greatly depending on the C:Chl and C:N ratio used. Depending on mass ratios used, the best feeding regime for phytoplankton biomass varied from 1 to 6 for northern sites and 1 to 5 for southern sites (Table 3). The best feeding regime for the phytoplankton biomass to total nitrogen ratio varied from 1 to 6 for both northern and southern sites (Table 3). The best feeding regime for the phytoplankton biomass to free nitrogen ratio varied from 1 to 4 in both northern and southern sites (Table 3).

Overall, the variability associated with using different combinations of mass ratios was greater than the variability between the northern and southern sites. The feeding regimes that best described the north and south were similar for all variables

examined when the same mass ratio was applied. Across all variables examined, the north and south were best described by the same feeding regime 11 times (Table 3). The best feeding regime was different for the northern and southern sites 9 times (Table 3). Of those, 8 times the best feeding regimes differed by 1 (e.g. regime 4 for north and regime 5 for south) and 1 time the best feeding regimes differed by 2 (Table 3). The best feeding regime was more copepod-like for the northern sites 4 times, while the best feeding regime was more copepod-like for the southern sites 5 times (Table 3).

2.3.3 Nutrient Reductions

Nutrient reductions showed little effect on model quasi-equilibrium outputs. Quasi-equilibrium outputs were similar to the original model simulations at appropriately reduced N_T values for both the sequential, small reductions and the singular, large reductions (Figure 10). For large nutrient reductions, a greater amount of nitrogen was removed from feeding regime 5, because there was greater quasi-equilibrium free nitrogen (Figure 10B). However, for both feeding regimes 1 and 5, no deviation from the original model simulations was apparent (Figure 10B). For small nutrient reductions, no deviation from the original model simulations was apparent, except in the simulation for $N_T=12.5$ with feeding regime 5 (Figure 10A). However, this deviation occurred only at an N_T where original model convergence was very slow. Once beyond that N_T value, the nutrient reduction results quickly returned to values near the original model simulations (Figure 10A).

2.4 Discussion

These results show an unexpected spatial pattern in plankton communities throughout BBLEH. The jellyfish-dominated feeding preference was based on *Chrysaora quinquecirrha* feeding preference. Therefore, I expected the jellyfish-dominated model output to be more similar to BBLEH plankton communities with higher *C. quinquecirrha* abundance (ie. sites in the northern region). However, the results of this study suggest the opposite is true. The most jellyfish-like site in the estuary was located in the southern region, where high salinity prevents *Chrysaora quinquecirrha* survival. The northern region, where *C. quinquecirrha* bloom, was modeled most accurately using a copepod-dominated feeding preference. These results show no evidence that increasing *C. quinquecirrha* abundances lead to more jellyfish-dominated community dynamics in BBLEH.

The copepod-dominance in northern BBLEH may actually be strengthened by *C. quinquecirrha* blooms because of interactions with other gelatinous taxa. Lift net data from 2012 show that *Mnemiopsis leidyi* is the most abundant gelatinous taxa and is inversely related to *C. quinquecirrha* abundance in BBLEH during the summer (Figure 11). Tow data from the same surveys shows similar results. *M. leidyi* is a ravenous grazer of microzooplankton (Mountford, 1980, Sandine, 1984) and has similar feeding preferences to *C. quinquecirrha*. *C. quinquecirrha* preys on *M. leidyi*, however, and can influence *M. leidyi* distribution and abundance. Laboratory-measured clearance rates suggest that *C. quinquecirrha* can eliminate *M. leidyi* from Chesapeake Bay tributaries (Purcell and Cowan Jr, 1995). *M. leidyi* was absent from the northern region of BBLEH during summer 2012. *M. leidyi* has wide environmental tolerances (Purcell et al., 2001)

and was unlikely to be excluded by physical/chemical factors, so I suspect that *C. quinquecirrha* excluded *M. leidy* from that region through predation (Figure 11). By consuming *M. leidy*, a voracious copepod predator, *C. quinquecirrha* may have indirectly caused the northern region of BBLEH to become more copepod-like. Predation rates on shared prey (e.g. copepods) are lower when *C. quinquecirrha* and *M. leidy* co-occur (Cowan Jr and Houde, 1992, Purcell et al., 1994). This idea is also supported by evidence from Chesapeake Bay, where *M. leidy* abundances fell and copepod standing stock rose when *C. quinquecirrha* became abundant (Feigenbaum and Kelly, 1984). Alterations to the base of the food web, driven by *C. quinquecirrha* and *M. leidy* interactions, have the potential to impact human interests in BBLEH.

The potential for *C. quinquecirrha* to alter New Jersey's fisheries merits further study, because both *C. quinquecirrha* and *M. leidy* feed on fish larvae (Cowan Jr and Houde, 1992), and may impact fish populations. Predation rates on ichthyoplankton (# of prey per predator per day) are higher for *C. quinquecirrha* than *M. leidy* (Cowan Jr and Houde, 1992). However, when both taxa are present, ichthyoplankton predation is lower than expected because of the handling time required for *C. quinquecirrha* to consume *M. leidy* (Cowan Jr and Houde, 1992). In locations where these taxa co-occur, *C. quinquecirrha* could reduce ichthyoplankton mortality through its interactions with *M. leidy* (Cowan Jr and Houde, 1992, Cowan Jr and Houde, 1993). Additionally, *C. quinquecirrha* predation on *M. leidy* may increase the standing stock of copepod prey available for more commercially important estuarine species (Feigenbaum and Kelly, 1984). The net effect of *C. quinquecirrha* on New Jersey's fisheries is largely unknown.

These results indicate that the impacts of a jellyfish invasion may vary depending on the taxa of invaders and presence of other gelatinous species. The outcome depends on the trophic level of the jellyfish and dynamics within the local ecosystem. An increase in *M. leidyi* abundance within BBLEH would likely cause the community-averaged feeding of the estuary to become more jellyfish-dominated, which appears to be true of the southern region of BBLEH (Figure 11). Additionally, the effect of *C. quinquecirrha* may have been different in the absence of *M. leidyi*. The presence of *M. leidyi* reduces *C. quinquecirrha* grazing rate on ichthyoplankton (Cowan Jr and Houde, 1992), while the presence of *C. quinquecirrha* influences the impact of *M. leidyi* on copepod standing stock (Feigenbaum and Kelly, 1984). I originally predicted that abundant *C. quinquecirrha* would lead to jellyfish-dominated ecosystem dynamics, and this prediction may have borne out in the absence of *M. leidyi*.

The BBLEH system is inadequate for testing the impacts of generalist invaders on a predominantly specialist system, because the jellyfish present are not strongly generalist feeders. The widths of prey size distributions are similar for the gelatinous taxa present and for copepods (Fuchs and Franks, 2010). Therefore, more dramatic impacts on plankton dynamics may be observed in higher latitudes, where salp-krill oscillations dominate the zooplankton (Loeb et al., 1997, Atkinson et al., 2004). Krill have more generalist feeding preferences than any of the taxa in the present study and salps have greater predator-prey size ratios and diet breadth (ie. are more generalist) than krill (Fuchs and Franks, 2010). Krill-salp dynamics influences vertebrate predator populations (Reid and Croxall, 2001) and chlorophyll-a concentrations (Loeb et al., 1997) in Antarctic food webs. Plankton functioning in high latitude is potentially starkly different

than the copepod-dominated mid- to low-latitudes, because the most generalist simulations in this study (regime 6) were most similar to the jellyfish-dominated simulations (regime 5). Additional simulations would be required to explore these possibilities.

The nutrient reduction scenarios simulated in this study show that the model is insensitive to initial values. Therefore, original simulations can be examined to predict the effects of reductions in nutrient loading in ecosystems with differing community averaged feeding preferences. Decreasing N_T in a copepod-dominated plankton community will lead to a greater reduction in phytoplankton biomass than in a jellyfish-dominated plankton community (Figure 5A). Conversely, decreasing N_T in a jellyfish-dominated community will lead to a greater reduction in free nutrients than in a copepod-dominated plankton community (Figure 8). Jellyfish have also been shown to influence the response of plankton to nutrient additions in mesocosms (Pitt et al., 2007). Zooplankton community composition should be considered when planning nutrient reduction strategies, because zooplankton feeding preference influences which types of management goals are more likely to be met. However, these observations would only hold true if reduction in nutrient loading did not affect the community averaged feeding preference. Phytoplankton biomass increased rapidly in the Dutch Wadden Sea following nutrient enrichment, but decreased more slowly in response to nutrient reduction (Philippart et al., 2007). Asymmetric responses of phytoplankton may arise from shifts in size-structure, feeding mode, or species composition (Philippart et al., 2007).

Some of the data used in this study were limited by sensitivity of instruments used. Dissolved nitrate plus nitrite and dissolved ammonia had the highest incidence of samples “below detection limit.” At all sites 30-67% of dissolved nitrate plus nitrite samples had to be excluded. Although I accounted for the excluded samples using a Monte-Carlo approach, sample exclusion still may have reduced the accuracy of calculations by reducing the sample size that could be used for curve fitting. Since the concentrations were low the uncertainty could cause a large error relative to the true concentration. Not surprisingly, the $\Sigma P^*/N^*$ had the worst performance for model-data matching (Figure 7). For this ratio, numerous sites were poorly matched to model outputs. For all other variables examined, only the unusual Toms River site (site 4) was sometimes poorly matched. These results highlight the need for more precise measurements when sampling dissolved nitrate plus nitrite and dissolved ammonia in estuarine environments.

The results of this study were also greatly impacted by the selection of the mass ratios (C:Chl and C:N). I interpreted results using the results using Barnegat C:Chl and Redfield C:N. I consider those to be the most reasonable options, because C:Chl was derived from Barnegat data for the appropriate time of year and no cellular nutrient concentration data was available to better constrain C:N. However, these ratios are highly variable among taxa (Brzezinski, 1985, Verity et al., 1992, Menden-Deuer and Lessard, 2000), as well as within taxa under various circumstances (Laws and Bannister, 1980, Falkowski et al., 1985). In cultured phytoplankton, C:Chl ratio have been recorded from <20 (Laws and Bannister, 1980) to 500 (Falkowski et al., 1985). Given the

potential range in these ratios, they are both difficult to constrain and vital to the proper interpretation of the results of this study.

By using different C:Chl and C:N ratios, the northern and southern regions of BBLEH could best fit either copepod-dominated or jellyfish-dominated ecosystems. With more detailed and accurate C:Chl and C:N data, it would have been possible to derive different ratios for the northern and southern regions of BBLEH. Larger phytoplankton cells and higher nutrient loading are found in the north (Olsen and Mahoney, 2001), both of which could cause variability in the C:Chl and C:N ratios. Addressing the uncertainty in these ratios would require a multi-year study to assess the relative abundances and cellular stoichiometry of BBLEH taxa. Such data would enable a more nuanced analysis of BBLEH plankton communities.

Despite uncertainties in mass ratios and the limitations of the observational data, the results of this study demonstrate that *C. quinquecirrha* has complex interactions ecosystems. In BBLEH, plankton communities with *C. quinquecirrha* have functioning and dynamics that more closely resemble copepod-dominated communities than plankton communities without *C. quinquecirrha*.

3. EXTENSIONS

3.1 Applicability of Results to Other Systems

The present study concluded that interactions between *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* play an important role in structuring the plankton communities in Barnegat Bay-Little Egg Harbor Estuary through top-down control. The results are consistent with other studies that have shown strong interactions between these two taxa in Chesapeake Bay (Feigenbaum and Kelly, 1984) and in mesocosm experiments (Cowan Jr and Houde, 1992). These general results may be relevant wherever *C. quinquecirrha* and *M. leidyi* co-occur. *C. quinquecirrha* is found along the Atlantic and Gulf coasts of the United States (Bayha, 2005) and *M. leidyi* is found along the Atlantic coast of both North and South America (Purcell et al., 2001). Therefore, the taxonomic makeup in the present study is likely to be replicated outside of estuaries along the eastern coast of the United States. Both scyphomedusa (Larson and Ameson, 1990) and *M. leidyi* have the capacity to be invasive (Purcell et al., 2001), so they are able to co-occur elsewhere.

Similar species interactions may also occur in taxa with similar feeding preferences to *C. quinquecirrha* and *M. leidyi*. Predatory jellyfish, like those in the genus *Beroe* (Swanberg, 1974), may influence plankton community functioning in estuaries where crustacean grazing jellyfish also occur. Such a situation occurs in the Bahamas, where ctenophore *Beroe ovata* preys on ctenophore *Bolinopsis virea* (Swanberg, 1974). In some locations, *Beroe* spp. may consume other jellyfish as its dominant food source (Nelson, 1925). Therefore, jellyfish interactions are potentially more impactful to plankton community functioning in the Bahamas than in Barnegat Bay-Little Egg Harbor

Estuary. Analogous situations with various jellyfish taxa may be found in estuaries throughout the world.

3.2 Applicability of Method to Other Systems

The methodology used in the present study could easily be adjusted to apply to different estuarine ecosystems. In other estuaries along the Atlantic coast of the United States, both *Chrysaora quinquecirrha* and/or *Mnemiopsis leidyi* may be dominant, so the model simulations in this study could re-used. Only the feeding preference for the jellyfish-dominated regime would need to be altered for most temperate and tropical estuarine ecosystems, because the mesozooplankton in those regions are usually dominated by copepods (Sommer, 2008). In polar regions, both feeding regime end members would need to be adjusted, due to the dominance of other zooplankton taxa, such as krill and salps (Loeb et al., 1997). The total nutrient range used for simulations in the present study covers oligotrophic to eutrophic conditions. However, some estuaries and coastal regions have higher than $50 \mu\text{mol-N L}^{-1}$ (Smith, 2006), and would require additional simulations with higher N_T .

To fully replicate this study in another ecosystem, however, independent samples would be needed from the system both with and without the jellyfish taxa. In the present study, geographic range was exploited for this, but temporal changes in jellyfish taxa may also be sufficient. One interesting location where such a study may be possible is in the Black Sea. *M. leidyi* was introduced to the Black Sea in the early 1980s (Purcell et al., 2001) and *Beroe ovata* was introduced in the mid 1990s (Konsulov and Kamburska, 1998). *B. ovata* introduction may be analogous to *C. quinquecirrha*, because both prey

on *M. leidyi* (Cowan Jr and Houde, 1992, Kideys et al., 2004). If nitrogen and chlorophyll-a data are available from those timeframes, the plankton community could be evaluated for a pre-jellyfish state, a one jellyfish state, and a two jellyfish state. It would be interesting to compare the results from Barnegat Bay-Little Egg Harbor Estuary northern and southern region to that of 1980s and 2000s data from the Black Sea, respectively.

If repeated for another system, several aspects of this study could be improved with additional observational data. The model used in this study resolves more ecosystem characteristics than was available in the BBLEH observational data, such as zooplankton biomass and plankton spectral slopes. Such data could be compared to model outputs using the same approach presented herein, but would present different challenges for data collection. Zooplankton data would need to be converted from abundance to $\mu\text{mol-N L}^{-1}$ using taxa-specific mass ratios. Size structured data could be collected using nets with varying mesh sizes or with sophisticated instruments, like FlowCam (Álvarez et al., 2011). These additional comparisons could provide new and interesting insights into plankton community functioning, and the impacts of jellyfish taxa on plankton community functioning.

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TABLES AND FIGURES

Table 1. Symbol definitions. Asterisks denote quasi-equilibrium values.

Symbol	Description
x	Log_{10} of equivalent spherical diameter
P	Phytoplankton biomass
Z	Zooplankton biomass
N	Free nitrogen
F^-	Feeding kernel
F^+	Redistribution kernel
N_T	Total nitrogen
a	Allometric coefficient
b	Allometric exponent
g	Feeding rate
k_s	Half-saturation constant
m	Mean of feeding kernel
s	Standard deviation of feeding kernel
γ	Assimilation efficiency
δ	Zooplankton mortality
λ	Phytoplankton mortality
μ_{max}	Maximum phytoplankton growth rate
N^*	Quasi-equilibrium free nitrogen
N^*/N_T	Quasi-equilibrium free nitrogen to total nitrogen ratio
ΣP^*	Quasi-equilibrium total phytoplankton biomass
$\Sigma P^*/N_T$	Quasi-equilibrium total phytoplankton biomass to total nitrogen ratio
$\Sigma P^*/N^*$	Quasi-equilibrium total phytoplankton biomass to free nitrogen ratio

Table 2. Sum of squared errors for each model feeding regime and region combination. Metrics listed are free nitrogen (N^*), phytoplankton biomass ($\sum P^*$), free nitrogen to total nitrogen ratio (N^*/N_T), phytoplankton biomass to total nitrogen ratio ($\sum P^*/N_T$), and phytoplankton biomass to free nitrogen ratio ($\sum P^*/N^*$). Results only shown for model-data comparisons using Barnegat C:Chl and Redfield C:N. The best feeding regimes are summarized in Table 3 for all mass ratios.

Region	North						South					
Regime	1	2	3	4	5	6	1	2	3	4	5	6
N^*	13.09	13.09	104.07	53.57	313.03	344.4	5.9	5.92	57.7	54.52	135.06	79.67
$\sum P^*$	254.38	259.69	734.35	834.45	1697.1	1840.77	117.07	109.72	249.8	338.95	567.3	439.14
$\sum P^*/N_T$	0.09	0.09	0.3	0.34	0.72	0.78	0.17	0.17	0.45	0.59	0.86	0.63
$\sum P^*/N^*$	647.63	669.53	2686.67	2527.16	3122.62	3148.54	271.98	283.56	1081.76	1123.4	1288.48	1161.42
N^*/N_T	0.01	0.01	0.04	0.02	0.13	0.14	0.01	0.01	0.06	0.06	0.13	0.07

Table 3. The model feeding regimes that are most similar to observational site data for various metrics and conversation ratios. Metrics listed are the same as in Table 2. All combinations of the Barnegat-derived (150) and Chesapeake-derived (50) C:Chl ratio and the Redfield (5.67), low (3.5), and high (12) C:N ratio are summarized. The most similar feeding regimes were determined by the lowest sum or squared error between the site observational data and the model output for the N_T values observed at those sites. N^* and N^*/N_T are only reported once because those values are invariant to the mass ratio assumptions.

Region	North						South					
C:Chl	Barnegat			Chesapeake			Barnegat			Chesapeake		
C:N	Redfield	Low	High	Redfield	Low	High	Redfield	Low	High	Redfield	Low	High
N^*	1	-	-	-	-	-	1	-	-	-	-	-
$\sum P^*$	1	1	5	6	4	6	2	1	5	5	5	5
N^*/N_T	1	-	-	-	-	-	1	-	-	-	-	-
$\sum P^*/N_T$	1	1	5	6	4	6	1	1	5	5	6	5
$\sum P^*/N^*$	1	1	2	4	2	4	1	1	3	3	2	4

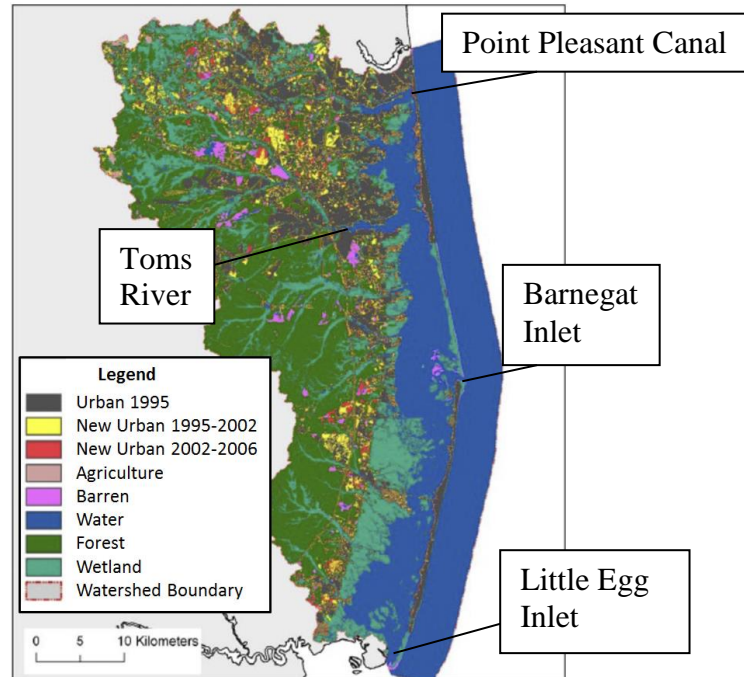


Figure 1. Map of development in the Barnegat Bay watershed, New Jersey in 2006. Coloring represents land usage type: grey (urban in 1995), yellow (became urban 1995-2002), red (became urban 2002-2005), beige (agricultural), pink (barren), blue (water), green (forested), and teal (wetland). Major inlets and rivers are also identified. Figure adjusted with permission from Kauffman and Cruz-Ortiz (2012).

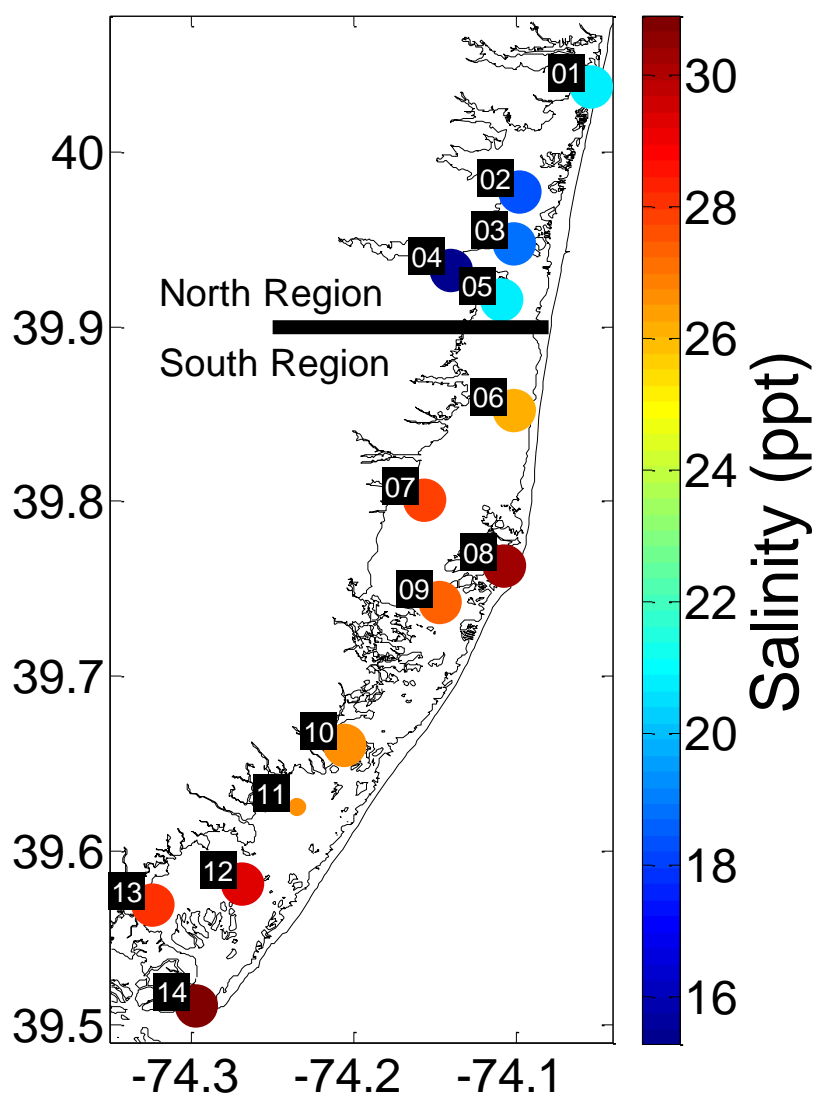


Figure 2. Map of surface salinity in Barnegat Bay-Little Egg Harbor Estuary for July and August 2012. Sites are numbered and the solid line denotes the division between northern and southern sites. Dot size is relative to the amount of data available at that site. Data courtesy of New Jersey Department of Environmental Protection, publicly available at <http://www.state.nj.us/dep/barnegatbay/bbmapviewer.htm>.

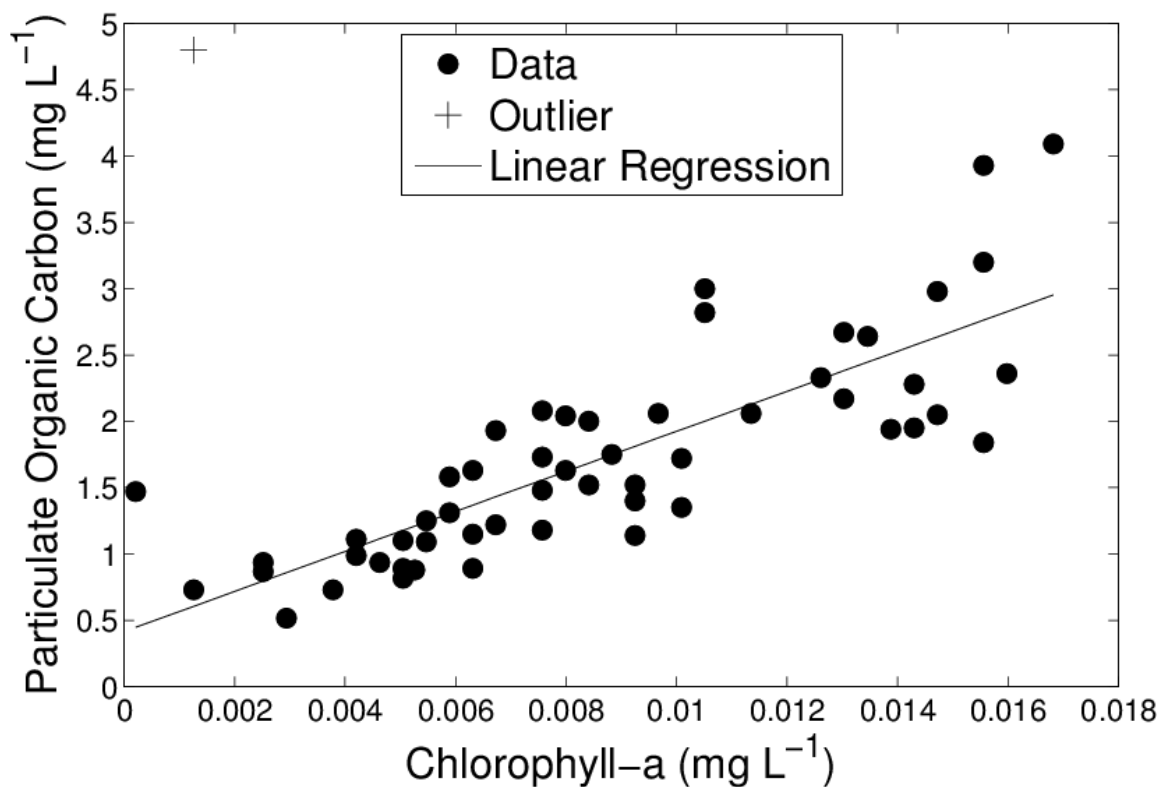


Figure 3. Regression of particulate organic carbon and chlorophyll-a in Barnegat Bay-Little Egg Harbor Estuary from July and August 2011. The regression equation is $y=150x+0.42$ ($R^2=0.6586$). Trendline slope is the carbon to chlorophyll-a ratio (mass:mass). One outlier (cross) was excluded prior to linear regression. Data source as in Figure 2.

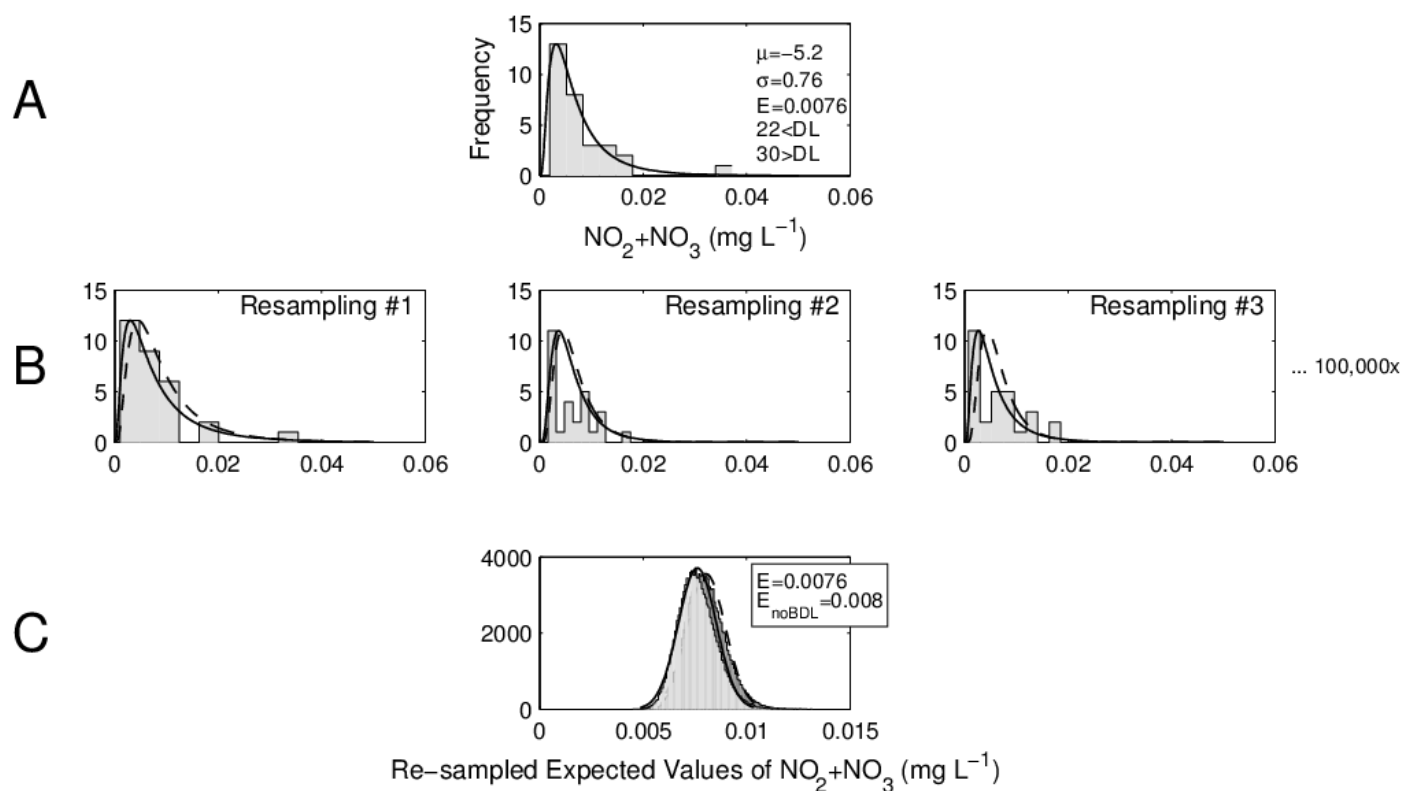


Figure 4. An example of the Monte-Carlo procedure used to generate 95% confidence intervals and quantify the bias effect of the detection limit. For simplicity, this example uses dissolved nitrate plus nitrite data instead of dissolved inorganic nitrogen, which requires fitting and resampling for both dissolved nitrate plus nitrite and dissolved ammonia. (A) Histogram and lognormal fit for the data. Fit parameters (μ and σ), expected value of the fit (E), and the number of samples below and above detection limit ($<DL$ and $>DL$) are reported. (B) Examples of resampled data. A lognormal distribution was fit to the data including (solid line) and excluding (dashed line) samples below detection

limit. Resampling was repeated 100,000 times and expected values from both fits were recorded. (C) Histogram of resampled expected values including (lighter gray) and excluding (darker gray) samples below detection limit. The mean of the resampled expected valued are reported for each.

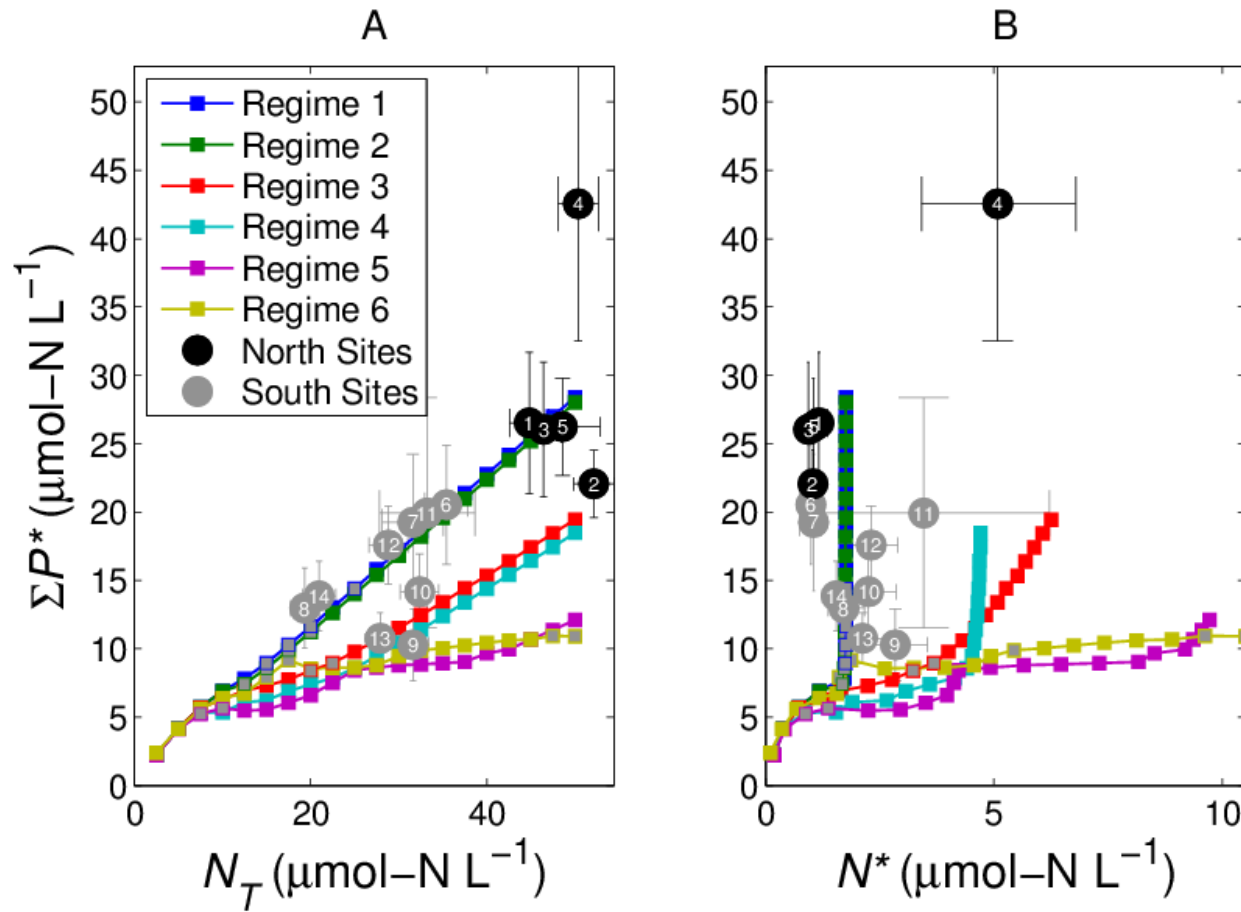


Figure 5. Barnegat Bay-Little Egg Harbor Estuary observational data for July and August 2012 overlaid on NPZ model outputs. (A) Phytoplankton biomass (ΣP^*) vs. total nitrogen (N_T). (B) Phytoplankton biomass (ΣP^*) vs. free nitrogen (N^*). Circles with error bars are expected values and 95% confidence intervals for data at sites denoted by numbers. Circle color denotes region (black for north, gray for south). Colored lines denote model feeding

parameterizations (Regimes 1-2 are copepod-dominated, Regime 3-4 are intermediate, and Regimes 5-6 are jellyfish-dominated). Squares with gray fills denote model simulations that required loosened quasi-equilibrium thresholds.

Data source as in Figure 2.

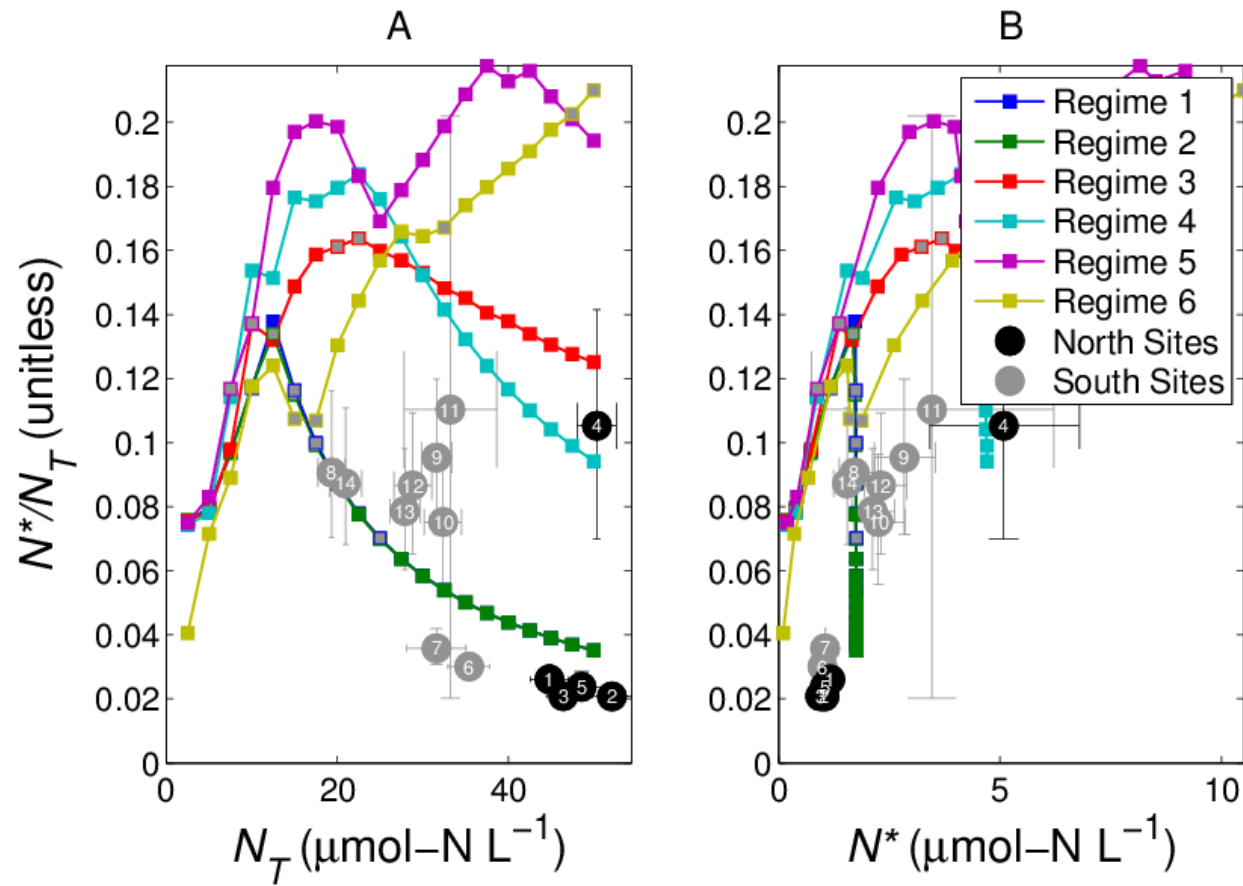


Figure 6. Barnegat Bay-Little Egg Harbor Estuary observational data for July and August 2012 overlaid on NPZ model outputs. (A) Free nitrogen to total nitrogen ratio (N^*/N_T) vs. total nitrogen (N_T). (B) Free nitrogen to total nitrogen ratio (N^*/N_T) vs. free nitrogen (N^*). Symbols, lines, and data source as in Figure 5.

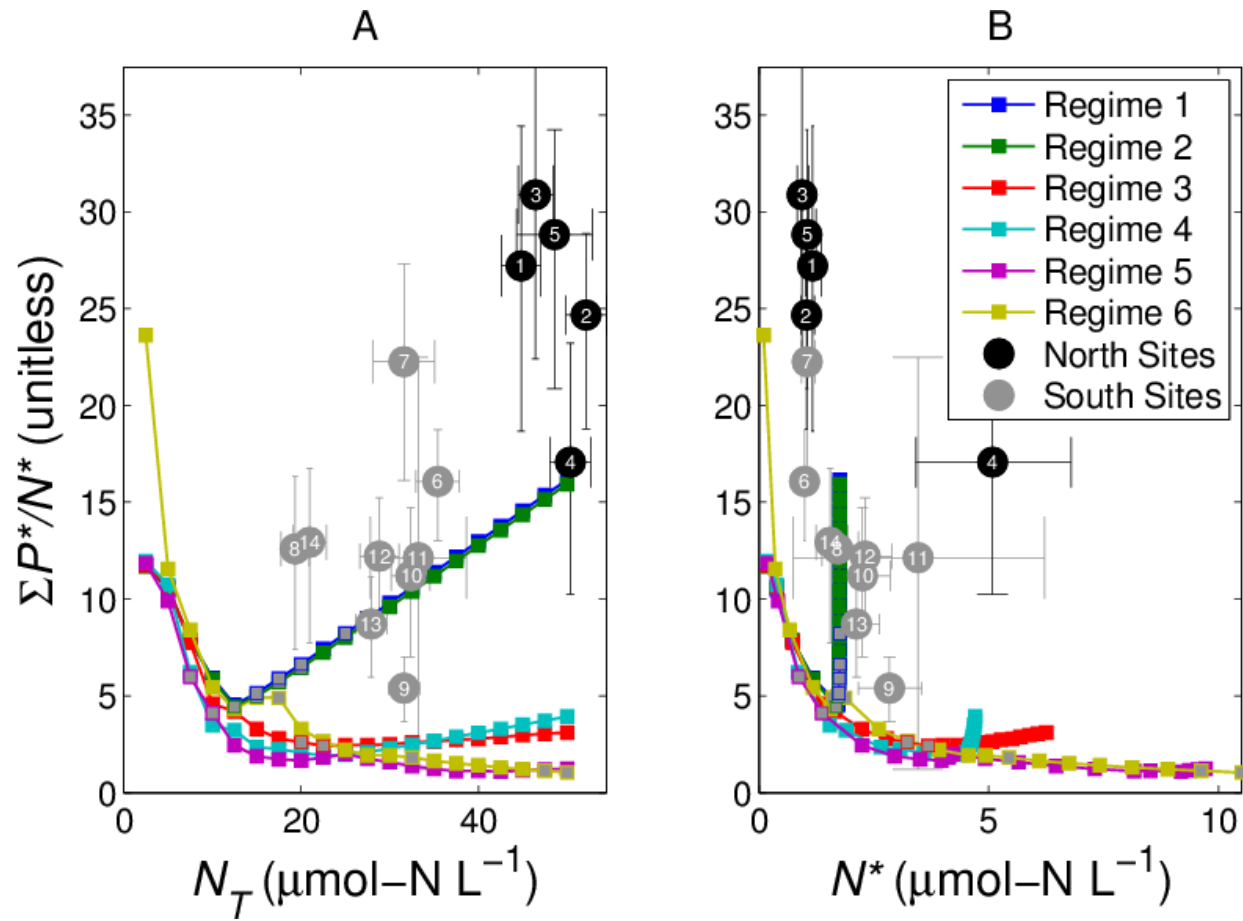


Figure 7. Barnegat Bay-Little Egg Harbor Estuary observational data for July and August 2012 overlaid on NPZ model outputs. (A) Phytoplankton biomass to free nitrogen ratio ($\Sigma P^*/N^*$) vs. total nitrogen (N_T). (B) Phytoplankton biomass to free nitrogen ratio ($\Sigma P^*/N^*$) vs. free nitrogen (N^*). Symbols, lines, and data source as in Figure 5.

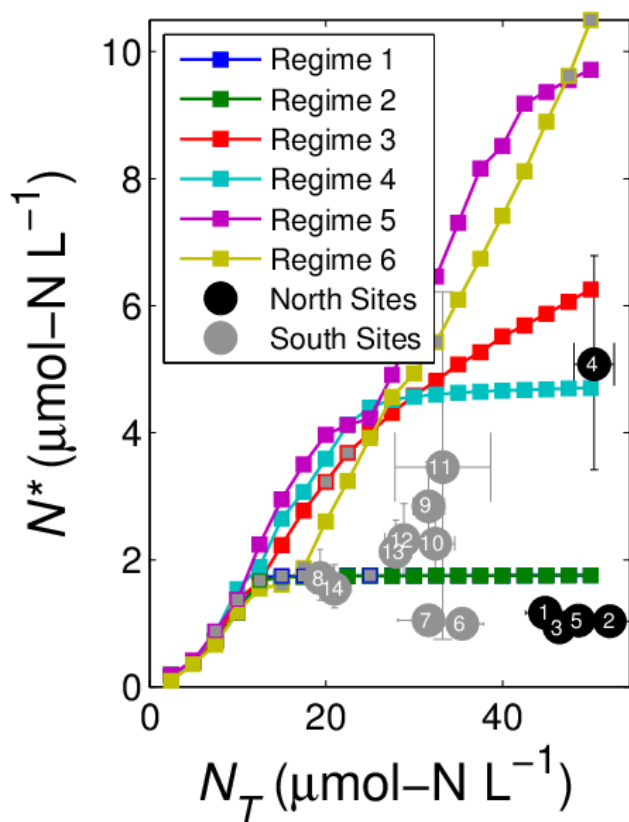


Figure 8. Barnegat Bay-Little Egg Harbor Estuary free nitrogen (N^*) vs. total nitrogen (N_T) data for July and August 2012 overlaid on NPZ model outputs. Symbols, lines, and data source as in Figure 5.

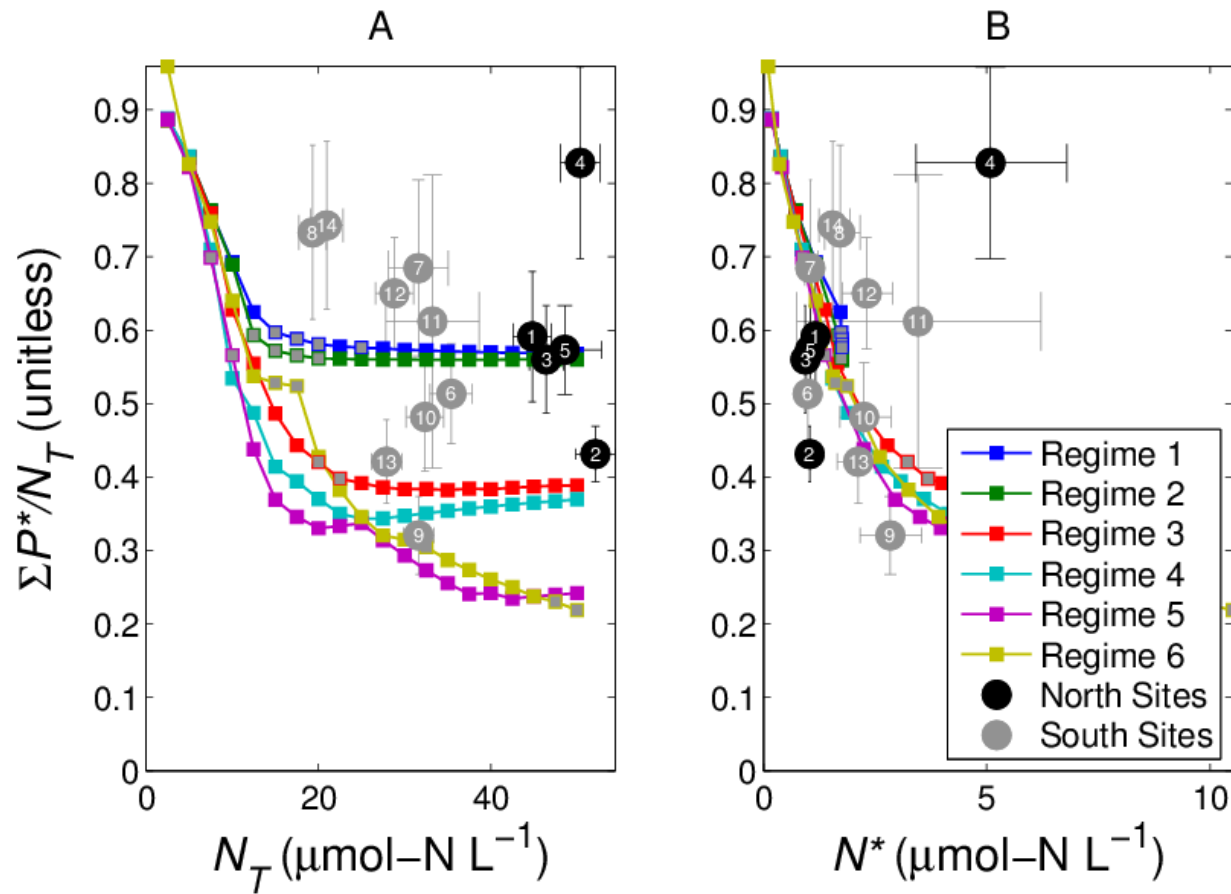


Figure 9. Barnegat Bay-Little Egg Harbor Estuary observational data for July and August 2012 overlaid on NPZ model outputs. (A) Phytoplankton biomass to total nitrogen ratio ($\Sigma P^*/N_T$) vs. total nitrogen (N_T). (B) Phytoplankton biomass to total nitrogen ratio ($\Sigma P^*/N_T$) vs. free nitrogen (N^*). Symbols, lines, and data source as in Figure 5.

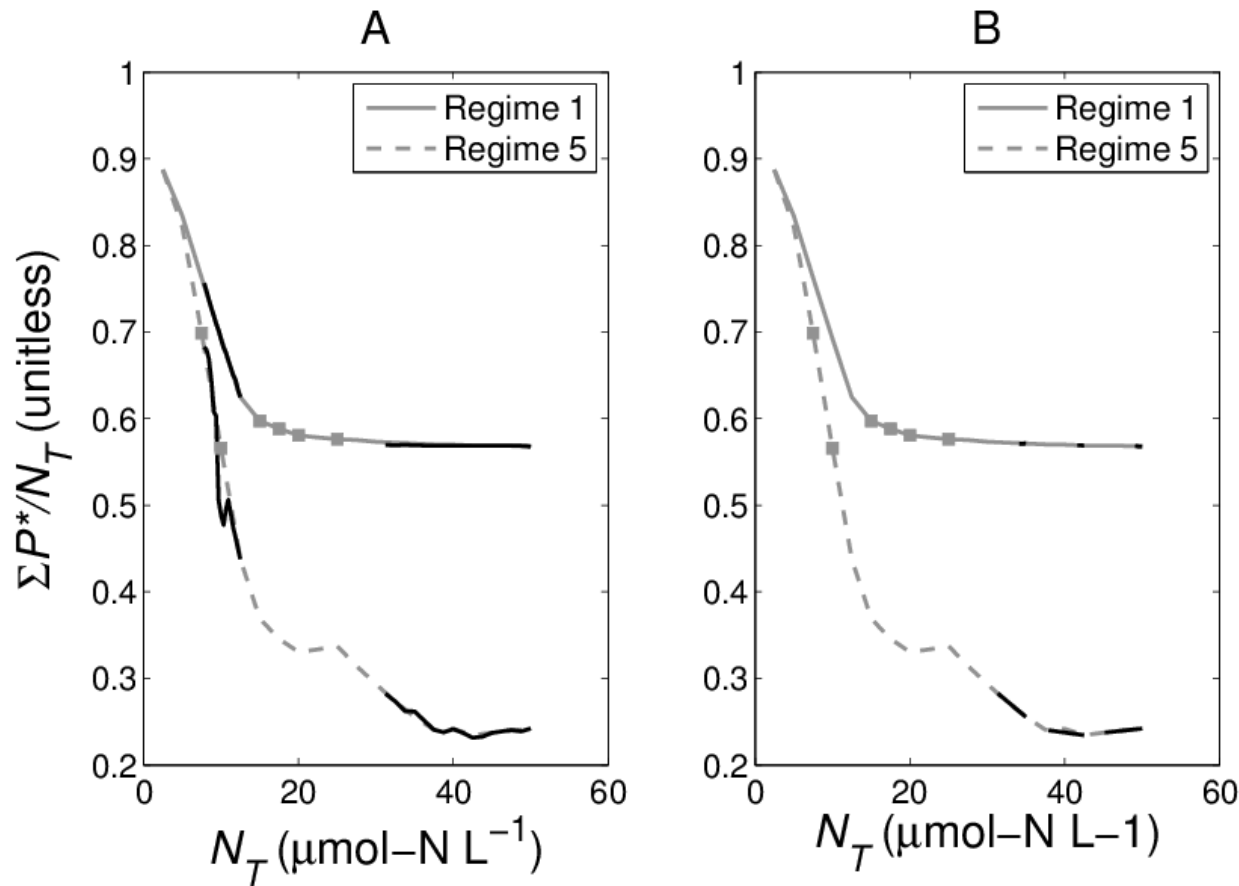


Figure 10. Phytoplankton biomass to total nitrogen ratio ($\Sigma P^*/N_T$) vs. total nitrogen (N_T) for nutrient reduction scenarios. (A) Singular, large nutrient reductions. (B) Sequential, small nutrient reductions. Grey lines denote original model simulations (solid is Regime 1, dashed is Regime 5) grey squares denote original model simulations that required loosened quasi-equilibrium thresholds. Solid, black lines denote nutrient reduction simulations.

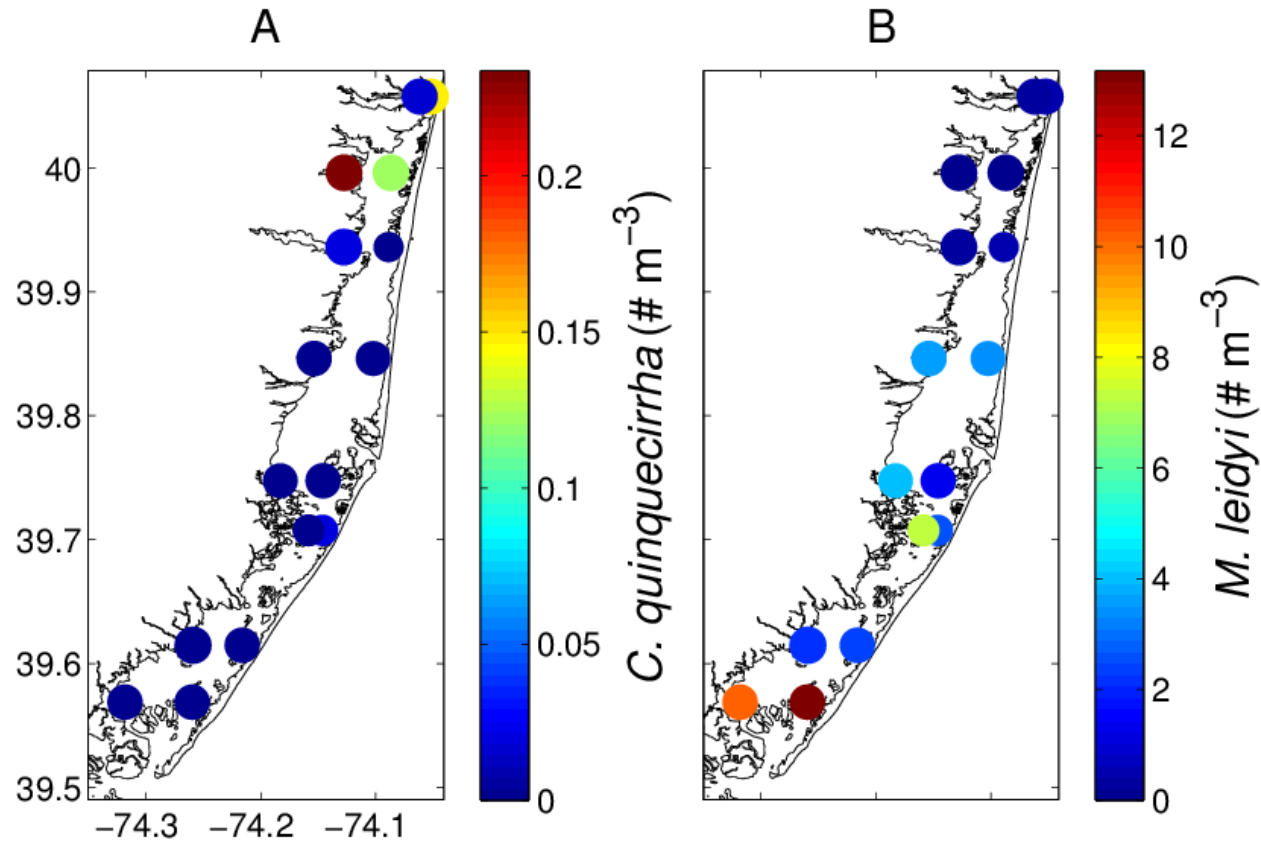


Figure 11. Map of jellyfish densities at various sites in Barnegat Bay-Little Egg Harbor Estuary for July and August 2012. Panels show lift net data for (A) *Chrysaora quinquecirrha* and (B) *Mnemiopsis leidyi*. Data courtesy of Paul Bologna and Jack Gaynor at Montclair State University.