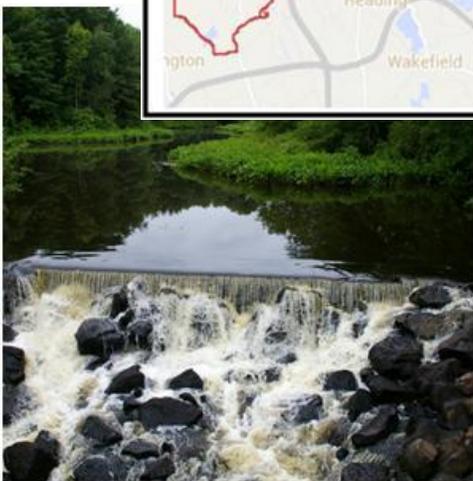
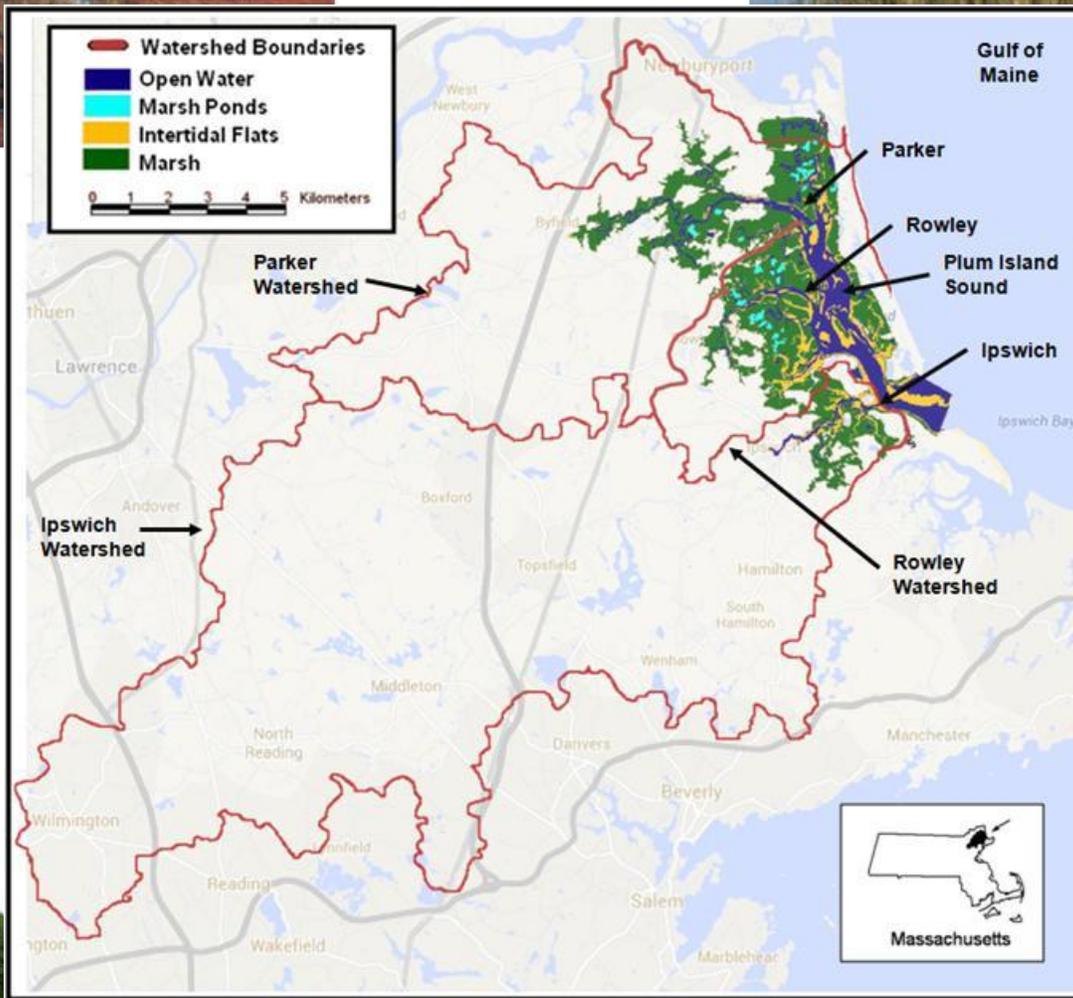
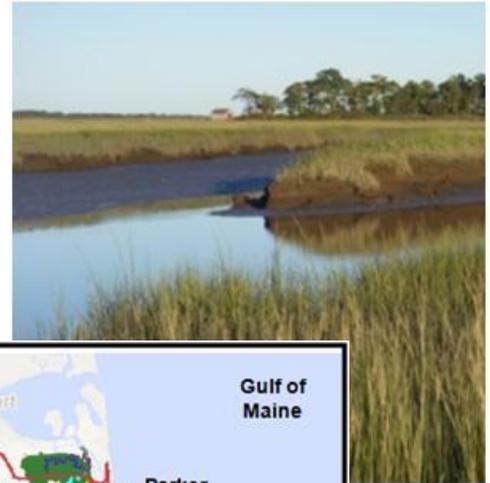
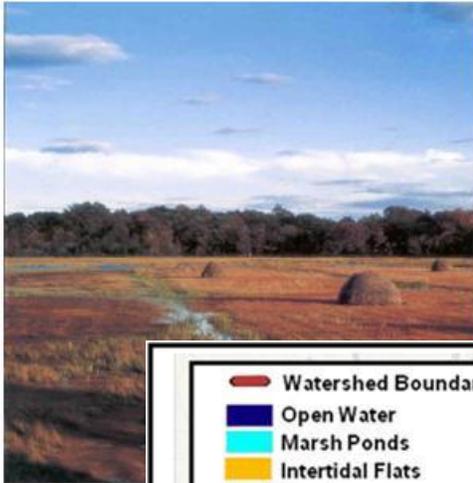


Plum Island Ecosystems (PIE) LTER Site Review Document 2014



1) INTRODUCTION

The Plum Island Ecosystems (PIE) LTER site consists of a linked watershed-marsh-estuarine system located north of Boston, Massachusetts (cover). The brackish and saline wetlands of the PIE site form the major portion of the “Great Marsh”, the largest intact marsh left on the northeast coast of the United States. These wetlands are influenced by three rivers, the Ipswich, the Parker and the Rowley, which collectively drain over 550 km² of upland.

PIE lies within the northern Acadian biogeographic province, a cold water environment connected to the Gulf of Maine. PIE salt marshes are geographically and biologically distinct from coastal ecosystems to the south of Cape Cod, Massachusetts, and lack all of the invertebrate species implicated in consumer controls on marsh production in some other marsh systems (Pennings and Silliman 2005). The marshes are macrotidal, with tidal excursions often exceeding 3 meters as opposed to more southerly US Atlantic marshes where tidal ranges are typically lower than 2m.

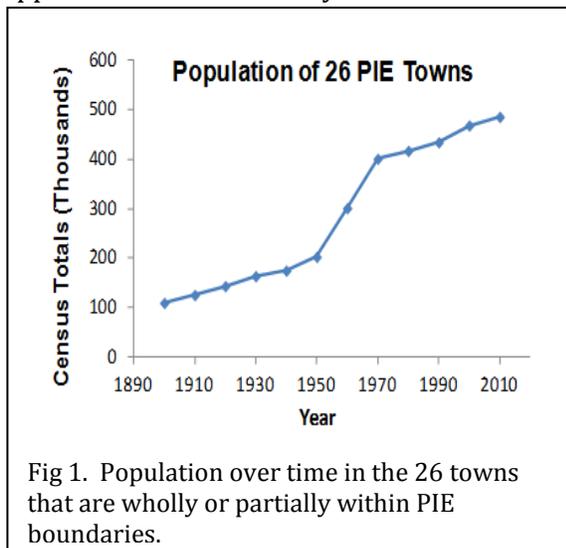


Fig 1. Population over time in the 26 towns that are wholly or partially within PIE boundaries.

Like most coastal areas worldwide, this region has experienced many human-driven changes both in the marsh and in the watershed. The watersheds were largely deforested by early European colonists for agriculture and the marshes were ditched to facilitate the harvest of *Spartina patens*, salt marsh hay. Early land clearing may have initially caused severe upland erosion and increased sediment export (Kirwin et al. 2011), but during the colonial period the rivers were dammed and the input of suspended solids to the estuary was greatly reduced, and remains quite low today. In the late 1800s the agricultural fields were abandoned and the watersheds once again became largely covered by forest. Marsh ditching continued and expanded in the 1920s and 1930s for mosquito control. Large freshwater

impoundments were created out of salt marsh habitat to attract nesting waterfowl. Then, shortly after World War II, forest cover was rapidly lost as the population increased (Fig. 1) and suburban areas expanded (Schneider and Pontius 2001).

Coupled with these local changes within the watershed and estuary are large-scale regional changes in climate and sea level. Precipitation has increased by nearly 20% over the last 70 years. However, this increase in water delivery to the watershed has been largely offset by increased evapotranspiration (ET) and human transfers of water out of the basin (Claessens et al. 2006). As a result, there has been little change in average annual river discharge to the estuary. However, discharge is highly variable and this variability seems to be increasing (Fig. 2) due to increased storminess (Hayden and Hayden 2003). At the same time, rising ocean temperatures are altering fish species distributions in the north Atlantic and may be extending the range of other organisms (NOAA 2013).

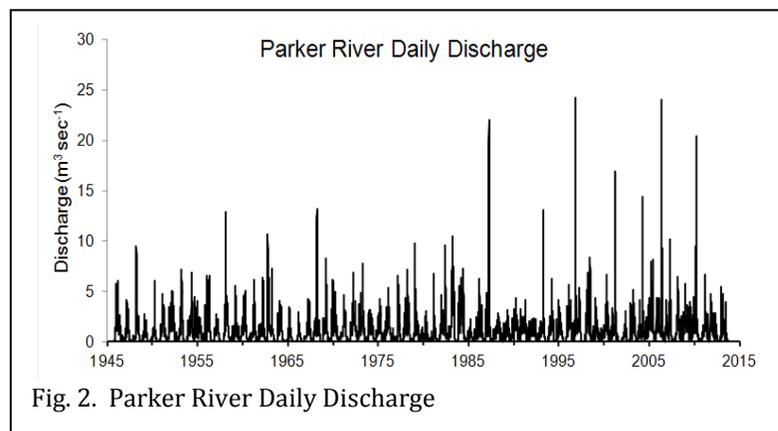
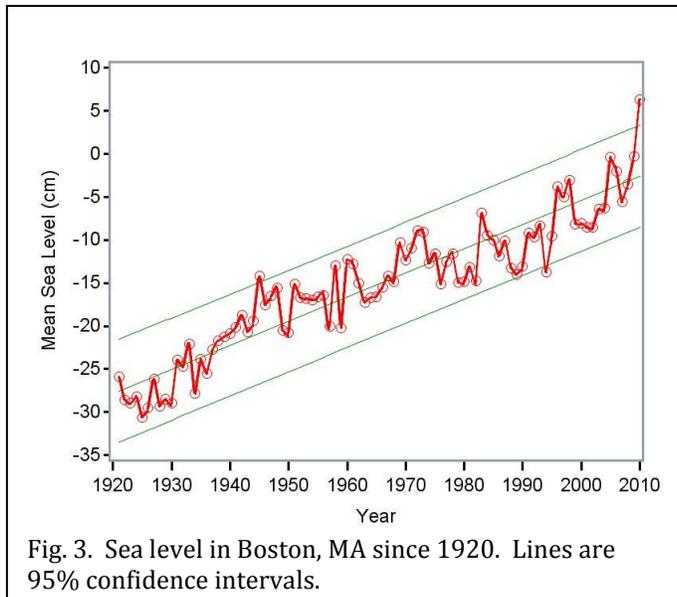


Fig. 2. Parker River Daily Discharge

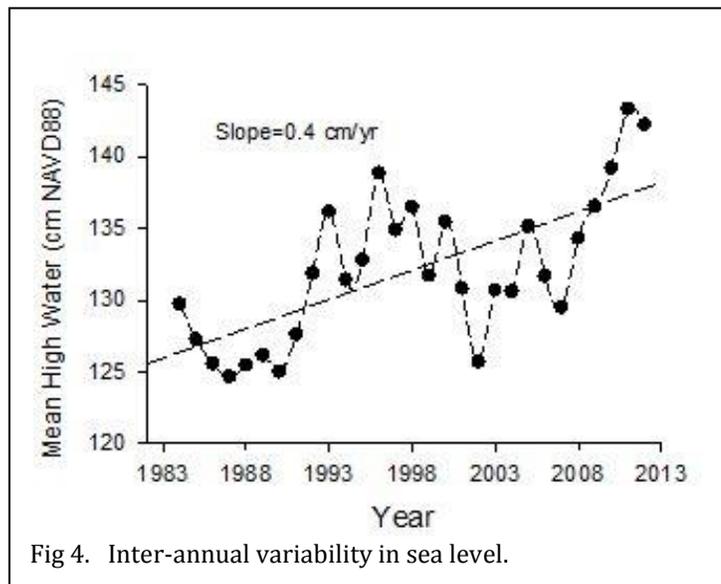


The long-term survival of marshes is linked to rates of sea level rise. Over the last 93 years mean sea level has risen at an average rate of 0.28 cm yr⁻¹ (Fig. 3). Mean high water (MHW) level is another important metric that determines productivity and overall marsh ecosystem function. The rate of increase in MHW in the Northeast since 1984 has been 0.4 cm yr⁻¹, significantly higher than the trend in mean sea level during the last century. While the long term trends are obviously important, there are a number of other factors which lead to substantial *interannual* variability in sea level rise. As a result, MHW averaged over the growing season has varied by 17 cm (Fig. 4). These interannual changes have turned out to be

extremely important for marsh functioning. Recognizing the impact of this variability has improved our understanding of the mechanisms by which sea level changes impact marsh primary productivity and accretion (see Q1b below).

HISTORY OF THE RESEARCH

The Plum Island Ecosystems (PIE) LTER was established in 1998. Since its inception our overall goal has been to develop a predictive understanding of the long-term response of coupled land-estuary-ocean ecosystems to changes in climate, sea level, and human activities. With this in mind we established a series of long-term monitoring activities (Table 1) designed to document changes to the major drivers influencing ecosystem function, and to record the responses to these changes. Both long-term and short-term experiments were begun to investigate the mechanisms behind these ecosystem responses (Table 2). Over the last 15 years our hypotheses and conceptual framework have evolved considerably.



In PIE I we asked, “How will trophic structure and primary and secondary productivity in estuaries be affected by changes in organic matter, nutrient, and water fluxes caused by changing land cover, climate, and sea level?”. A primary hypothesis tested in PIE I was that the interaction of inorganic nutrients with the quality and quantity of organic carbon and organic nitrogen plays an important role in determining the trophic structure, production, and efficiency of estuarine food webs. Our findings did not support this hypothesis but instead demonstrated that *hydrology* played an enormous role in structuring the food web by altering the residence time of water and plankton. The effect varied widely depending upon the physical characteristics of different parts of the estuary.

In PIE II we continued to study the questions we addressed in PIE I but focused much more heavily on the importance of the interactions of changing nutrient, water, and organic matter inputs with the “*hydrologic and geomorphic template*” of our estuary. During PIE II it became evident that rather than viewing the system as a template we had to incorporate *geomorphic change* into our conceptual model. Human actions that alter stream flow directly as well as indirectly were leading to major geomorphic changes in the river network. In addition we were seeing substantial changes in the abundance and distribution of vegetation, ponds, and creeks throughout the salt marsh.

In PIE III we have begun to directly address how geomorphic change shapes organic matter and nutrient transformations in linked watershed and coastal ecosystems. **Our overarching goal for PIE III is to understand how external drivers, ecosystem dynamics, and human activities interact to shape ecological processes in a mosaic of coastal landscapes and estuarine seascapes.** Understanding how landscapes and seascapes evolve and change, and how those changes control ecosystem processes, is both a fundamental science question and a critical management question for coastal policy makers. We continue to study the effects of *temporal change and variability* in climate, sea level rise and human activities on ecological process through our long-term monitoring. In the current funding round we have initiated activities under two new themes that explore how these changes affect the way that ecosystems and habitats within the landscape are arranged and connected.

Theme 1) What controls the spatial arrangements and connectivity between ecological habitat patches in the coastal zone?

The two questions under this theme, detailed below, examine the physical and biological processes that alter geomorphology and connectivity within and between the watersheds and the marshes. We should point out to reviewers not familiar with salt marshes that the causes of marsh geomorphic changes are not well understood (See article by Kintisch under “Other Background Material” at <http://pie-lter.ecosystems.mbl.edu/content/pie-review>). The relative importance of sea level rise (Morris et al. 2002; Mudd et al. 2009; Fagherazzi et al. 2013), sediment legacies (Kirwan et al. 2011), and nutrient inputs (Deegan et al. 2007), which are all being investigated within our program, are being vigorously debated in the community as a whole. We believe that the collaboration of researchers with somewhat different points of view within one team is a real strength of PIE and is helping move the field forward.

Theme 2) How do the spatial arrangement and connectivity between ecological habitat patches in coastal watersheds and estuarine seascapes influence ecological processes?

Four of the questions under this theme directly relate to how arrangement and connectivity alter material transport, biogeochemistry, food webs, and habitat use by specific key consumers. The final question explores an approach to modeling microbial systems which we believe holds promise for modeling biogeochemistry in complex systems.

We have allocated LTER resources to all of these questions but our progress would be slower without the engagement of other researchers and other funding. From 2010 to the present there have been 22 projects closely collaborating with the LTER (Table 3). An additional 9 projects have involved PIE research in cross-LTER or regional synthesis activities. Twelve more are intellectually and conceptually linked with PIE LTER (e.g. modeling projects) although they do not take place on site. How these interactions are managed is described in the management section.

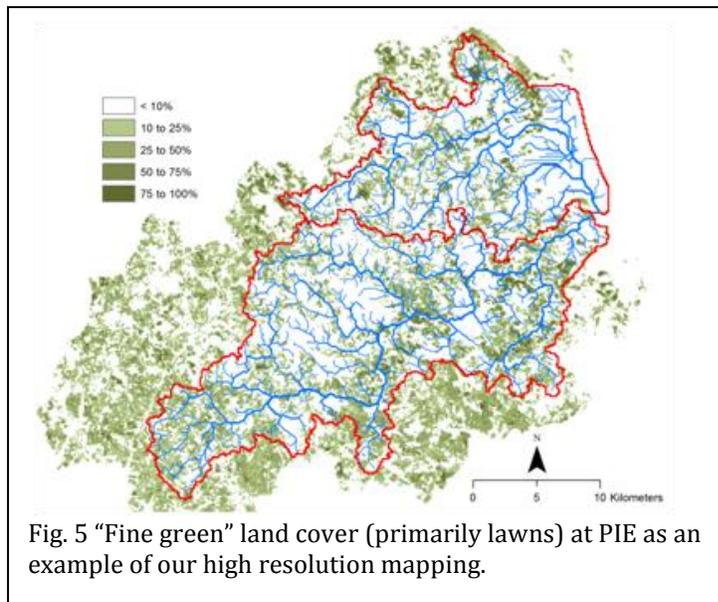
The section below describes our progress to date on each of the research questions. The results are focused on LTER supported work and bring in findings from our long-term monitoring.

2) RESEARCH QUESTIONS AND FINDINGS

Theme 1 Q1A. How do human land use, infrastructure placement, and species management impact the connectivity of terrestrial areas to the river network and different aquatic patches within the network?

The theoretical basis for much of our watershed research lies within the framework of hierarchical patch dynamics (Wu and Loucks, 1995), which integrates many subsidiary theories of aquatic ecosystem function at landscape scales (Poole 2002, Thorp et al. 2006). Our major goal in using this framework is to understand how function at the watershed scale emerges from the interactions of human activity, terrestrial ecosystem processes, and aquatic ecosystem processes. Our major hypothesis is that the spatial distribution of sources and sink “patches” within the watershed, interacting with climate variability, strongly influence watershed function and resulting linkages with the estuary. Because our basin lies on a shallow-sloped geological setting, geomorphological changes associated with relatively small modifications (i.e. road crossings, beaver dams) can have a large influence.

Under this question, we explore how human activities and climate alter spatial heterogeneity and connectedness in an urbanizing watershed. We hypothesize that spatial arrangement of urban land cover and infrastructure, relative to hydrologic flow paths, and intersections with hotspots of retention (e.g. wetlands), are important factors defining nutrient delivery to the surface water network. Hence, urbanization patterns strongly affect biogeochemical fluxes through river systems and delivery to the coastal zone.



Connectivity between patches is governed by hydrological factors, such as flow quantity and timing, which are influenced by land and water use within and across basin boundaries, as well as legacies of such use (Bain et al. 2012a, b; Wollheim et al. 2013). Thus, our work has focused on understanding the controls of spatial arrangement of patches on land and in water, and quantifying connectivity by understanding hydrological changes and linkages among aquatic patches.

HUMAN IMPACTS ON LAND COVER AND HYDROLOGY

We have completed very high resolution mapping (0.5m) of the location of key terrestrial patches and socio-ecological processes (Polsky et al. 2012; Giner et al. 2014), with associated applications focusing on urban infrastructure, land cover (imperviousness, lawns; Fig. 5), and water management (lawn watering rates, water-use restrictions, location of water withdrawals) (Harris et al. 2012a, b; Polsky et al. 2012; Giner et al. 2013; Runfola et al. 2013). High resolution is essential in this watershed to account for accurate location relative to flowpaths due to shallow slopes. The inclusion of the sociological data is very important as land cover alone does not adequately describe terrestrial patch characteristics because of differential management. For example, the spatial distribution and size of lawns are best explained by population density, which is town specific. Further, rates of lawn watering and fertilizer application also vary across the region, again driven by socioeconomic factors. This approach developed for PIE has been used by co-PI Polsky as a

platform for similar work in other areas (Gober et al. 2012; Harris et al., 2012a, b; Foo et al. 2013; Larson et al. 2013; Polsky et al., 2014).

Spatially distributed hydrology modeling that integrates the location of different urban patches in the watershed indicates that human activities have led to higher flows throughout much of the river network (Wollheim et al. 2012). Model results show that increased runoff from urban headwater catchments occurs because impervious surfaces increase storm runoff and reduce

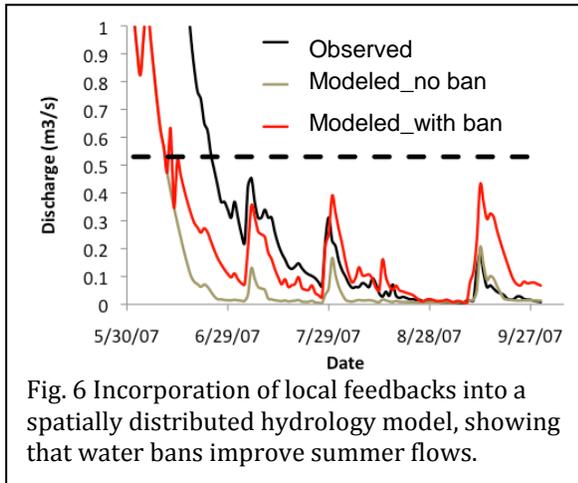


Fig. 6 Incorporation of local feedbacks into a spatially distributed hydrology model, showing that water bans improve summer flows.

catchment ET, lawn watering increases soil moisture levels and thus capacity to absorb rainwater, and septic waste management uses water transferred to the catchment from the river mainstem or from outside the basin (Wollheim et al. 2013; Claessens et al. 2006). However, at the scale of the large rivers, this wetting is offset by water withdrawals, so flows measured at the mainstem gauging stations are similar (annual) or less (summers) than in preindustrial times. These spatially distributed findings are consistent with our previous whole watershed water budgets (Claessens et al. 2006) and have important implications for characterizing terrestrial-aquatic linkages, upstream-downstream connectivity, and the role of aquatic nutrient sinks.

Incorporation of socio-ecological feedbacks into hydrological models indicates that such feedbacks are influencing hydrological conditions and therefore watershed estuarine connectivity (Wollheim et al. 2012, 2013, Fig. 6). For example, our modeling indicates that water bans enacted by communities that rely on local water are improving summer flow conditions in the mainstem, and are therefore an effective feedback mechanism (Fig. 6). Polsky has examined how water bans are increasing in communities in eastern MA (Hill and Polsky 2005, 2007; Polsky et al. 2009; Milman and Polsky, in prep). Water bans are a local, short time-scale feedback. Longer term socioecological feedbacks, such as alterations to interbasin transfers, are also at work, further improving flow conditions. These feedbacks are resulting in a decline in residential dependence on local water, reduced interbasin water export, and reduced reliance on local water sources in favor of regional services (Wollheim et al. 2013).

Historical reconstruction of water and nutrient budgets indicates that watershed-estuarine connectivity is changing over time due to ongoing regionalization of the water supply by communities nearby and within the watershed. Net interbasin transfers out of the watershed averaged ~20% of mean annual runoff for much of the 20th century (Wollheim et al. 2013). Negative impacts such as rivers drying and fish kills, which occur particularly during summer low flows, have contributed to decision making that lead to declines in net water use. Through regionalization of water supply, more towns within the basin are now importing water from existing urban infrastructure of Boston. In contrast, similar decisions have not been made regarding nitrogen loading, which continues to increase. There is continued reliance on watershed ecosystems for N removal, with only limited construction of sewer systems that export N from the basin. Watershed N removal rates continues to remain high, independent of changes in loading (i.e. no evidence of saturation), but are currently largely driven by variability in discharge (Wollheim et al. 2013; Morse et al., in review).

CONNECTIVITY IN THE RIVER NETWORK

We continue to quantify longitudinal (upstream-downstream), lateral (channel-surface transient storage), and vertical (channel-hyporheic) connectivities within the river network

(Wollheim et al. 2008; Stewart et al. 2011; Briggs et al. 2010; Smith and Mather 2013; Lawrence 2014). In our watershed, the return of beaver is having a particularly large impact on connectivity. The North American beaver is a well-studied ecosystem engineer (Rosell et al. 2005) that can dramatically modify aquatic habitats (e.g. Johnston and Naiman, 1990). However, the role of beaver dams and other physical discontinuities has not been quantified at riverscape scales (Burchsted et al. 2010). Beaver dams are widespread and are increasing aquatic heterogeneity in the Ipswich and Parker R. watersheds. Along the Ipswich mainstem, 1.1 beaver structures occur every kilometer of river length, with ~50% of water elevation change controlled by beaver dams (PIE unpublished data). By quantifying in-stream habitat and fish assemblages above and below all beaver dams and at select control sites within the entire Fish Brook stream network of the Ipswich River, Smith and Mather (2013) found that beaver dams altered habitat within streams by changing stream width, depth, velocity and substratum. As a result, beaver dams increase habitat heterogeneity and help maintain native stream fish biodiversity.

We are also conducting hydrological studies to understand how the connectivity between stream channels and both surface transient storage (STS) zones and hyporheic transient storage (HTS) changes with stream size (Briggs et al. 2009, 2010). Briggs et al. (2009) developed a new technique for estimating hydrologic parameters of two transient storage zones within stream channels, and then quantified changes with increasing stream size (Briggs et al. 2010). They found that both vertical and lateral connectivity is fairly constant with increasing stream size within reaches with natural channel banks. Connectivity with surface transient storage (side pools) was much greater than with the hyporheic zone. However, modeling work indicates that at the river network scale, the probability of encountering the hyporheic zone increases. Because residence times are much longer in hyporheic zones than in surface transient storage, at network scales the HTS is likely to have a strong impact on biogeochemical fluxes (Stewart et al. 2011). We are now extending this work to fluvial wetlands and floodplains, which are abundant and increasing due to beaver activity.

We have begun analysis of terrestrial and aquatic heterogeneity using new LiDAR data, which was flown in spring 2011. Initial analysis made by the PIE group discovered errors in the original data product, so our analyses were temporarily delayed. We will be using the high resolution LiDAR derived digital elevation map (DEM) in conjunction with the high resolution terrestrial maps of land cover (Fig. 5) to quantify flowpath distances between potential source areas for water and nutrients and receiving surface waters. Preliminary results indicate that actual flow path distances are 2.5x longer than straight line distances to surface water, which has large implications for nutrient retention in the catchment. We will incorporate potential terrestrial nutrient sinks (wetland soils) that occur between sources and river systems, as well as information regarding management. We can thus characterize mean distance of sources and the probability of encountering sinks. We plan to instrument and sample (flow, conductivity, nutrients, sediments) several headwater catchments that vary with source-sink position, which we hypothesize contributes to the unexplained variability in loading concentrations in headwater streams. We will conduct similar analyses of aquatic heterogeneity in relation to road crossings, and other hydraulic structures. We are collaborating with the Parker-Ipswich-Essex River Restoration (PIE-Rivers) group, which is conducting a census of road crossings and habitat impacts to identify inadequate road culverts. Mapping of beaver pond locations will also be used (Smith and Mather, 2013) to quantify at the network scale the impact of ponds relative to their position within the network.

Theme 1 Q1B How will tidal marsh area, configuration, and elevation (relative to mean sea level) change with rising sea level and changes in sediment delivery?

Changes in sea level are important to the biological, sedimentological, and geochemical functioning of salt marsh ecosystems, as well as to the spatial arrangements and connectivity of

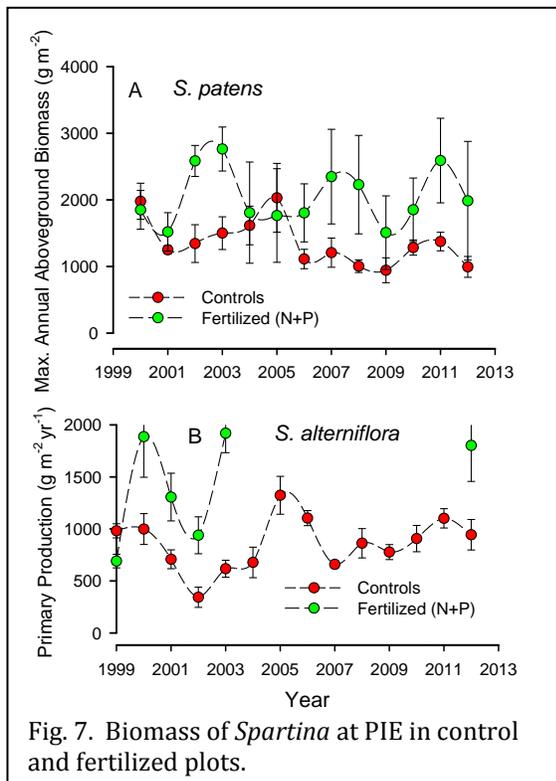


Fig. 7. Biomass of *Spartina* at PIE in control and fertilized plots.

Net annual primary production of both *S. patens* and *S. alterniflora* at PIE has been quite variable through the years (Morris et al. 2013, Fig. 7). We have found a significant correlation between *S. alterniflora* aboveground net primary production and MHW at Plum Island ($r^2=0.37$, $p=0.02$) (Fig. 8). The same relationship has not been found for *S. patens*.

The duration of flooding (i.e. marsh hydroperiod) is a critically important variable for coastal wetland plants. It is determined by



Fig. 9. A marsh "organ"

habitats within them. The ability of the marsh to respond to relative sea level rise (RSLR) is highly dependent on interactions among various factors, such as sediment and nutrient supply, changes in hydrology and temperature, and others which collectively determine the elevation, vegetative composition and extent of the marsh platform. Our research is guided by a theoretical model, the Marsh Equilibrium Model (MEM) that uses feedbacks among the plant community, sediments and tides to predict how the relative elevation of a salt marsh is affected by rising sea level (Morris et al. 2002; Morris et al. 2012). At the heart of this model are the feedbacks among hydroperiod, primary production, and sedimentation that together maintain relative marsh elevation within the tolerance of marsh vegetation, provided that the rate of sea level rise is below a critical limit. A goal of our research is to determine the value of this critical limit and the factors that control it.

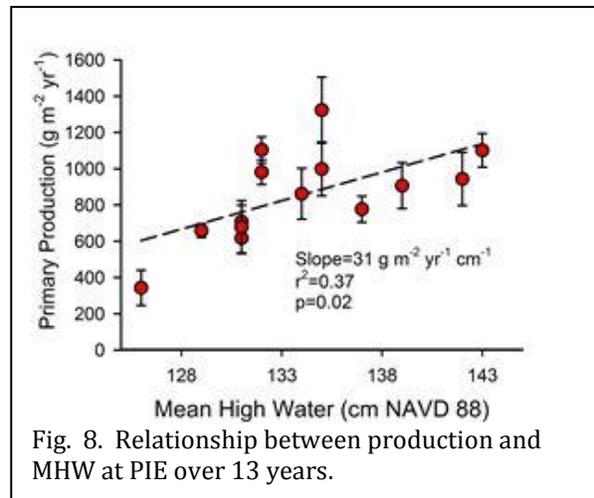


Fig. 8. Relationship between production and MHW at PIE over 13 years.

the relative elevation of the marsh within the intertidal zone. For marsh elevations between MHW and MSL, depth below MHW is a good proxy for hydroperiod and accounts for changes in both mean sea level and tidal amplitude. The sensitivity of vegetation to changes in sea level varies as a function of elevation within the intertidal zone, and should be greatest near the upper and lower vertical limits of growth. Growth should be greatest in the middle of the range, and less sensitive to change.

The effect of hydroperiod is being tested using planters constructed of PVC pipe, termed "marsh organs", placed in Plum Island (Fig. 9) and North Inlet, South Carolina, salt marshes to simulate growth of vegetation at different relative elevations. Pipes were filled with sediment taken from the adjacent mudflat and planted in

the spring with *S. alterniflora* plugs taken from the marsh. All of the pipes had open bottoms resting on tidal mudflat, and their lengths differed by approximately 15 cm between rows (6 pipes per row). The weights of harvested plants varied with relative elevation in both estuaries (Fig. 10) and growth responses in these bioassays are consistent with those of *in situ* net primary production to anomalies in MHW, and conclusively demonstrate the feedback between growth and relative elevation. This important feedback helps to explain how marshes track rising sea level.

The North Inlet growth response shows upper and lower limits and a mid-range optimum (Fig. 10). This is a good example of Shelford's Law of Tolerance (1931). With respect to *S. alterniflora*, at the high end, osmotic stress from hypersalinity or drought most likely limits growth, while the lower limit is probably a function of hypoxia. The direction of the response will depend on the relative elevation, which can be either superoptimal or suboptimal. At suboptimal elevations the response of growth to a rise in sea level should be negative and destabilizing, except in situations where high sedimentation rates build marshes. The suboptimal side of the curve is destabilizing because an increase in sea level will decrease primary production, leading to a decline in sediment organic matter accumulation and accretion of mineral sediment. Plum Island marshes are closer to the local MHW level, a superoptimal elevation for growth, than are most North Inlet marshes and will be more tolerant to some rise in MHW.

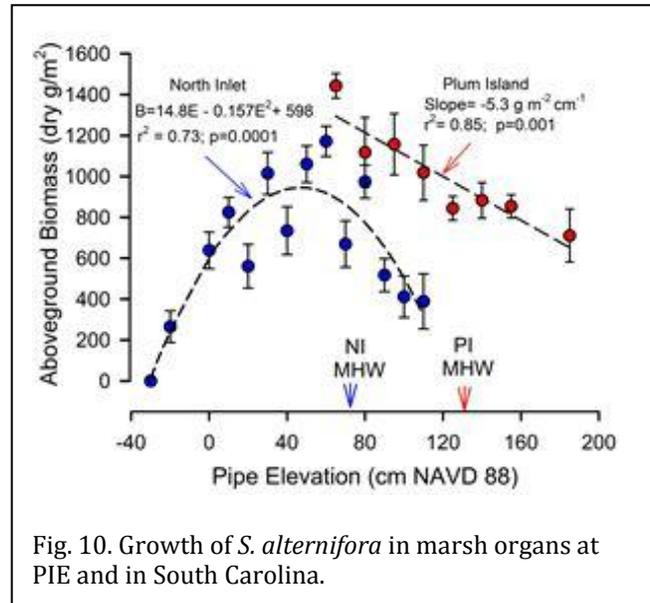


Fig. 10. Growth of *S. alterniflora* in marsh organs at PIE and in South Carolina.

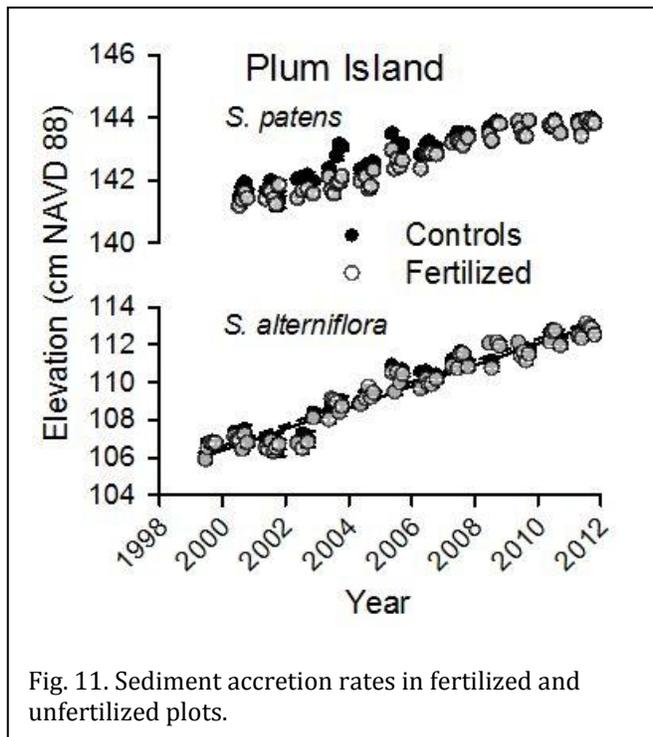


Fig. 11. Sediment accretion rates in fertilized and unfertilized plots.

We are now examining whether interannual variations in net ecosystem production track above ground primary production. We have installed two eddy covariance systems to measure CO₂ fluxes (see progress report and later sections).

RESPONSES TO NUTRIENTS

Experimental plots started at Plum Island in 1999 have been treated with nitrogen and phosphorus fertilizer, and both *Spartina* species responded positively to fertilization after 1 year. Fertilizer has been added approximately monthly from April through September. In plots of *S. alterniflora* treated with both nitrogen and phosphorus, biomass increased nearly 50% (Fig. 7B). The biomass on fertilized plots of *S. patens* increased 62% when treated with nitrogen and phosphorus (Fig. 7A), and 45% and 31% when treated solely with nitrogen or phosphorus, respectively. The enhanced

production in the fertilized plots shows no indication of increasing further or declining, even after 13 years of fertilization.

We have combined fertilization studies with measurements of marsh elevation in marshes in Plum Island and North Inlet. The change in elevation (from the slope of a linear regression) in the Plum Island *S. alterniflora* marsh has been 0.57 cm yr⁻¹ in both reference and fertilized plots (Fig. 11). In the *S. patens* marsh, which is almost 40 cm higher in elevation than the *S. alterniflora* marsh, the change in elevation has been 0.22 cm yr⁻¹ in the reference site and 0.25 cm yr⁻¹ in fertilized plots. In neither marsh type did the control elevations differ from those in the fertilizer treatments. MEM would suggest that fertilized plots should gain elevation by trapping more sediment. However, Plum Island is an estuary with low concentrations of suspended sediments and its marshes are perched high in the tidal frame (mean high water = 1.3 m) with limited access to sediment. The increase in marsh elevation at Plum Island appears to be largely driven by organic matter accretion

from roots and rhizomes and a small amount of suspended organic matter derived from the erosion of peat that is occurring around the margins of tidal creeks. Hence, Plum Island marshes are cannibalizing themselves.

Nutrient concentrations in control plots and plots that have been continuously fertilized with N and P since 1999 generally increase with depth. There is a remarkable difference in nutrient (NH₄ and PO₄) concentrations between the *Typha* site and the *Spartina* sites (Fig. 12).

Porewater ammonium concentrations at the *Typha* site in all plots average about 11 μM, but are always higher at the saltwater sites, reaching 274 μM at depth in the fertilized *S. patens* marsh

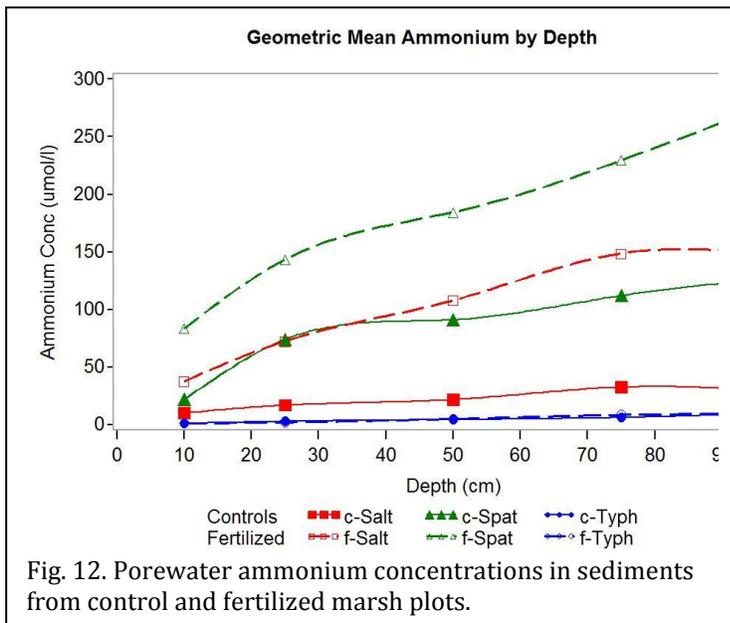


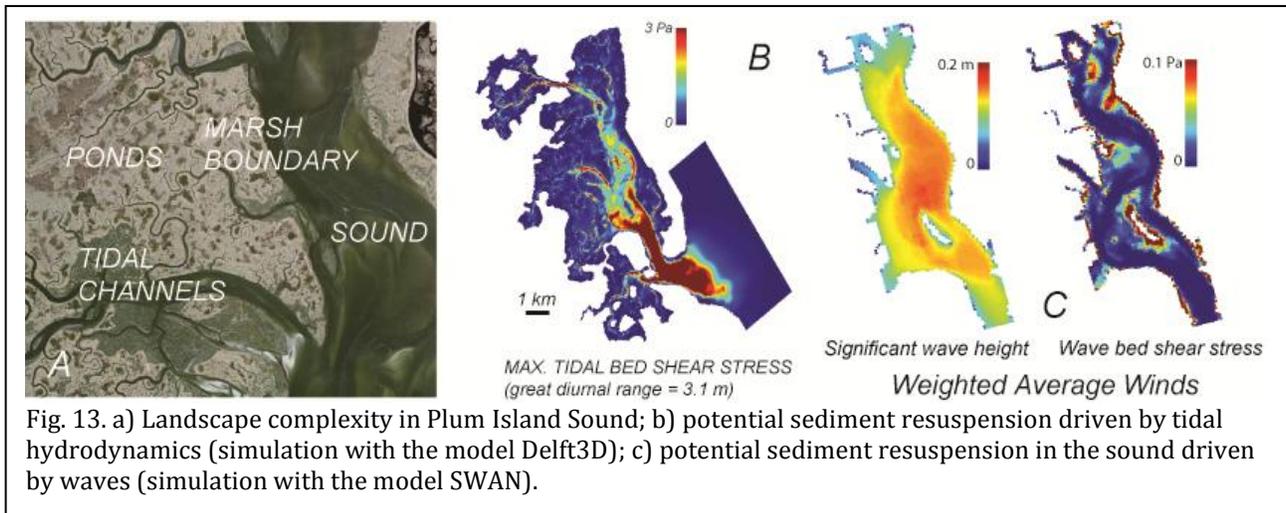
Fig. 12. Porewater ammonium concentrations in sediments from control and fertilized marsh plots.

and with intermediate concentrations in the *S. alterniflora* marsh. The same relative ranking of porewater ammonium among sites is true of phosphate. Although there are large differences between sites, porewater nutrient concentrations in the salt marshes are orders of magnitude greater than what we see in the surface water of creeks in the estuary, demonstrating the importance of any porewater drainage as a significant net supply of nutrients to the creeks and open estuary.

COMPLEXITY OF THE SALT MARSH LANDSCAPE

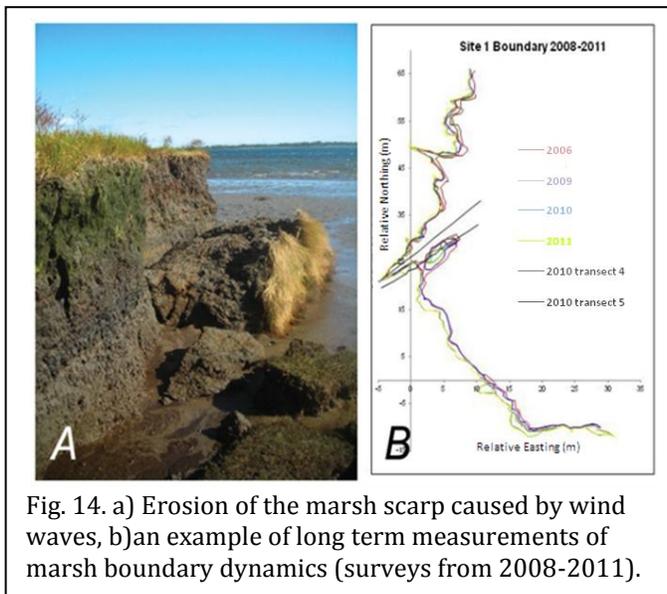
PIE marshes are a complex succession of ponds, channels, and vegetated surfaces at different elevations with an irregular boundary that separates them from Plum Island Sound (Fig. 13a). This landscape complexity needs to be accounted for to understand the long-term fate of the salt marsh and to determine the spatial distribution of related ecosystems. Recent research indicates that salt marshes are relatively stable along the vertical direction *if* enough sediment is available (Kirwan et al. 2010), whereas they are inherently unstable along the horizontal direction (Mariotti and Fagherazzi 2010). The availability of sediments plays an important role in marsh survival, and with limited riverine sediments entering the estuary, sediments eroded from shorelines are likely the primary source for the marsh platform at PIE. The only mechanism that can counteract lateral erosion by waves is seaward marsh expansion driven by deposition of large amounts of sediment in sheltered areas (Mariotti and Fagherazzi 2013).

Marsh deterioration is also a complex phenomenon, often involving the formation and enlargement of ponds at the marsh surface and the widening of tidal creeks (Hartig et al. 2002, Fagherazzi and Mariotti 2013). In a series of long-term studies and models (Fig 13b,c) we are accounting for this landscape complexity at Plum Island Sound.



LATERAL DYNAMICS OF SALT MARSHES

We have been collecting data on the dynamics of the marsh boundary for five years at three locations in PIE, including geotechnical parameters and the stabilizing effect of roots (see Fig. 14). We are planning an instrument deployment to quantify the effect of waves and storm surges on



scarp erosion. The goal of this task is to determine the processes responsible for the long-term erosion of the marsh and resulting effects on the overall partitioning of the intertidal area between salt marshes and tidal flats (Fagherazzi et al. 2006, 2007). In 2013 we started a set of measurements in areas where *S. alterniflora* is encroaching on tidal flats in order to determine the conditions under which stable vegetated surfaces can form, which counteract marsh erosion. The collected data will refine an already existing model for marsh boundary evolution (Mariotti and Fagherazzi 2010). A similar effort is underway at VCR-LTER led by Fagherazzi and Wiberg, so this project represents an example of cross-site comparison, shedding light on the different response of macrotidal and microtidal systems to global change.

COUPLING BETWEEN MARSHES AND SURROUNDING TIDAL FLATS

Future 3D modeling at PIE will build off of the framework established by the NSF funded LENS project. In particular, Fagherazzi's team is modeling the co-evolution of salt marshes and tidal flats by quantifying the exchange of sediments between Plum Island Sound and the marshes. To this end the 3D sediment transport model Delft3D was set up for the entire Plum Island System, and coupled to the wave model SWAN (see Fig. 15). The model will be tested using data collected from

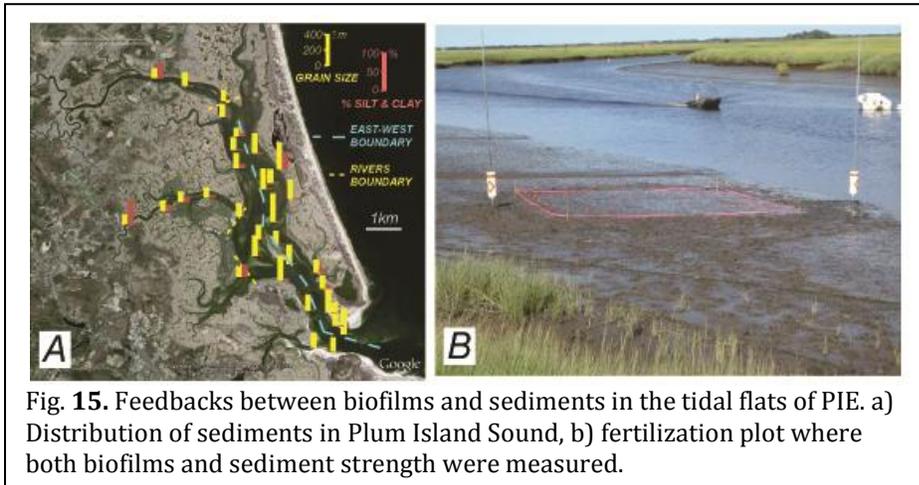


Fig. 15. Feedbacks between biofilms and sediments in the tidal flats of PIE. a) Distribution of sediments in Plum Island Sound, b) fertilization plot where both biofilms and sediment strength were measured.

acoustic doppler current profilers deployed within the tidal channel network and in the sound, and by collecting suspended sediments and nutrients. We are also determining the potential resuspension of tidal flat sediments, and how this source of material might be transported to the marsh platform, thus

promoting marsh accretion. In particular, we are studying how biogeochemical processes (e.g. formation of biofilms) affect sediment mobilization and stability in tidal flats, and how sediment availability in these systems might change under different storm conditions and different rates of sea level rise.

MORPHODYNAMIC EVOLUTION OF TIDAL CHANNELS DISSECTING THE MARSH PLATFORM

Recent observations indicate that the widening of marsh creeks is a leading process for the deterioration of marshes (Hartig et al. 2002; Deegan et al. 2012). While sea level rise has long been thought to affect marshes, long-term experimental manipulation of nutrients in tidal creeks (TIDE Experiment; Deegan et al. 2007) has shown that increased nutrient loading may be a driving factor in the loss of creek bank marsh and the widening of channels (Deegan et al. 2012). Nutrient enrichment can affect soil properties such as decomposition rate, root mass, porosity, bulk density, and tensile strength (Turner 2011, Deegan et al. 2012), which in turn can affect the susceptibility of the marsh-edge to erosion (Fagherazzi et al. 2013). Positive feedbacks with geomorphic features, such as cracks and slumps, and hydrology/hydrodynamics may accelerate decomposition, leading to continued loss of marsh edge and the widening of creeks. Measuring change over time of geomorphology, creek bank characteristics and plant distributions can test both nutrient and sea level rise hypotheses.

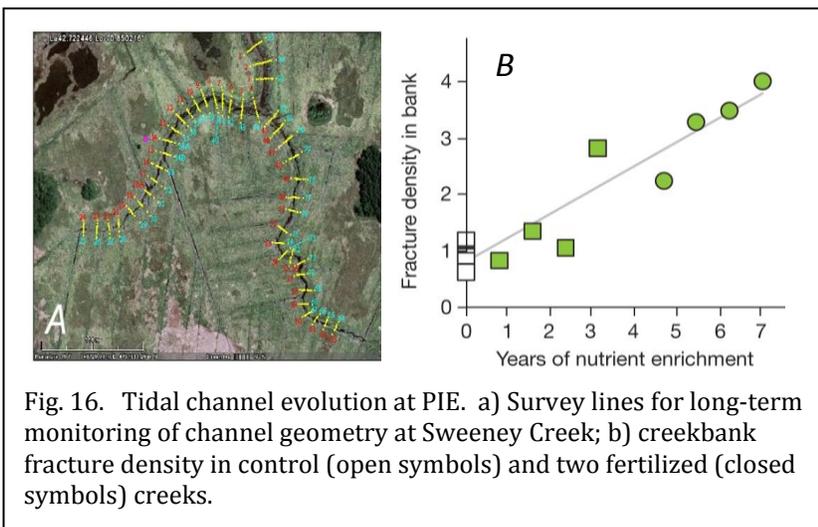


Fig. 16. Tidal channel evolution at PIE. a) Survey lines for long-term monitoring of channel geometry at Sweeney Creek; b) creekbank fracture density in control (open symbols) and two fertilized (closed symbols) creeks.

We have been measuring erosion of channel banks in fertilized and reference saltmarsh creeksheds and we will add more sites in the near future. The loss of marsh edge with fertilization was not apparent until after 6 years of increased nutrients, suggesting long-term monitoring is essential to understanding this phenomenon. Data collected in the field will drive high resolution models of channel hydraulics and sediment transport. The models simulate

the long-term evolution of tidal channels, and how they respond to sea level rise, sediment availability, and nutrient loading (Fagherazzi and Furbish 2001, D'Alpaos et al. 2006) (See Fig. 16).

Theme 2 Q2A. Have changes in the spatial arrangement and connectivity of aquatic patches in the watershed led to reduced longitudinal and increased lateral connectivity? Has altered connectivity resulted in changes in material flows, consumer biodiversity, and mobility of fish?

Using the hierarchical patch dynamics framework, we are investigating how the processes within component elements (i.e. patches) vary, and how these processes then aggregate to influence biogeochemical patterns at the broad spatial scale of the entire river network. We explore the emergent properties resulting from the meta-structure (location, abundance, and connectivity of patches) using a river network modeling framework. In particular, we have focused on quantifying and integrating heterogeneity in the four dimensions of connectivity (Ward 1989): longitudinal, lateral, and vertical, all of which vary over time (the fourth dimension).

We have focused primarily on aquatic ecological processes, quantifying the variability of biological demand for nutrients. We hypothesize that heterogeneity is associated with biogeochemical hotspots. We have used our PIE LTER long-term biogeochemical data set (1993-2010) to examine how nutrient fluxes to the estuary have changed over time (Morse and Wollheim, in review). We originally hypothesized the increase in watershed population between 1990 and 2010 (a 19% increase) and associated land cover and N loading over the period would have resulted in increased N export. However, surprisingly we found no significant long term trends, in part because interannual variability in flux was large and driven by precipitation variability (Fig. 2).

The lack of a trend may be because nutrient fluxes on a per unit area basis from the entire watershed were already relatively high, suggesting that suburbanization had already led to elevated exports by 1993, and that additional increases were not detectable given the strong climate control. Overall retention of N in the watershed during the period is high (80-90%), but annual runoff drives variability in watershed N retention (Wollheim et al. 2013). An additional factor leading to the lack of change may be the increased abundance of beaver ponds. Modeling results suggest increased N retention by beaver ponds could explain why watershed nutrient export is not currently increasing despite higher nutrient loading (Fig. 17).

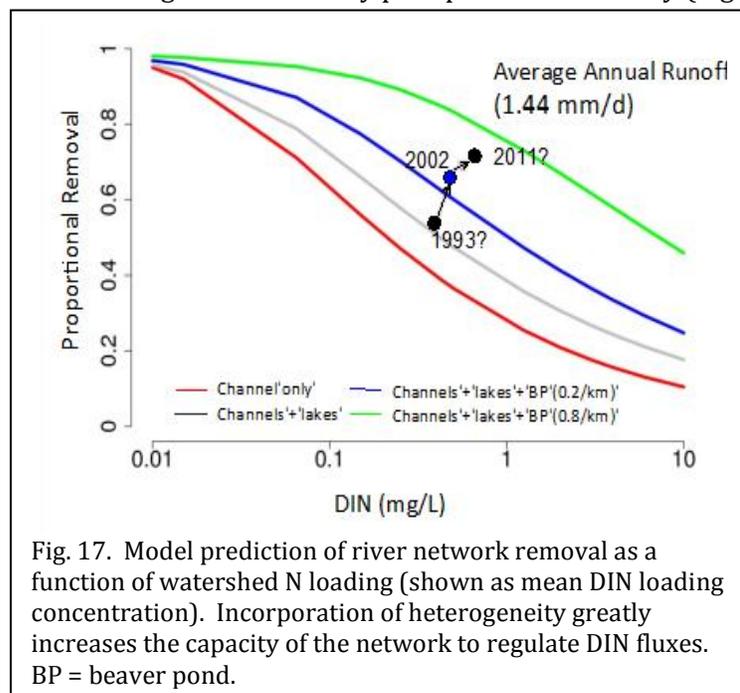


Fig. 17. Model prediction of river network removal as a function of watershed N loading (shown as mean DIN loading concentration). Incorporation of heterogeneity greatly increases the capacity of the network to regulate DIN fluxes. BP = beaver pond.

Biogeochemical reaction rates (i.e. demand for nutrients) within fluvial patches are an important factor defining the potential role of patch types at the river network scale. We have therefore quantified reaction rates in a variety of habitat patches including stream channels of various size, surface transient storage within channels, fluvial wetlands (Wollheim et al. in press), and streams of varying N and P stoichiometry. We found that nitrate reaction rates in larger streams differed from each other but were consistent with previous estimates from headwater

streams. Nitrate reaction rates in surface transient storage (STS) zones within larger streams were higher than rates estimated at the whole-stream scale. Nitrate reaction rates in fluvial wetlands were higher than in streams at elevated nitrate concentrations. Both streams and wetlands demonstrated efficiency loss at high N concentrations. Our data so far demonstrate that STS, particularly fluvial wetlands, are hotspots of biogeochemical activity and should be integrated into network scale biogeochemical models, as suggested by Helton et al. (2010).

While potential reaction rates from individual patches may be high, they may only translate into hotspots at basin scales if they are connected to areas of high nutrient inputs and are not source limited. For example, a fluvial wetland dominated reach in the Upper Ipswich watershed was able to entirely strip nitrate entering from a suburban headwater catchment. This indicates high reaction rates and high connectivity with advective inputs. High nitrate reactivity is clearly related to low oxygen conditions induced by high rates of metabolism as water flows through the wetland dominated system. Ongoing work is quantifying connectivity, metabolism, and the dominant processes and sub-patches contributing to N removal. We are also expanding this analysis to understand the link between aquatic metabolism and nutrient removal in other areas with different configurations of beaver pond and fluvial wetland distribution.

Unlike many estuaries in the U.S., much of the urbanized land in PIE watersheds is concentrated in the headwaters, some distance upstream of the estuary. This spatial arrangement allows for many potential interactions between nutrients delivered from headwater sources and sinks in the river network. One of the key findings from our work is that although hyporheic zones are not major zones of N removal at the reach scale they contribute significantly to N removal at the larger river network scale. This is because at network scales the probability of a nutrient molecule entering the hyporheic zone increases considerably, and once in these zones residence times are long. Further, heterogeneity within the river network greatly enhances network scale N removal (Stewart et al. 2011). As a result, PIE estuaries have been spared most of the adverse impacts of watershed N loading which are common in other nearby systems. We are now using this network scale modeling to comparing N removal ecosystem services of different watersheds throughout New England (Whittinghill et al. 2013).

Heterogeneity is a fundamental feature of ecological systems that can alter the outcomes of species interactions and ecosystem processes (Scheiner and Willig 2011). Ecological theory suggests that the diversity of species in an ecosystem is positively related to habitat heterogeneity (e.g. Dodd, 2009; Munguia et al. 2011), but the amount and configuration of heterogeneity that maintains biodiversity within ecosystems is not well understood. Abundant beaver dams in PIE watersheds provide opportunities to address this question. Beaver dams are a source of heterogeneity that can influence hydrology (Andersen and Shafroth, 2010), biogeochemistry (Naiman et al. 1994), assemblages of invertebrates (Fuller and Peckarsky 2011) and fish (Kemp et al. 2012). At 15 beaver dams in Fish Brook, a tributary of the Ipswich River, diversity and abundance of fish around beaver dams were positively related to habitat heterogeneity. Faster water and the coarser substratum below beaver dams increased the amount of fluvial habitat available to native fish (Smith and Mather 2013). This alteration can be critical for fish with life histories that depend on flowing water and hard substrata. Because biodiversity is declining more rapidly in aquatic than terrestrial systems (Jelks et al. 2008), these results are timely for providing scientific insights into maintaining functioning ecosystem. They provide guidance for efforts aimed at maintaining biodiversity throughout stream networks, on the design of catchment monitoring, and provide a scientific basis for decisions regarding the removal of beaver dams.

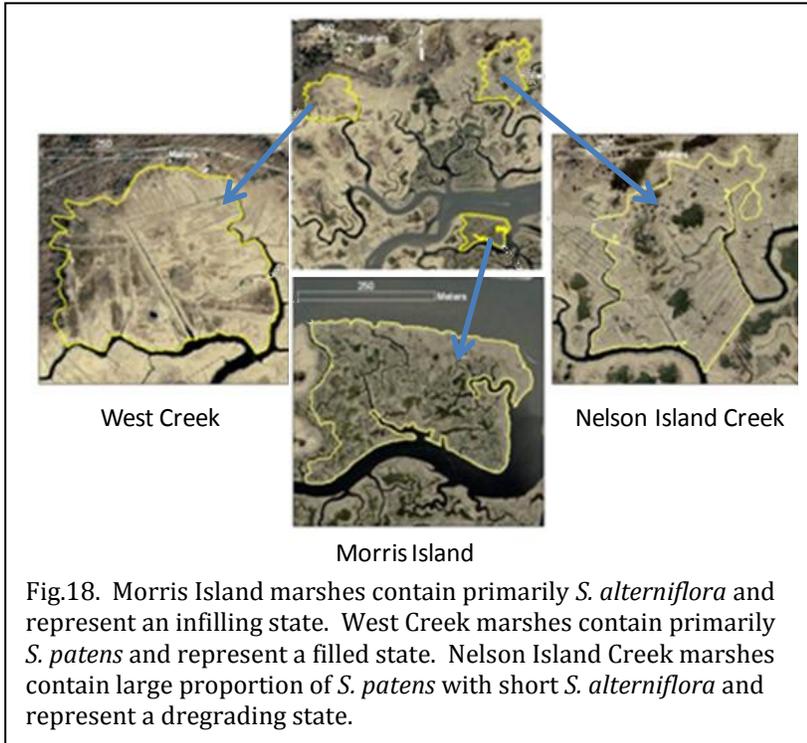
Theme 2 Q2B. How do changes in riverine inputs, marsh productivity, and sea level interact with the arrangement and connectivity of patches in the estuarine seascape to influence C and N biogeochemistry?

The relatively long (24 km), linear orientation of the Plum Island estuary (60 km²) with its fringing tidal wetlands (39 km²), widely distributed riverine inputs (7 sources over 23 km), and large tidal range leads to a system where the relative influence of watershed inputs and fringing wetlands varies tremendously along the length of the estuary. We learned early in our studies that the spatial arrangement of watershed-estuarine connectivity played a major role in defining the estuarine seascape, the distribution of habitats, and even the distribution of marsh. Importantly, 87% of river discharge enters in the lower half of the estuary, but estuarine water residence times and salinity distribution are controlled almost exclusively by the 13% of discharge that enters at the head of the estuary (Vallino and Hopkinson 1998). The relative distribution of marsh and tidal waterbodies is another important landscape feature that plays a major role in controlling ecological processes. The ratio of marsh area to water area is high in the upper 6 km of the estuary, reaches a maximum between 7 and 12 km, then decreases in the lower reaches of the estuary in Plum Island Sound.

During PIE I and II, our research findings clearly demonstrated the importance of changes in the coupling between the watershed and estuary in controlling estuarine ecological processes and biogeochemistry. During the spring, and often in the fall, the river and the estuary are highly connected, with salinity, material inputs, and water residence time determined by river discharge. During the summer and winter, internal processes increase in importance and connections between the marsh and the estuary dominate. Three major findings were: 1) Annual shifts in surface water and porewater salinity due to huge annual swings in river discharge cause major changes in benthic NH₄⁺ flux, denitrification, and nitrification in the upper estuary while the lower estuary is largely unimpacted (Weston et al. 2010; Giblin et al. 2010; Hopkinson et al. 1999; Bernhard 2007). During spring, rivers dominate nutrient inputs while in summer benthic ammonium release in the upper-to mid-estuary becomes the primary N source (also see poster by Davenport); 2) The combination of river discharge in the upper estuary and tidal mixing control water residence time, which in turn controls spatial patterns in phytoplankton and bacterial populations. Residence time further plays a major role in foodweb structure. In the upper estuary, when residence time is long, a planktonic foodweb structure dominates, while in the lower estuary, where residence time is short and controlled by tidal mixing a benthic foodweb structure dominates (Holmes et al. 2000; Hughes et al. 2000); 3) Spatial differences in water residence time interact with the spatial distribution of watershed, marsh, and ocean organic carbon (OC) sources to control the pattern of metabolism in the estuary. Terrestrial OC fuels metabolism only in the upper estuary in summer, when temperature is high and residence time long. During the rest of the year material is rapidly flushed through the estuary. Oceanic phytoplankton fuels metabolism in the lower estuary, especially in spring when offshore blooms come in with tides. The region of greatest heterotrophy is in the mid-reaches of the estuary, and here metabolic mass balance analyses and $\Delta^{14}\text{C}$ - and $\delta^{13}\text{C}$ evidence indicate fringing marshes to be an important allochthonous source (Raymond and Hopkinson 2003; long-term monitoring data). This is the region where the marsh:water ratio and drainage density are highest in the estuary. Our initial calculations suggest that DOC input from drainage of the marsh edge porewaters is many times greater than total DOC loading from the Parker River (Gardner and Gaines 2008).

These initial findings of how changes in river discharge and sea level interact with key habitats along the length of the estuary to control ecological processes now lead us to focus more on how changes in the distribution of marsh and aquatic habitats control ecological processes. We are examining our long-term record of estuarine metabolism to determine the importance of changes in the frequency and duration of marsh flooding and variations in marsh edge drainage. Not only do we see great differences in marsh:water area along the length of the estuary, we also see great differences in the density and size of ponds on the marsh surface, and in the density of tidal creeks. Many of these changes are occurring rapidly, especially the number and size of marsh

ponds and the density of tidal creeks, which translates directly to substantial changes in total “edge” and marsh edge drainage.



PONDING

Aerial photos readily show that ponds on the marsh surface are primarily limited to the lower 15 km of the estuary, and are most abundant in the marshes adjacent to Plum Island Sound. Comparisons of maps and photos over time show that there has been a dramatic increase in ponding over the past 60 yrs, but these changes are not distributed uniformly (Fig 18). For instance, pond coverage and size range from about 50 m² ha⁻¹ and 20 m², respectively, in the West Creek marshes to about 1200 m² ha⁻¹ and 90 m² in the Nelson Island marshes.

We have begun to examine the metabolism of marsh ponds to better

understand ecological processes involved in their development and the potential importance of ponds on watershed – estuarine connectivity. We want to know how the C balance of a pond influences C balance of the marshes in which they are embedded and how ponds influence the exchange of organic and inorganic C with adjacent tidal creeks. As an integrated measure of total system production (P), and respiration (R), we measure diurnal oxygen changes in pond water (Fig. 19, left) and calculate biological activity after correcting for air-sea gas exchange. We find that ponds have extremely high rates of gross primary production (GPP) (attributable to *Ruppia* and benthic microalgal mats - *Enteromorpha*) but even higher rates of R. Thus most ponds consume considerably more OC than they produce internally (Fig. 19, right). Ponds are also significant sources of dissolved organic matter. When ponds are flooded they can become a source of labile DOM for adjacent tidal creeks.

The formation and enlargement of ponds on the high marsh platform represents a

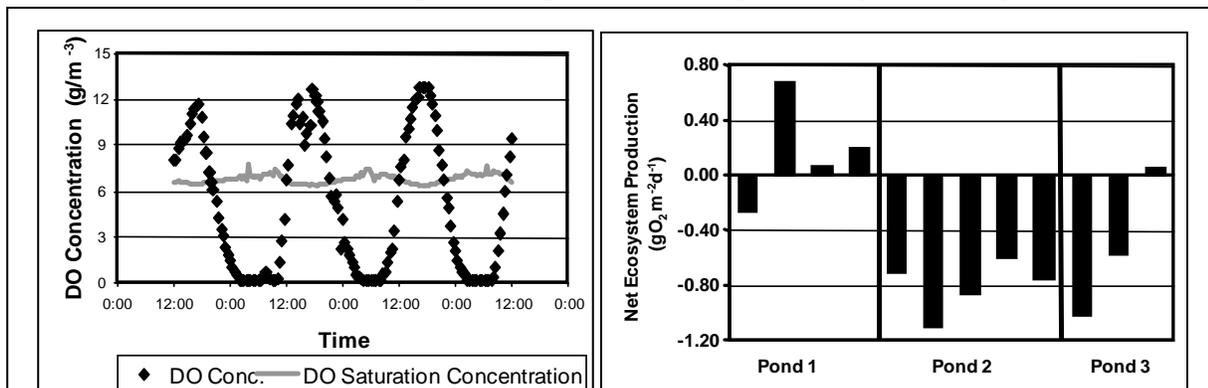


Fig. 19. Diurnal changes in oxygen concentrations (left) show that rates of primary production and community respiration are very high in marsh ponds but the overall net ecosystem production (NEP) for most ponds is negative (right), i.e., consuming more organic matter than produced. Parallel sediment incubations show that it's marsh peat that is being lost and that thru this process ponds increase in depth over time.

significant loss of C stores from marsh sediments that are released to the atmosphere as CO₂, or drain to tidal creeks as dissolved inorganic (DIC) or organic (DOC) carbon. Pond metabolism, coupled with elevation gain by the surrounding marsh, results in ponds increasing in depth. Our calculations suggest that net ecosystem respiration (NEP) accounts for 50% of observed pond deepening. DOC production and loss via flooding represents another potentially important C loss term that we hope to quantify over the next several years.

LINKAGES BETWEEN MARSH PLATFORM AND TIDAL CREEKS

While experiments and modeling (Q1B) suggest that our marshes are currently maintaining elevation relative to SLR, we need to understand the extent to which marsh ponding, erosion, and creek elongation are impacting overall system net ecosystem carbon storage. We are using the non-intrusive eddy covariance method to study the vertical exchange of energy, CO₂ and H₂O between marsh and the atmosphere at a scale (km²) that can capture the changes occurring at larger scales. This method (the flux tower approach) provides continuous flux measurements of net ecosystem exchange (NEE) at the ecosystem scale. While this method has been employed in terrestrial ecosystems for >30 yrs, measurements in tidal, coastal ecosystems have only recently started.

A key uncertainty in this environment is the effect of flooding on NEE. Some have concluded that NEE is lowered during flooding, implying that SLR will decrease marsh sustainability but this is contrary to the results of our “marsh organ” experiments. It is our assumption that metabolism is not reduced during flooding but that respiratory CO₂ enters floodwater rather than the atmosphere and then is exported as TCO₂ during ebb tide as lateral transport (Troxler et al. 2013). We also suspect that flood tide water is enriched with DOC from ponds and marsh porewaters. To quantify the “horizontal” flux of DOC and TCO₂, we have installed instrumentation to measure the fluxes of water, DOC, pCO₂ and pH (which enable TCO₂ to be calculated) in a tidal creek that drains a portion of the flux tower marsh.

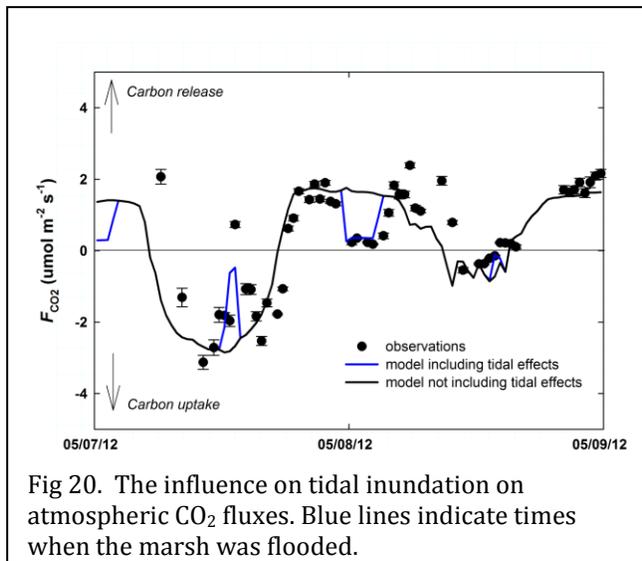


Fig 20. The influence on tidal inundation on atmospheric CO₂ fluxes. Blue lines indicate times when the marsh was flooded.

Tidal influences on NEE are apparent when the high marsh platform is submerged. We observed decreases in fluxes from the marsh during spring tides both during day- and nighttime (Fig. 20). This is primarily due to the temporary reduction of leaf area exposed to the atmosphere and to short-term blockage of diffusion, but does not necessarily imply a stop of photosynthesis or respiration (Winkel et al. 2011). To consider this uncertainty in our estimates of NEE, gross primary production (GPP) and ecosystem respiration, we modeled the fluxes during submergence as follows: One model is fitted to low tide conditions only (maximum fluxes), while the second one is fitted to all fluxes (including minimum fluxes during

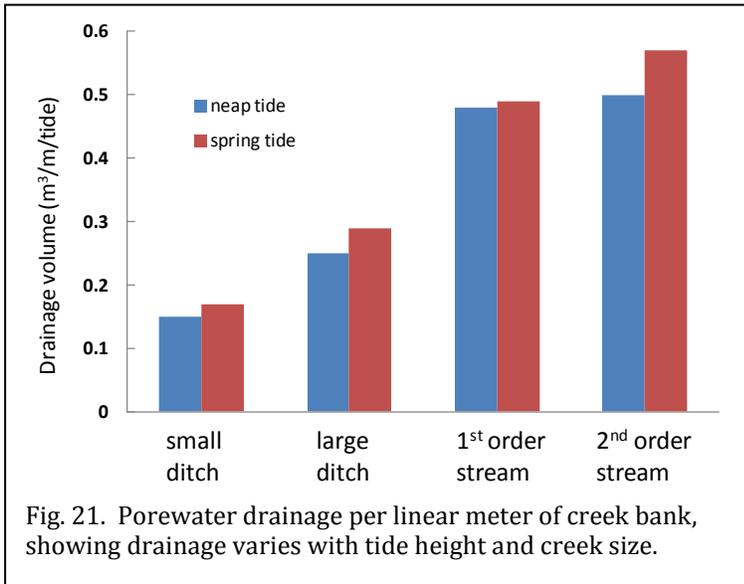
submergence). The difference between these two values can give us an estimate of how great the tidal influence is (Kathilankal et al. 2008). We can then compare these estimates with the fluxes we measure in draining creek water.

We are also examining the linkage between marshes and tidal creeks via tidal flooding and creekbank edge drainage and how that controls C and N biogeochemistry. We have quantified whole creek export of N₂ in reference and fertilized tidal creeks to better understand the relative importance of various habitats within a marsh-tidal creek system. Denitrification produces N₂, and increases in the net tidal creek flux of N₂ (measured relative to argon) can be used to calculate

whole system (marsh platform, creekbank edge, creek sediments) denitrification. We have used this approach to “find” the N missing from a whole marsh/creek fertilization study (see proposal) and we are working on using other noble gases to improve the sensitivity for non-fertilized creeks.

CREEKBANK EDGE

We are beginning to examine our long-term record of marsh creekbank drainage to examine how changes in mean sea level and the frequency and duration of marsh flooding affect drainage volume and to quantify nutrient and OC linkages between marshes and tidal creeks. Surveys in a



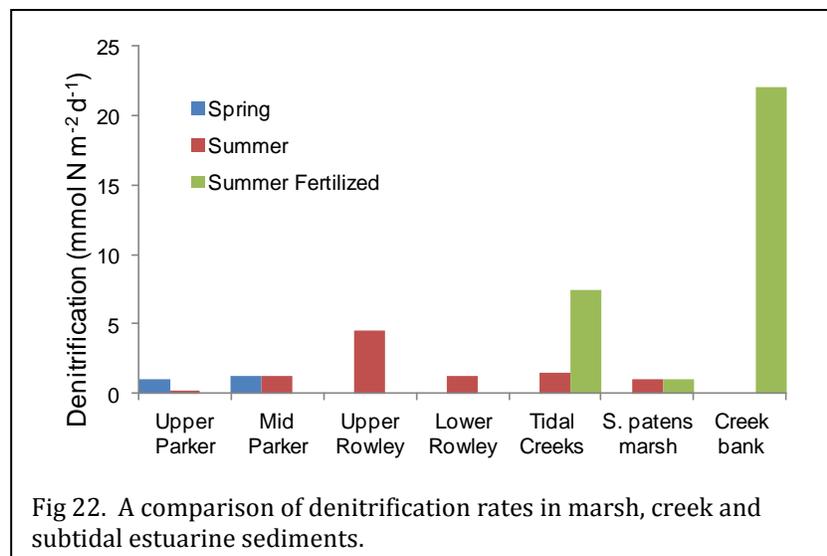
variety of creeks and ditches show that drainage volume is proportional to creek size and daily tidal range: the larger the head of water, the larger the drainage volume (Fig. 21). Additional factors, such as evaporation further contribute to large daily variation in drainage volume. When scaled to the entire estuary, the magnitude of creekbank drainage volume exceeds that of Parker River discharge by a ratio of 8:1.

Our porewater measurements show that the water draining from the marsh (see Q1A) contains substantial concentrations of inorganic N and DOC indicating the

marsh is a source of both constituents for autotrophic and heterotrophic communities in tidal creeks. We clearly see these marsh porewater signals in the water column in both concentrations and in C isotopes. Using porewater and well data we can calculate the flux of carbon and nitrogen from the marsh to creeks. From March to December (unfrozen period) the flux is on the order of 4-20 gN m⁻¹ shoreline and 140-170 gC m⁻¹ shoreline (*Typha* vs *S. patens*). With drainage volume and nutrient concentrations being substantially greater than river fluxes for much of the year, drainage inputs must play a major role in controlling estuarine biogeochemistry and ecological processes.

We note that this is NOT new water entering the estuary, rather it is water entering the creekbank edge during high tide and draining during low tide. But as the concentrations of DOC, NH₄⁺ and PO₄ are substantially higher in creekbank drainage than in the river water entering the estuary, the nutrients become a new source of nutrients for the aquatic system.

The role of creekbank exchange in supplying nutrients to the water column may be reversed in estuaries with high nutrient loading. Experiments in PIE fertilized creeks clearly showed that the creekbank edge is a major hotspot of denitrification.



Indeed, mass balance and $N_2:Ar$ suggest that the rate of denitrification in the creekbank edge under moderate $NO_3^-:N$ loading is 2X higher than in any other creek-marsh habitat (Fig. 22). Extrapolated for a year, this rate of nutrient removal would exceed the average input of ammonium from porewater drainage.

Theme2 Q2C. What are the implications of the configuration and connectivity of different habitat patches and changing drivers on spatial variations in organisms and food webs across the estuarine seascape?

Over the history of the PIE LTER we have empirically tested food web concepts including the relative strength and spatial location of top-down (consumer-limited) and bottom-up (resource-limited) control (Deegan et al. 2007; Fleeger et al. 2008; Johnson et al. 2009), green (algal) vs. brown (detrital) energy pathways (Deegan and Garritt 1997; Davis et al. 2010; Marcarelli et al. 2011; Galvan et al. 2011), the role of omnivory (Massol et al. 2011; Lockfield et al. 2013), and abiotic (hydrodynamic) influences (Hughes et al. 2000; Haas et al. 2009). In this current round we continued our food web work, but have emphasized the crucial role of migratory animals as connectors of spatially separate ecosystems, either as ecosystem process controls (e.g., mobile predators as top down control; Lundberg and Moberg 2003; Deegan et al. 2007; Flecker et al. 2010; McCauley et al. 2012; Casini et al. 2012) or as ecosystem subsidies (Deegan 1993; Polis et al. 2004; Nelson et al. 2013).

The discontinuity concept is one of several approaches (e.g., network dynamics, ecotones, patch dynamics) developed to understand the ecological implications of patterns of physical heterogeneity at larger spatial scales (Benda et al. 2004; Poole 2010; Winemiller et al. 2010). At the landscape scale, a spatially heterogeneous and temporally variable landscape has the potential to create ecological hotspots of energy transfer and nutrient cycling (Kennedy 2013). Physical features such as marsh/open bay edges, sand bars, and channel confluences may create ecological hotspots, either by increasing local productivity or by concentrating motile prey and predators. For example, we have found that although the production from the highly productive saltmarsh surface is inaccessible to striped bass, it is gathered by smaller motile organisms (e.g. mummichog and shrimp) and moved to hotspots formed by the confluences of landscape features, where it is consumed by larger predators (trophic relay; Kneib 1997; Deegan et al. 2000; Ferry and Mather 2012). These landscape features may amplify top down predator effects, alter food webs, and facilitate trophic connectivity between multiple habitats.

We have been experimentally testing hypotheses about the role of omnivory versus top down controls and fast (algae, low quantity, high quality) and slow (detrital, high quantity, low quality) multichannel foodwebs in salt marshes. High nutrient availability, high basal resource quality (algal), and simple communities, such as algal-based planktonic food webs, are typical of food webs with trophic cascades. However, in more complex food webs, especially those with large detrital inputs and many omnivorous species, the role of detritus in supporting the food web, and the existence and strength of trophic cascades are debated (Deegan et al. 2007; Leroux and Loreau 2008; Massol et al. 2011). Coastal ecosystems, especially marshes, are replete with omnivorous species and organic matter inputs are dominated by inputs of low quality vascular plant material, thus direct tests of top-down vs. bottom-up controls on saltmarsh food webs are needed.

We have conducted a long-term ecosystem scale nutrient enrichment experiment (TIDE) that for several years was crossed with the removal of a meso-consumer (*Fundulus heteroclitus*) suggested to be at the top of the saltmarsh trophic cascade. In the first 3-5 years of the nutrient enrichment experiment we observed a bottom-up stimulation of the marsh food web including increases in the production of benthic algae, grazing epibenthic invertebrates, and nekton (fish and shrimp) (Deegan et al. 2007). We found that algal production, despite its overall lower availability, is very important in fueling marsh food webs and this importance was amplified by nutrient enrichment (Galvan et al. 2008; Galvan et al. 2011). Nutrient enrichment stimulated benthic

microalgal (BMA) production by a factor of five (Ritter 2012), while macrophyte litter production (e.g., *Spartina alterniflora*) increased only ~5% (Deegan et al. 2012). Only a few invertebrate species on the high marsh surface benefited from the increased litter decomposition stimulated by increased nutrients (Short 2012) while stimulation of algae led to many omnivorous species switching from poor quality detrital sources to high-quality algal carbon sources to maximize energy uptake (Galván 2008; Galvan et al. 2011; Lockfield et al. 2013; Pascal and Fleeger 2013; Pascal et al. 2013; Mitwally and Fleeger 2013).

Omnivory also muted the food web response to potential top-down control by fish. Contrary to top-down predator control theory and what was posited in the literature for

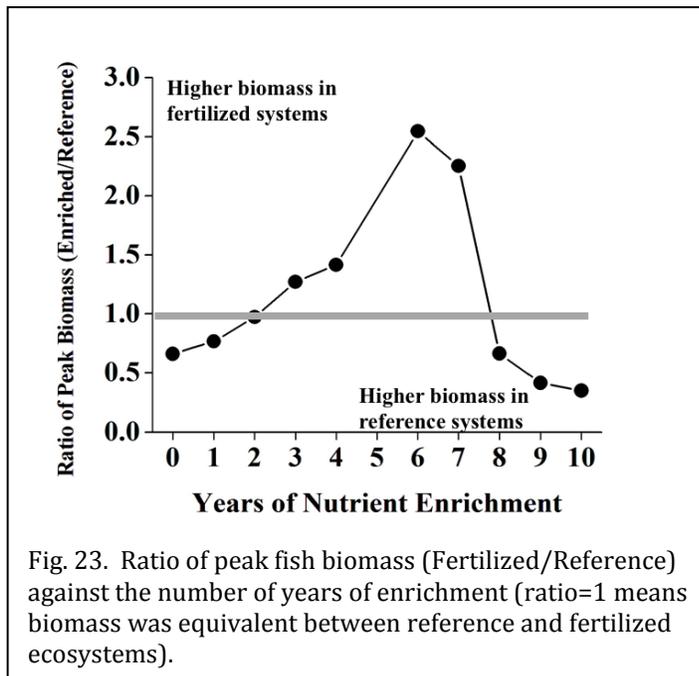


Fig. 23. Ratio of peak fish biomass (Fertilized/Reference) against the number of years of enrichment (ratio=1 means biomass was equivalent between reference and fertilized ecosystems).

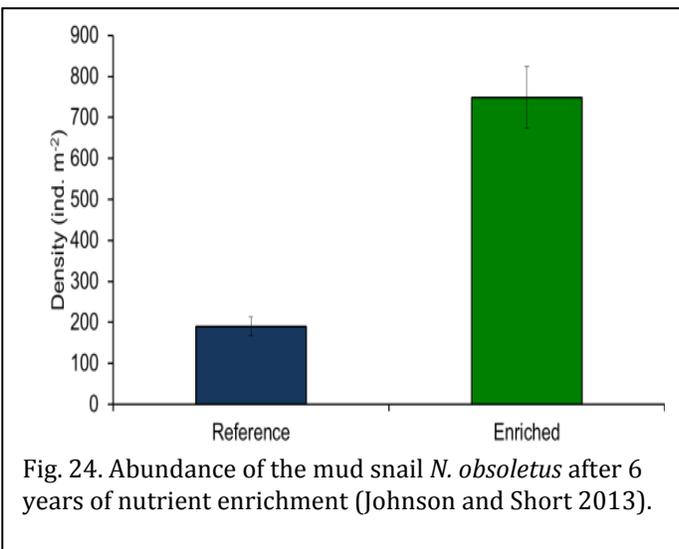
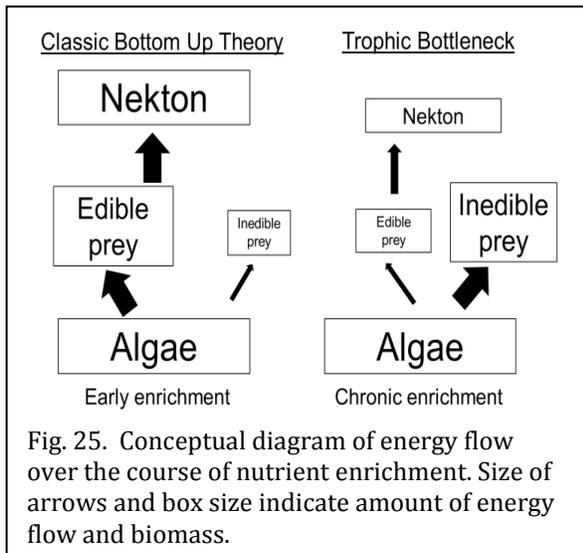


Fig. 24. Abundance of the mud snail *N. obsoletus* after 6 years of nutrient enrichment (Johnson and Short 2013).

saltmarshes, *Fundulus* removal did not elicit strong prey responses in the marsh creek, in part because omnivorous grass shrimp (*Palaeomonetes pugio*) switched from an algal-based diet to animal-based diet and replaced mummichogs as a predator (Lockfield et al. 2013). Switching from slow energy transfer channels (detritus) to fast energy channels (algae) should lead to increased energy production of higher trophic levels (e.g., classic bottom-up theory). Bottom-up control of consumer production, however, is predicated on increased efficiencies between trophic levels and simple linearity of food webs. In complex food webs, such as those in salt marshes, nutrient enrichment may decouple the top and the bottom of the food web if enrichment stimulates prey largely unavailable to predators, which may decrease predator-prey trophic efficiency (Davis et al. 2010).

In fertilized creeksheds at PIE, we have observed significant declines in mid-level consumer (fish and shrimp) production in the last 4 years (years 6 – 10) of nutrient enrichment, suggesting attenuation of trophic flows, or perhaps alterations of habitat (Fig. 23; Nelson et al. in prep.). Concurrently, we have found a four fold increase in the abundance of mud snail (*Nassarius obsoletus*) in fertilized mudflats (Johnson and Short 2013; Fig. 24). Once past a size threshold, these snails are inedible to nektonic consumers. Additionally, through habitat disturbance,

they decrease infauna production, reducing the availability of prey for young-of-the-year mummichog (Kelaher and Levinton 2003). The mud snail is long-lived (>10 years; Curtis et al. 2000) and resident within salt marsh creeks, allowing biomass to accumulate in our system where

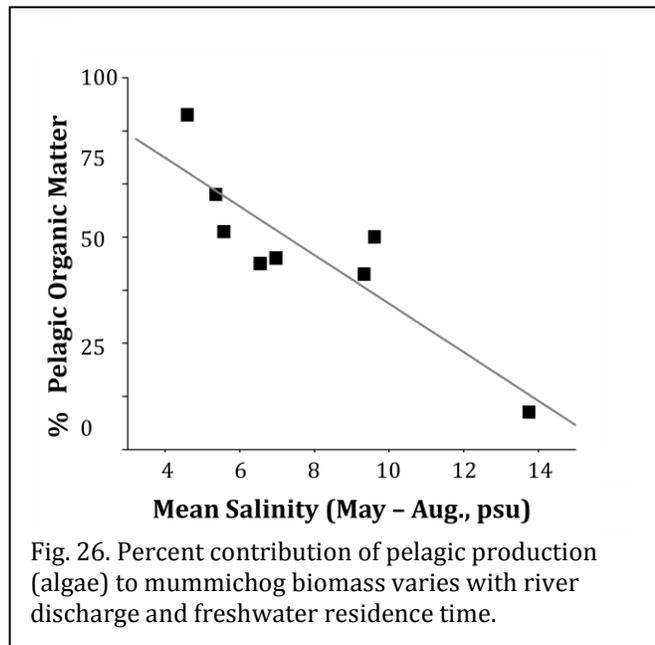


they have few predators. Thus, nutrient enrichment may have led to a trophic bottleneck as energy is truncated into trophic dead-ends (mud snails), reducing flow to higher trophic levels (Fig. 25).

This hypothesis, however, is confounded by the unexpected geomorphic alteration in the last 4 to 5 years resulting from creek bank fragmentation and loss of tall *S. alterniflora* along the creek edge (Deegan et al. 2012). Creek edge habitat is critical to nekton (fish and shrimp) for foraging, spawning, and refugia; thus, its recent loss may contribute to the decline in mobile meso-consumer biomass. While we are still uncertain of the relative weight of the two proposed mechanisms, the net effect is that nutrient enrichment reduces the abundance of small prey

fish and shrimp and therefore reduces the trophic subsidy of marshes to the open bay provided by their cross system movements (Fig. 23). Future work will combine the work on algal productivity, grazing rates and estimates of productivity of different species to determine if the increase in snails is sufficient to induce a trophic bottleneck, while continued monitoring of habitat and work on the habitat quality of the slumped creek banks (see poster) will help determine the role of loss of creek edge habitat.

Our long-term monitoring of the stable isotope values of the major trophic guilds in PIE revealed freshwater delivery and residence time are important factors controlling the primary source of secondary production and nutrient retention in the estuary. The hydrological and biological dynamics of the oligohaline transitional zone, where nutrients and organic matter from the upper water shed first enter an estuary, can significantly impact the biogeochemical cycling and productivity of the entire estuarine ecosystem (Holmes et al. 2000; Giblin et al. 2010). This zone serves as habitat for a unique suite of species capable of tolerating the extreme changes in environmental conditions (Hughes et al. 2000). Coupling between pelagic primary production and benthic secondary production in the oligohaline zone increases the retention of allochthonous nutrient and organic matter inputs within the estuary (Eyre and Ferguson 2006; Hughes et al. 2000). This can increase secondary production and provide greater food web stability (Carpenter et al. 2005; Huxel and Mccann 1998). Benthic-pelagic coupling is relatively strong in the upper, oligohaline zone of the Parker River estuary. There is an increase in nutrient delivery during high flow periods, typically in the spring. Phytoplankton bloom in response to these nutrient inputs as soon as residence times in the system are long enough to prevent wash out. The increased production in the pelagic zone fuels benthic production by either



direct grazing of phytoplankton by benthic invertebrates, or through remineralization and subsequent uptake by benthic primary producers. However, the physical factors that control the degree of benthic-pelagic coupling in this important transitional area are poorly understood. During years when freshwater discharge remained relatively high, we observed mummichog (*Fundulus heteroclitus*), an indicator species that feeds exclusively in the benthos, derived the majority of its energy from pelagic production. Under low discharge conditions, nutrient delivery to the upper portion of the estuary is too low to stimulate high pelagic production. During these years, salinity rises and the system becomes supported by benthic nutrient regeneration and production, and marsh macrophytes (Fig. 26). This is consistent with PIE work on benthic regeneration of nutrients that suggests under low river inputs, local regeneration of N is more important than river inputs. High river discharge also increases the areal extent of the riverine influenced food web.

Theme 2 Q2D. What are the configurations of habitats, geomorphic features, and hydrodynamics that create regions of high production and efficient energy transfer to higher trophic levels?

Heterogeneity in the distribution of predators through space and time affects the functioning of ecosystems through direct and indirect effects on prey communities, top-down ecosystem impacts, and other transformations and translocations of energy and nutrients (Estes et al. 2011, Altieri et al. 2012). Relatively little is known about seascape-scale predator distribution, abiotic and biotic correlates of these patterns, or the resulting ecological consequences (Pittman et al. 2011).

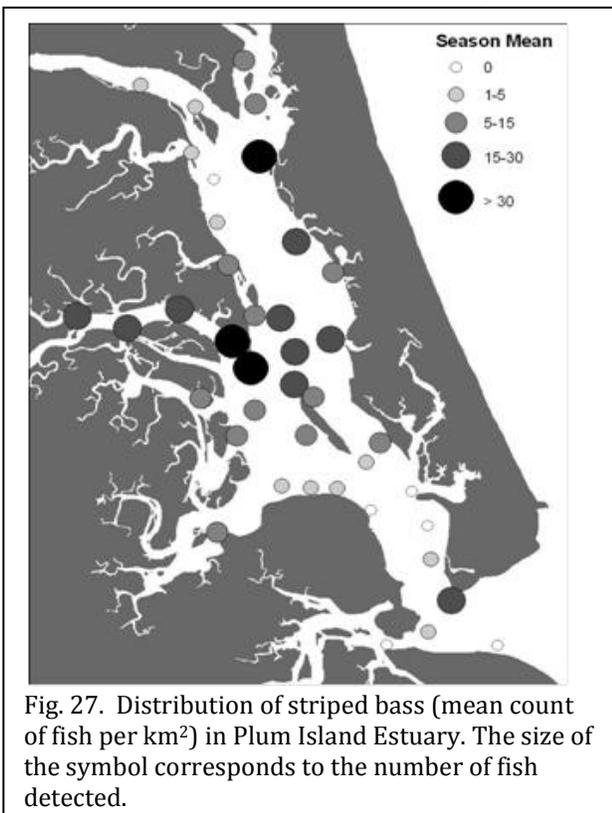


Fig. 27. Distribution of striped bass (mean count of fish per km²) in Plum Island Estuary. The size of the symbol corresponds to the number of fish detected.

Although we have shown that migratory striped bass (*Morone saxatilis*) predators establish seasonal residency in PIE (Mather et al. 2009) and concentrate within localized regions of PIE (Pautzke et al. 2010), little is known about their use of specific estuarine habitats. Consequently, we have begun to test predictions about how physical structure aggregates secondary productivity (e.g., predators) using the discontinuity conceptual framework (i.e., can rare or unusual seascape-scale physical features create ecological hotspots).

When we mapped the distribution of 50 acoustically-tagged striped bass within PIE, we found that these highly mobile predators were clustered at ecological hotspots in the middle region of PIE in response to combinations of sandbar area, intermediate bottom unevenness, channel networks, and, to a lesser extent, confluences and drop-offs (Fig. 27; Kennedy 2013). Furthermore, the highest predator counts occurred at sites with the greatest additive habitat complexity (i.e., where sandbars, drop offs, and confluences co-occurred). This suggests

that certain types and spatial arrangements of seascape-scale geomorphic structures aggregate striped bass predators through some combination of physical habitat changes, increased local secondary production, or aggregation of motile prey from adjacent habitats (e.g. salt marshes). These predator aggregations can also have ecosystem-wide impacts. For example, striped bass can

have potential top-down effects on prey populations at the habitat hotspots that we identified and these concentrations of predators can potentially affect primary production through trophic cascades.

We have recently (2012) begun to examine how one specific confluence is being used by mobile consumers as a foraging space and the impact of these predators on prey behavior and abundance. Previous work identified the confluence of West Creek, which drains a large saltmarsh area, and the adjacent Rowley River as consistently used by sub-adult striped bass (Pautzke et al. 2010). In contrast to many top predators which often have empty guts, nearly all (98%) of the striped bass that visit PIE, as part of a coastal feeding migration, had fresh prey in their stomachs (Ferry and Mather 2012). Striped bass ate predominately marsh-derived prey; initially shrimp (*Crangon septemspinosa* and *Palaemonetes pugio*) with small fish (*Fundulus* and *Menidia*) increasing in number at the end of the season as the prey fish migrated out of the marsh to the open bay area to overwinter. The observed consistent presence of striped bass at the confluence of saltmarsh creeks with the larger open bay, the movement of striped bass into the creeks with the incoming tide, and a diet of marsh-dependent prey species suggest that marsh channels are one important foraging ground for striped bass. These distinct foraging areas at small salt marsh creek confluences may result in a higher net energy flux per unit area than larger “realized foraging areas” as predicted by food web theory (McCann and Rooney 2009). This interaction between movement and foraging could lead to differential patterns of top down control throughout the PIE marsh-estuary ecosystem.

Similar to our work with striped bass, we have initiated work on hotspots of foraging and the potential role of wading birds, particularly Snowy Egrets (*Egretta thula*) and Great Egrets (*Ardea alba*), within the estuary. Like striped bass, these wading birds are seasonal inhabitants of the Plum Island system, but they also make daily movements out of the system to offshore nesting islands or late summer roosts. We are interested in defining the geomorphic and productivity characteristics of hotspots of feeding activity. We found that feeding by both species of egrets on small fish was concentrated in pannes, ponds, and tidal creeks at low and mid-tides. Although probably not abundant enough to be estuarine-wide top down controls on their prey populations, the temporary concentrated use of some locations (e.g., certain salt pannes) suggest that egrets could create local prey depletion between spring tide cycles. This is a question we have begun to explore by sampling of prey populations in ponds before and after egret feeding events.

Migratory fish can translocate nutrients and energy and consequently propagate events from one estuary to another (Deegan 1993; Reiners and Driese, 2001; Mather et al. 2013). However, variations in how fish migrate can weaken or intensify these across-system effects and determine the degree of connectivity between PIE and other estuaries. Our research has shown a strong connection between striped bass that feed in PIE and bass that overwinter in the Hudson and Delaware Rivers (Mather et al. 2010; 2013). Because of their strong fidelity and specificity, striped bass can act as transport vehicles to export nutrients and energy from PIE to these other estuaries hundreds of kilometers away. For example, the biomass that striped bass gain in a single estuary like PIE could increase spawning stock of coastal striped bass in the Hudson and Delaware estuaries. This increased striped bass biomass may then feed back to intensify predation pressure on prey in other estuaries. Thus, our research on predator movement has advanced what is known about patterns of biotic connectivity, especially the complexity and heterogeneity of fish migration. This long term research focus at PIE allows for the development of increasingly complex questions that could not be anticipated a priori (Dodds et al. 2012). Our research started with simple top predator ‘where are they and what are they eating’ questions (Ferry and Mather 2012), progressed to local within estuary patterns (Pautzke et al 2010), evolved to coastal movements (Mather et al. 2010), and most recently advanced to making connections across estuaries (Mather et al. 2013). This type of sequential, focused, in-depth research on variations in fish migration is essential for a much-needed understanding of how biotic connectivity affects coastal ecosystems.

Theme 2 Q2E. Do microbial systems organize towards a state of maximum entropy production (MEP), and can this principle be used to understand estuarine biogeochemistry in a spatially complex seascape?

One of our modeling objectives in the PIE LTER program is to develop more robust estuarine biogeochemistry models that produce reliable predictions of estuarine biogeochemistry under conditions likely to occur under global change. While classic, organismal-based, biogeochemistry models work well for interpolating between observational data sets, they are not

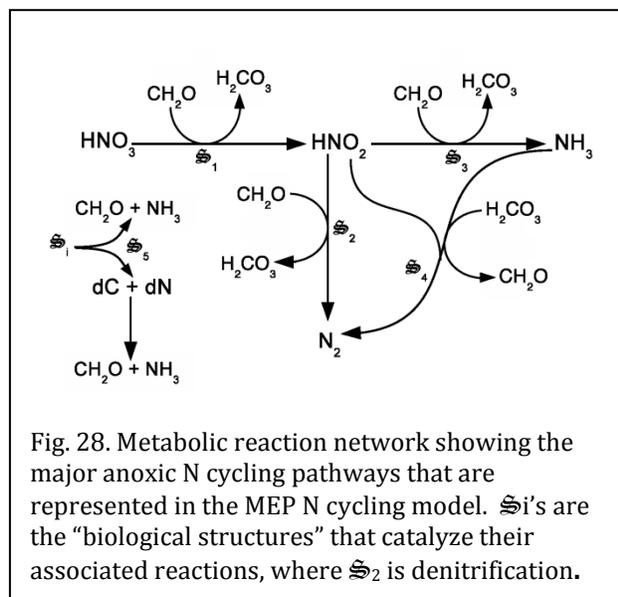


Fig. 28. Metabolic reaction network showing the major anoxic N cycling pathways that are represented in the MEP N cycling model. \mathcal{S}_i 's are the "biological structures" that catalyze their associated reactions, where \mathcal{S}_2 is denitrification.

robust in predicting system dynamics under conditions that lie outside the data envelope used for model calibration (Vallino 2000). Consequently, we have begun developing models based on the maximum entropy production (MEP) principle (Dewar 2003; Dewar 2005). During our last funding cycle, we used methanotrophic-based microcosms for development of both mathematical and numerical frameworks for implementing MEP concepts (Vallino 2010; Vallino 2011). During the current funding cycle, our objective is to apply the previously developed mathematical and numerical tools for understanding and predicting estuarine biogeochemistry at PIE.

Our basic approach is to represent ecosystem biogeochemistry as a distributed metabolic network (Vallino 2003), where each metabolic function, such as CO_2 fixation,

denitrification, sulfate reduction, etc., is catalyzed by an associated biological structure, \mathcal{S}_i (i.e., an aggregation of molecular machines with a defined metabolic function) (Fig. 28). Each biological structure participates in a reaction that both catalyzes the given redox reaction, such as $\text{CH}_2\text{O} + \text{O}_2 \rightarrow \text{CO}_2 + \text{H}_2\text{O}$, as well as produces more catalyst, such as $\text{CH}_2\text{O} + \text{N} + \text{P} \rightarrow \mathcal{S}_i$ (i.e., each reaction is autocatalytic). A single control variable determines the extent of catalyst synthesis versus redox reaction extent, which allows any reaction in the network to be up-regulated or down-regulated. By changing the values of the control variables over time, we can change the amount of free energy that is dissipated (or entropy produced). Obviously this approach assumes that the microbial community has sufficient diversity to conduct the most favorable reactions or that microbes with those functions will quickly colonize the area. We are not currently investigating the microbial community composition as part of the LTER program. However, we are examining this in a number of collaborating projects including the TIDE project, MBL-Brown IGERT project and the project examining sulfur and nitrogen interactions (SONICC). Several of these groups will have posters at the site review.

To examine how and if MEP organizes microbial biogeochemistry in a manner consistent with experiments or observations, we have developed an algorithm that determines allocation of biological structures across the metabolic network by solving a receding horizon optimal control problem (Vallino et al. 2014). *Two exciting results that have derived from application of the MEP principle to microbial biogeochemistry are 1) a theoretically-based distinction between biotic and abiotic processes and 2) a mathematically-based hypothesis that supports the development of cooperation of metabolic function over space to maximize the dissipation of available free energy.* Our modeling work indicates that abiotic processes, such as fire, maximize instantaneous entropy production. In contrast, biological systems can maximize entropy over a finite interval of time by

executing temporal strategies from information stored in their genome and acquired via evolution (Vallino 2010; Vallino et al. 2014). By avoiding the steepest descent approach, biological systems under appropriate conditions can outcompete abiotic systems in free energy dissipation. Using rationale similar to the temporal problem, we have also shown that systems that coordinate function over space can increase total entropy production compared to systems that maximize entropy production locally (Vallino 2011). Quorum sensing is one example of how bacteria can and do coordinate function over space, which is consistent with our MEP-based conclusions.

Having developed the MEP approach using experimental microcosms, we have recently begun expanding our approach to address problems and questions of more relevance to estuarine and ecosystem biogeochemistry. Because of the

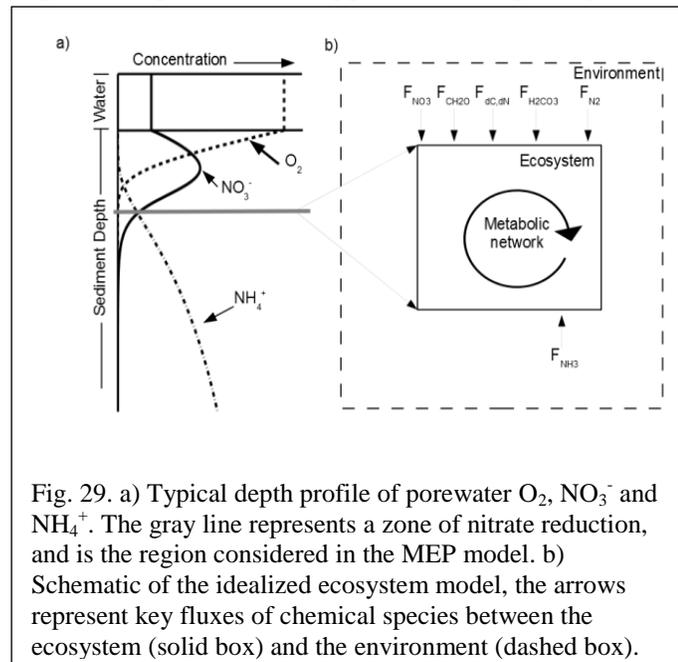


Fig. 29. a) Typical depth profile of porewater O_2 , NO_3^- and NH_4^+ . The gray line represents a zone of nitrate reduction, and is the region considered in the MEP model. b) Schematic of the idealized ecosystem model, the arrows represent key fluxes of chemical species between the ecosystem (solid box) and the environment (dashed box).

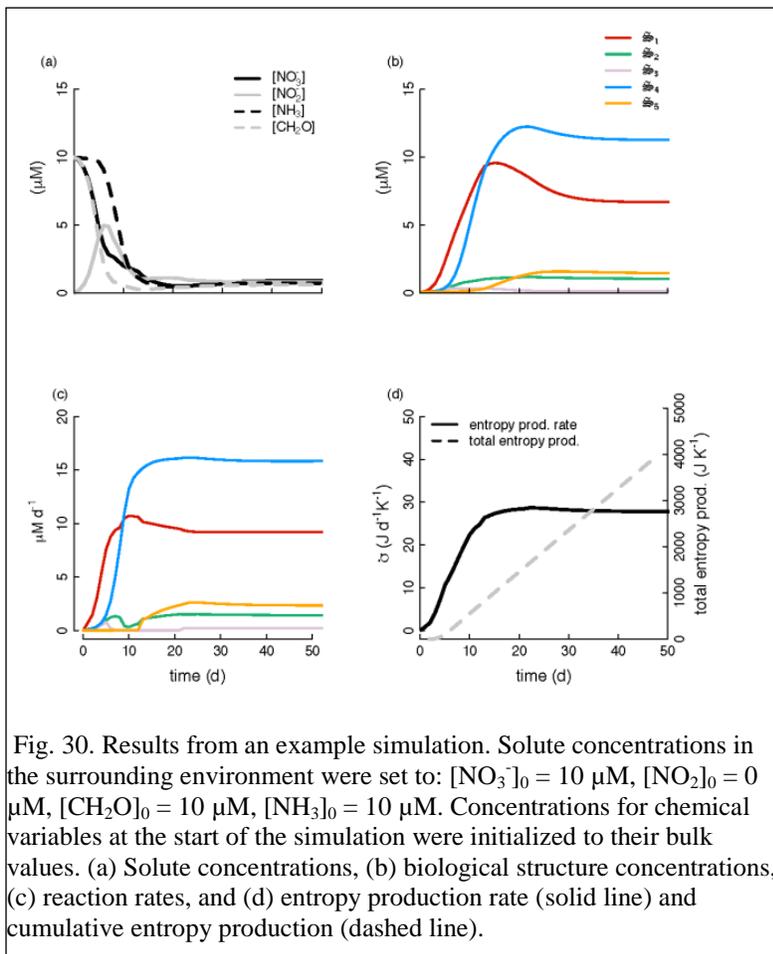


Fig. 30. Results from an example simulation. Solute concentrations in the surrounding environment were set to: $[NO_3^-]_0 = 10 \mu M$, $[NO_2^-]_0 = 0 \mu M$, $[CH_2O]_0 = 10 \mu M$, $[NH_3]_0 = 10 \mu M$. Concentrations for chemical variables at the start of the simulation were initialized to their bulk values. (a) Solute concentrations, (b) biological structure concentrations, (c) reaction rates, and (d) entropy production rate (solid line) and cumulative entropy production (dashed line).

importance of N processing in estuaries as well as the extensive data sets we have on sediment N-cycling at PIE, our first estuarine MEP-based model has focused on examining the controls and environmental conditions that underlie metabolic switching between denitrification, anammox and dissimilatory nitrate reduction to ammonium (DNRA). The first phase of model development examines the microbial metabolic network (Fig. 28) that operates in a thin anaerobic sediment layer where nitrate is available (Fig. 29), which allows us to focus on metabolism instead of transport processes (i.e., model domain is only subject to simple diffusion into and out of a thin sediment layer). Once boundary conditions are given for concentrations of nitrate, ammonium, labile organic carbon (CH_2O), and detrital C (dC) and N (dN), we can determine metabolic fluxes through the network (Fig. 28), concentrations

of the N and C species, and the amount of protein catalyst (S_i) allocated to the 5 reactions as a function of time by maximizing entropy production rate, as shown in the example simulation (Fig. 30). Because most of the model's degrees of freedom are embedded in the optimal control variables used to solve the MEP optimization problem, the model only contains two adjustable parameters; however, we have not attempted to tune these parameters and are using the same values used in testing the model with the methanotrophic microcosms. Nevertheless, the model produces results that are consistent with experiments and observations (Algar and Vallino, 2014).

In one of our model analyses, we examined metabolic switching that occurs as the relative rates of labile carbon to nitrate availability are varied from low ratios (C lacking) to high ratios (excess C). In these simulations (Fig. 31) we found that anammox dominates the nitrite reduction rate at low C to N ratios. As the amount of labile carbon relative to nitrate is increased, denitrification becomes more important. Finally, at high C to N ratios, DNRA dominates nitrite reduction. Even though denitrification has the highest free energy yield per mole of C, at high C to N ratios, it is the electron acceptor (nitrite) rather than carbon that is limiting. DNRA reduces nitrate to a lower oxidation state than denitrification (6 electrons transferred per mole of N reduced for DNRA compared to only 3 for

denitrification). The result is that DNRA makes more efficient use of the available electron acceptor and over time results in more carbon oxidized and more entropy produced than would be accomplished through denitrification despite the greater free energy of denitrification per extent of reaction. While the MEP model certainly produces results consistent with the standard redox cascade model (i.e., use of oxidizers: $O_2 > NO_3^- > Mn^{4+} > Fe^{3+} > SO_4^{2-} > CO_2$), our results also show that the redox cascade is not always followed due to other limitations, which the MEP approach can account for.

Our model results are consistent with the current understanding of the controls on N cycling in marine environments (Burgin & Hamilton 2007), as well as with the observations that anammox appears to dominate nitrite reduction in deep carbon-poor marine sediments (Dalsgaard *et al.* 2005), but is relatively unimportant in organic rich salt marshes where DNRA is very important (Koop-Jakobsen and Giblin 2009; Koop-Jakobsen and Giblin 2010). What is most exciting about our results, however, is that no parameters were tuned to obtain the results shown in Fig. 31. The results derive solely from maximizing entropy production given the metabolic network constraints. This work gives us further confidence that this modeling approach will likely lead to new understanding and insights into estuarine biogeochemistry as we expand its application vertically into the sediments as well as longitudinally in the water column along the length of the estuary.

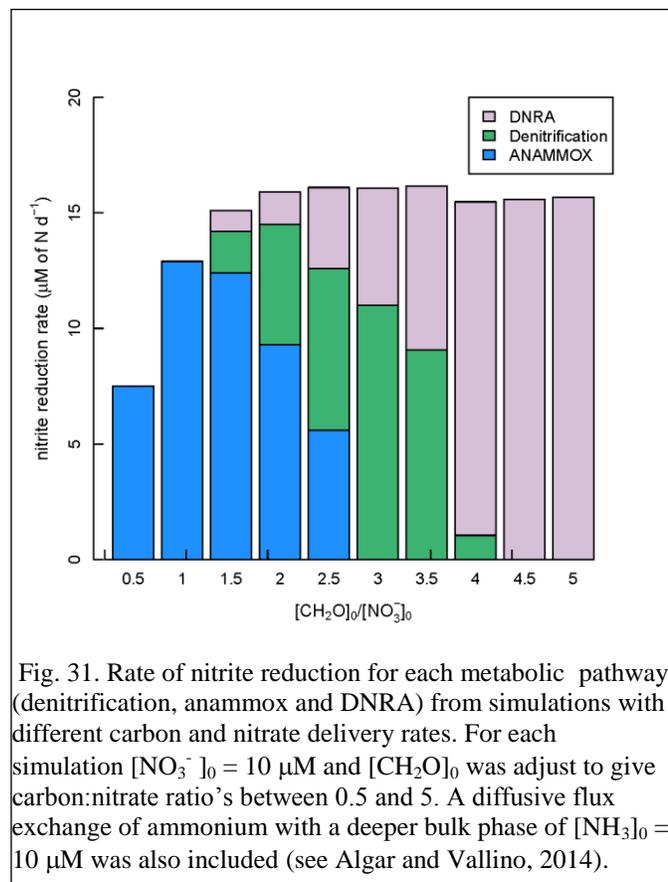


Fig. 31. Rate of nitrite reduction for each metabolic pathway (denitrification, anammox and DNRA) from simulations with different carbon and nitrate delivery rates. For each simulation $[NO_3^-]_0 = 10 \mu M$ and $[CH_2O]_0$ was adjusted to give carbon:nitrate ratios between 0.5 and 5. A diffusive flux exchange of ammonium with a deeper bulk phase of $[NH_3]_0 = 10 \mu M$ was also included (see Algar and Vallino, 2014).

3) OUTREACH AND EDUCATION PROGRAMS

PIE LTER helps support and participates in a wide range of educational and outreach activities. These activities emphasize the importance of long-term data to understand ecosystem change, provide opportunities for hands on learning, and address local and regional issues of concern.

K-12 EDUCATION

The major goals of our K-12 education programs are to: 1) excite students and teachers about coastal science by collecting and interpreting field data, 2) encourage students to consider a career in science, and 3) foster environmental stewardship. PIE educators and scientists work together in developing education activities and have forged solid working relationships with local schools and other educational institutions to accomplish these goals (Table 4).

A centerpiece of our education effort is Mass Audubon's Salt Marsh Science Project (SMS) (<http://www.massaudubon.org/saltmarsh>) initiated in 1996 and supported by NSF Schoolyard Supplements and other leveraged funding. Students from grades 5-12 investigate how marsh vegetation and the fish community in their towns are changing as a result of invasive species, sea level rise, and hydrological alterations and restoration actions. In 2011, PIE's education coordinator, Elizabeth Duff, was honored by the Massachusetts Marine Educators Association with the prestigious "Massachusetts Marine Educator of the Year" award for this project. In 2010-2014, Ms. Duff provided students and teachers with training and on-going support and maintained a database and web site so that students could compare their results with those collected in previous years.

NSF Schoolyard supplements have also supported teachers at the Governor's Academy, a local private high school, in implementing science modules. Students monitor ribbed mussels and intertidal marsh plant distribution. From 2010-2013 eleven students from the Academy worked as paid interns in PIE research over the summer and carried out independent projects. Over the last two years, an RET grant allowed a Governor's biology teacher and four students to conduct research on striped bass.

PIE scientists from UNH have mentored honors marine biology student at Triton Regional High School, the local public high school. Students are involved in stream sampling. In 2013, more than two dozen students chose to focus on the Plum Island Ecosystem LTER for their honors projects.

PIE LTER scientists and educators have been involved with the Gulf of Maine Institute (GOMI), a nonprofit educational institution whose mission is to inspire young people to take a leadership role in the stewardship of the Gulf of Maine (<http://www.gulfofmaineinstitute.org/>). Giblin serves on its Board of Directors, and Duff is a regular teacher, most recently having led climate change and solutions themes and teaching a total of 53 high school students. Other PIE scientists have given presentations and led field trips during summer workshops.

Fish are of widespread interest in the region and are a natural focus of PIE education efforts. PIE educators and scientists have collaborated on developing a striped bass curriculum for middle and high school schools in coastal Massachusetts (<http://www.massaudubon.org/saltmarsh/stripes/>). These lesson plans and resources are based on Massachusetts Science Curriculum Frameworks and are currently being used in selected schools in coastal Massachusetts. In 2013, lessons from the striped bass curriculum were included in the LTER Digital Library. An Inland Fish and Warming Waters Curriculum recently developed by Duff was presented at the April 2014 meeting of the National Science Teachers Association and is now available on the PIE LTER website (<http://pie-lter.ecosystems.mbl.edu/content/inland-fish-and-warming-waters-curriculum>).

UNDERGRADUATE EDUCATION

PIE LTER has involved undergraduates in research by providing summer research opportunities and hosting classes and honors projects during the school year (Table 4). From 2010-2013 funding from NSF has allowed us to host eleven undergraduates in the Research Experience for Undergraduates (REU) program. The students live at the field station, are mentored by PIs, help out in joint projects, carry out their own research projects, and conclude their summer with a presentation at the Marine Biological Laboratory. Additional REU students working at PIE have been funded by grants to our partnering universities. Several REUs have gone on to present their findings at national meetings, such as those hosted by the Coastal and Estuarine Research Federation (CERF).

During the school year, undergraduates from a number of universities have used PIE LTER as an outdoor laboratory and have received class credits for independent research projects. PIE Co-PIs Fagherazzi (Boston University) and Pontius (Clark University) have been particularly active in involving their students in PIE research (Table 4). Eleven Clark undergraduates received awards for presentations on their work at scientific meetings. The Ecosystems Center's Semester in Environmental Science (SES) program includes an annual field trip to PIE. A number of SES students carry out their independent projects at PIE.

GRADUATE AND POSTGRADUATE EDUCATION

Thirty-seven M.A., M.S., and Ph.D. students have carried out their research on the PIE LTER project from 2010-to present (Table 4). Additional students (e.g., from Boston University and the University of Houston) have used the facilities and field sites at PIE to carry out their own research projects. PIE LTER has also hosted five postdoctoral fellows during this time period.

An exciting recent educational development for graduate students is the IGERT program, an outgrowth of the collaboration between Brown University and the Marine Biological Lab. Students work with Giblin and other MBL and Brown faculty exploring how next generation sequencing techniques can be used to explore important and interesting ecological questions at PIE field sites.

Last fall (2013), PIE scientists collaborated with scientists from the other east coast LTERs sites to teach an on-line course "Linking biology and geomorphology in coastal wetlands (and other habitats)". The course was offered for credit at 9 universities. Over 140 people participated, including graduate students and faculty members at over 30 academic institutions, and staff at 9 National Estuarine Research Reserves and 2 Federal Agencies.

OUTREACH

Scientists from the PIE LTER are actively engaged in sharing their knowledge and presenting their findings to federal, state, and local agencies, nonprofit environmental organizations, and the general public. The science carried out at PIE has influenced environmental policy nationally, regionally and locally. PIE scientists serve on numerous advisory committees for federal and state commissions and nonprofit environmental organizations (Table 4). They also engage the general public through presentations, articles in newspapers and magazines, and citizen science.

PIE research and scientists are influencing national policy. Morris participated in a 2012 workshop at the National Conservation Training Center in West Virginia designed to advise the USFWS on a change in policy regarding Open Marsh Water Management for mosquito control. Based on Morris's widely used MEM model and data obtained at PIE on sediment accretion, the ditch plugging of peat marshes in New England will likely be restricted in the future. Deegan's TIDE project is being used by EPA to inform critical nitrogen loads in estuaries. Deegan also serves on the Ecosystem Sciences and Management Working Group of the NOAA Science Advisory Board.

Polsky serves on an NAS/NRC committee setting strategic goals for geographic research over the next decade.

PIE LTER has a solid working relationship with the Parker River National Wildlife Refuge (PRNWR). Giblin and Buchsbaum have attended meetings and provided input for the Refuge's Comprehensive Conservation Plan (currently in process). They have also been involved in providing information to the Refuge on its vulnerability to climate change. Giblin gave a presentation at a workshop run by the PRNWR aimed to help citizens reduce their water and nitrogen use. Duff, using data from the Salt Marsh Science Project, produced a report for the Refuge outlining the results of long term studies of vegetation in one of the impoundments that has been invaded by common reed (*Phragmites australis*). The report was intended to assist in planning for the future management of this impoundment.

The PIE LTER has provided information and advice to Massachusetts state agencies in addressing their management concerns. LiDAR data collected by the state with support from PIE was instrumental in determining the locations of coastal climate change adaptation zones that were incorporated into the Massachusetts's BioMAP conservation assessment. LiDAR data and the circulation model have contributed to an understanding of the causes of recent common reed invasions in the north section of Plum Island Sound. Morris alerted the state to a discrepancy in the most recent raw LiDAR data, and the state was then able to get their contractor to correct the error. Bathymetry, sediment, and nutrient data provided by PIE were used to delineate potential eelgrass restoration sites for a Massachusetts Bays Program (National Estuaries Program) project. Finally, PIE scientists will be collaborating with the Massachusetts Office of Coastal Zone Management on an EPA funded grant to assess the vulnerability to climate change of coastal wetlands in the Parker River watershed.

PIE LTER scientists have been actively engaged with nonprofit environmental organizations and local towns. Buchsbaum and Duff are on the staff of Mass Audubon, the largest environmental organization in New England, and have informed the membership of PIE activities through presentations and articles in the organization's journal. PIE scientists have been active in PIE-Rivers, a committee comprised of watershed associations, land trusts, local planners, and state agencies whose goal is river restoration in the Parker, Ipswich, and Essex Rivers. Giblin gave the keynote address at their first public conference, Wollheim provided critical comments on their proposal to map the culverts, and Buchsbaum serves on the task force. Other presentations are shown in Table 4. The public has had the opportunity to participate in PIE through citizen science projects sponsored by Mass Audubon and the watershed associations, including bird and water sampling.

Polsky is writing a book for the LTER illustrated book series that will focus on lawns and their impact on watersheds. The book is nearing completion.

PIE scientists have engaged journalists. Neill ran MBL's Hands-on Logan Science Journalism Program at PIE from May 19-27, 2011. Eight journalists participated and a number of PIE LTER scientists contributed their expertise. Johnson writes regularly for the local newspaper and maintains a natural history blog on PIE topics (www.manayunkia.com), which receives about 50 hits per day.

We have used the web as an outreach tool. Our PIE LTER website has provided overall summaries of our work, links to our data, and to our education programs. It is currently being updated to conform to LTER guidelines. In addition, Mather along with other faculty and graduate students at UMass-Amherst and Deegan at MBL developed an Ipswich River Herring website. This website (<https://sites.google.com/site/ipswichriverherring/>) was the basis for our successful Adopt-A-Herring outreach program. It describes the research we conducted on river herring biology and management that uses radiotelemetry, and it includes information on river herring behavior and habitat use. It also provides opportunities for individuals, organizations, and schools to be involved in river herring restoration efforts.

4) PROJECT MANAGEMENT AND SITE MANAGEMENT

Our management structure is described in the proposal and is fairly typical of an LTER site. Overall direction and management are provided by lead PI, Anne Giblin, and the executive committee. The executive committee consists of Giblin, and the leaders of major program areas (Wollheim-watershed, Morris-marsh, Hopkinson-estuarine biogeochemistry, Deegan-consumers, Vallino-modeling, Pontius-human dimension, Buchsbaum-outreach). These program areas, and these scientists, have provided principal investigator supervision for our long-term monitoring, continuity in data, and integration across disciplines in the cross-cutting experiments since the inception of the PIE LTER. They also provide conceptually logical points of contact for investigators working on collaborating projects.

Over the next three years we do not anticipate any major changes in senior personnel (see Table 4). Looking further ahead to PIE IV, Giblin will lead but would expect to overlap with the next PIE leader before the end of the next 6-year period. Hopkinson will move off of the executive committee after this round to devote his time to the PIE LTER synthesis book. Nat Weston will take over lead of the estuarine biogeochemistry program area. We anticipate that the other new scientists who have joined the PIE LTER will take on leadership roles in the next 3-6 years.

We coordinate closely with Federal (US Fish and Wildlife, Parker River Wildlife Refuge), state, town, and private owners of estuarine and watershed areas (e.g., Mass Audubon, Essex Country Greenbelt Association, a number of smaller NGOs, and individuals). They have been extremely cooperative, allowing us to conduct long-term experiments, such as TIDE (which takes place on marshes owned by the Town of Ipswich, the Greenbelt Association and private landowners) and deploy gear such as the flux towers (on USFWS Refuge owned marsh). Giblin, Buchsbaum, and Deegan have coordinated work in the estuary and marsh, while Wollheim coordinates with watershed groups.

The PIE LTER, the collaborating projects, and other researchers not closely associated with PIE use two field facilities. The Rowley House is owned by the Essex County Greenbelt and provides water access on the Rowley River. The Marshview House is owned by the MBL and open to all doing research at PIE. There is an on-line calendar for sign up for the houses. Facilities are basic. There is usually an MBL post-doc or research assistant in residence at Marshview throughout much of the field season who provides on-site supervision. The MBL has local contractors who handle both repairs and property management.

OPPORTUNITIES AND CURRENT CHALLENGES

The LTER has been very successful in attracting new researchers to the PIE site, adding new thinking, depth and breadth to our program. However, as the number of projects grows, keeping track of the people involved (which now often do not include a PIE LTER PI), their research sites, and their need for field facilities becomes a management challenge.

Field facilities in particular have been at capacity and we have only a small lab at Marshview. As a result, groups have had to plan *not* to overlap in the field, which reduces interactions and coordination, and most of our K-12 educational activities have to be held off-site. Fortunately we were awarded an NSF facilities grant to add a field lab onto the existing barn at Marshview. This addition (about 1,200 sq ft) increased our lab space by 5-fold. It will allow for more interaction, more efficient use of field time, and provide a better experience for our summer students as more groups will be on site rather than rushing back to their home institutions to process samples.

One of our challenges, common to every LTER, is bringing in new investigators and keeping them engaged in the LTER. These investigators often start by becoming involved in separately funded projects in collaboration with the LTER. The challenge becomes having them maintain

involvement with the LTER when those projects end. We often can provide very little in the way of direct financial resources as much of our budget is already programmed into long-term observations, long-term experiments and data management. We are trying to address this by providing new investigators with field logistics, by allowing them to request REUs and other summer students, and, to the extent possible, helping them secure other funding.

PIE has been very successful in outreach and education and we routinely receive requests to speak at meetings or for information. Recently, there has been a great deal of interest in understanding sea level rise and extreme events such as flooding. As a result we have been asked to participate in both high level planning efforts (such as with the US Fish and Wildlife and the Northeast Climate Science Center) and on grants to analyze the vulnerability of the region to sea level rise (Mass Coastal Zone Management). These are very important opportunities to directly put PIE research into the management and policy arena and to the extent possible we have been following up on them. However, it has stretched the team thin and we are looking for ways to engage some of the new investigators in these vital activities, and to continue and enhance the personal relationships we have developed with some of these organizations over the years.

Finally, PIE is a system where the actions of humans can often trump natural changes. Early in PIE we considered humans predominately as “external drivers”, disconnected from the results of their actions on the ecosystem. We now have evidence from PIE and cross-site work on water bans, water use, and lawn care that humans can change their behavior in response to environmental stimuli and act more like internal feedbacks than external drivers. The controls on these human feedbacks, like all feedbacks, need to be understood better if we expect to predict the long-term trajectory that coastal ecosystems will take into the future. We have two excellent social scientists on the team who received the majority of their funds through LTER supplements for social science. These supplements have now ended. However, our social scientists have been very successful finding other sources of funding to keep this vital aspect of our program going and they have remained well integrated with the LTER .

5) INFORMATION MANAGEMENT

OVERVIEW OF DATA AND INFORMATION MANAGEMENT

The goal of the PIE LTER data and information system is to provide a centralized network of information and data related to the Plum Island Ecosystem. This network provides researchers access to common information and data in addition to protected long-term storage. Data and information are also easily accessible to local, regional, and state partners and the broader scientific community. Researchers associated with PIE are committed to the integrity of the information and databases resulting from the research.

Access by the public and scientific community to data and information is provided by the web site, <http://pie-lter.ecosystems.mbl.edu>. The web site contains information on research, data, education and outreach, personnel and publications. Datasets are accessible via the PIE web site [data section](#) and searchable using the LTER Metacat and LTER PASTA Data Portals. PIE maintains an Intranet site with archived datasets from which the PIE web site is updated.

PIE information and data are stored on a MBL Microsoft Windows server with a level 3 RAID array that is backed up on an external drive nightly. The external drive is replaced every 1 – 3 months and stored in an offsite location. The PIE web site (Drupal Content Management System) is managed using Aegir on a Linux virtual machine, Ubuntu 12.04, LAMP system. The database and file system is backed up to another machine daily at 1 PM and 5 PM for a 30 day cycle. MBL researchers can directly access archived data on MBL’s server and MBL provides software and network storage capability for backing up MBL researcher’s individual computers. Non-MBL researchers have access to a secure FTP web site at MBL for archival back up of their data (both unprocessed and processed). PIE maintains a server at the Rowley Field station to manage streaming of telemetry

data from weather, water quality and eddy flux remote stations. Near real time data (helpful when planning research schedules) are available on the [PIE home page](#).

DATA MANAGEMENT AND DESIGN OF RESEARCH PROJECTS

Data management and design of research projects is coordinated through an information management team. The information management team consists of: Anne Giblin (Lead PI), Joe Vallino (PI), Robert (Hap) Garritt (IM), Jane Tucker (SRA), Gil Pontius (PI) and research assistants associated with program areas. The team has the necessary leadership, knowledge and technical expertise for creating and maintaining the PIE research information. Continuity of the system relies on the multi-person management team to provide experiential memory of the system. Guidelines for the PIE Information System are available on the web, <http://pie-ter.ecosystems.mbl.edu/content/information-management>, and include Data Policies and Protocols, Description of Information Management and Data Submission documentation. Hap Garritt, a senior research assistant with The Ecosystems Center, MBL, has been the information manager (IM) since 1998 and has the responsibility for overseeing the overall integrity of the data and information system for PIE LTER. Hap has been involved with the design and execution of many of the research projects, which allows for a smooth incorporation of data and information into the PIE database. Several meetings each year provide each researcher the opportunity to communicate with the PIE information management team regarding the design of the specific research project and subsequent incorporation of data and information into the PIE LTER database.

CONTRIBUTIONS OF DATA TO DATABASE

Individual researchers are responsible for providing metadata and data via a [PIE LTER Excel Metadata Template](#) for each of the core research areas. Researchers on the PIE LTER are expected to follow the LTER Network data release policy defined on the LTER web page, <http://lternet.edu/policies/data-access>. Researchers using the facilities of the PIE LTER are expected to comply with the LTER policy even if they are not funded by the LTER. Data files must include accompanying documentation files that completely describe the data. PIE currently uses a Microsoft Excel spreadsheet template for managing metadata and data. The Excel template provides utility for: 1) consistent metadata entry, 2) subsequent conversion via a visual basic macro to XML structured Ecological Metadata Language (EML 2.1.0) according to EML Best Practices for LTER Sites and 3) QA/QC checks for uploading to the LTER Network Metacat and PASTA Data Portals. Individual researchers are responsible for quality assurance, quality control, data entry, validation and analysis for their respective projects. Researchers are reminded about contributions to the database several times during the year via email, teleconference calls and field sampling trips, in addition to announcements during our Annual Spring PIE LTER All Scientists Meeting.

DATA ACCESSIBILITY AND TIMELINESS

Researchers on the PIE LTER are required to contribute data to the PIE LTER database. It is recognized that investigators on PIE LTER have first opportunity for use of data in publications but there is also the realization for timely submittal of data sets for incorporation into the PIE LTER database. PIE strives to make data available within 1-2 years. The variability in time is dependent upon the time required for sample analysis and corresponding QA/QC of data and metadata. Many logger data sets, such as sonde water quality, water level, discharge and meteorological observations and data that do not require a great deal of post-collection chemical or other analysis, are available within 3-6 months of collection. Selected data (weather, water level and water quality) are made available in near real time to provide timely awareness of local conditions. PIE follows the data release policy for the LTER network that states:

“There are two types of data: Type I (data that are freely available within 2 years) with minimum restrictions and, Type II (Exceptional data sets, rare in occurrence that are available only with written permission from the PI/investigator(s)).”

PIE strives to make datasets easily accessible to PIE LTER scientists, local, regional, and state partners and the broader scientific community. Datasets are available across the broad breadth of PIE research in the watersheds and estuary. We currently have no registration requirements for either observing or downloading data from our web site, which has resulted in seamless access to all PIE LTER data. PIE data downloads on our web site are accompanied by a metadata document, which requests (based on the honor system) users of the data to notify the corresponding Principal Investigator about reasons for acquiring the data and resulting publication intentions (see [PIE LTER Data Use Agreement](#).) PIE currently has 346 data packages in the LTER Network Metacat and contributes routinely to network databases of ClimDB/HydroDB, Personnel, Bibliography and Site DB. Contributions of data and metadata to the LTER Network PASTA Data Portal are actively ongoing with 250 of 346 data packages currently available in PASTA. We are continuing to QA/QC the remaining data for EML 2.1.0 compliancy and PASTA readiness. The remaining data should be available in PASTA by mid 2014.

NETWORK PARTICIPATION

The PIE LTER program participates in the annual LTER Information Managers meetings and contributes to network level databases of ClimDB, HydroDB, Personnel, Bibliography, Site DB, LTER Data Portal (Metacat and PASTA) and EcoTrends. Over the past 3 years Hap Garritt has participated as a member of the Unit Dictionary, DEIMS and Governance and GIS working groups. PIE researchers Wil Wollheim (PI) and Inke Forbrich (Post-Doc) participated in the 2011 SensorNIS workshop Hubbard Brook, NH, October 2011. Hap Garritt (IM) participated in the 2013 Software tools and strategies for managing sensor networks workshop, Albuquerque, NM, April 2013. Jim Morris is involved with the Veg-DB working group in designing a LTER database portal for vegetation data.

ACCOMPLISHMENTS 2010 -2014

Upgrading the PIE web site to a more modern, user friendly, functional web site has been a major priority over the last several years. The new PIE web site, <http://pie-lter.ecosystems.mbl.edu>, based on a Drupal 6 content management system, provides a comprehensive and easily navigable interface through use of dynamic menus and search capabilities. The PIE web site is a product of our Drupal Ecological Information Management System (DEIMS) collaborative with other LTER sites (SEV, LUQ, NTL, ARC, JRN,LNO), the MBL/WHOI Library and Encyclopedia of Life. The web site will be further improved upon with our anticipated migration to a Drupal 7 version of DEIMS, <https://drupal.org/project/deims>, in the coming year. In the open source community, Drupal 7 is more widely supported than Drupal 6 which will allow for standardization across the DEIMS collaborative.

PIE also prioritized improving PIE data accessibility on the web and in the LTER NIS. We have been updating metadata from EML 2.0.1 to EML 2.1.0 to provide high quality data and metadata for the PIE web site and the LTER Metacat and PASTA data portals. PIE developed a script to convert our legacy GIS metadata from MS Word FGDC metadata to EML 2.1.0. PIE legacy GIS information is now EML 2.1.0 compliant and available via Metacat and PASTA. We are currently using the ESRI2EML script developed by the LTER IM community to convert Clark University half-meter resolution urban lawn ESRI metadata to EML 2.1.0 which will allow subsequent upload of data to Metacat and PASTA.

6) PUBLICATION SUMMARY

Since 2010 the PIE LTER has produced 87 journal articles and 10 book chapters. Students have completed 5 Ph.D. dissertations, 19 MS theses and we have had 8 undergraduate do senior honors projects with us. A complete list of 2010-2014 publications is on the PIE web section for the reviewers, <http://pie-lter.ecosystems.mbl.edu/content/pie-review>.

Table 1. Long-term core measurements conducted at regular intervals in watersheds, estuary and coastal ocean. Data sets and methods are available on the PIE LTER web site (<http://pie-ter.ecosystems.mbl.edu/content/data>). LTER core areas: 1) Primary production, 2) Organic matter, 3) Nutrients, 4) Disturbance, 5) Dynamics of populations.

RESEARCH AREA & LOCATIONS	CORE AREA	VARIABLES	FREQUENCY	METHOD
WATERSHED NADP sites (Lexington & Truro, MA)	1	Wet/Dry temperature (T), insolation, precip, wet & dry N/P deposition	Hourly	NADP program
WATERSHED PIE weather station, Marshview Field Station	1	Temp, precipitation, humidity, wind speed/direction, barometric pressure, solar radiation, PAR	15 minute and daily	Campbell Scientific weather station
WATERSHED NCDC sites (Boston, Groveland, Bedford, Haverhill, Lawrence, Marblehead, Middleton, Reading, Ipswich & Newburyport, MA)	1	Temperature, precipitation	Daily	NOAA, National Climatic Data Center
WATERSHED Sub-catchment headwater streams of Ipswich & Parker Rivers (suburban, forest, and wetland dominated catchments)	2, 3, 4	Temp, H ₂ O level, NH ₄ ⁺ , NO ₃ ⁻ , PO ₄ ³⁻ , DO(N, P & C) PO(C&N), TSS	Monthly grab samples	Data logger and grab samples, Alpkem autoanalyzer, Lachat autoanalyzer, Shimadzu TOC/TN, CHN, gravimetric
WATERSHED Sub-catchment headwater streams of Ipswich & Parker Rivers	2, 3, 4	NO ₃ ⁻ , Total nitrogen, carbon, and phosphorus	Monthly composite samples (4x per day)	SIGMA autosampler and logger, Alpkem autoanalyzer, Shimadzu TOC/TN
WATERSHED Export at Ipswich, & Parker dams	2, 3	Temp, NH ₄ ⁺ , NO ₃ ⁻ , PO ₄ ³⁻ , DO(N, P & C) PO(C&N), TSS (grabs). NO ₃ ⁻ , Total C, N, and P (autosamplers).	Monthly grabs, plus two-day composite sampling using autosampler	SIGMA autosampler and logger, Alpkem autoanalyzer, Shimadzu TOC/TN, CHN, gravimetric
WATERSHED Export at Ipswich & Parker River dams	4	Riverine discharge	Daily	USGS station

MARSH Parker & Rowley River marshes	1	Macrophyte productivity	Monthly-semi monthly, during growing season	Phenometric
MARSH & ESTUARY Parker & Rowley River marshes	1	Algal biomass	Monthly during growing season. 5 benthic habitats in marsh	Pigment analysis
MARSH Parker & Rowley River marshes	2, 3	Accretion	Monthly, during growing season, semi-annual	SET tables, marker horizons, sedimentation plates
MARSH Parker & Rowley River marshes	2, 3, 4	Porewater - NH_4^+ , NO_3^- , PO_4^{3-} , DO(C&N) Eh, pH, S^2 , conductivity	Monthly - bimonthly	Diffusion samplers
MARSH Parker & Rowley River marshes	4	Groundwater height	5 minute intervals during growing season	Pressure transducers
ESTUARY Parker River and Plum Island Sound	1, 2, 3, 4, 5	Light, DO, T, Cond, NH_4^+ , NO_3^- , PO_4^{3-} , DO(N,P,C), PO(C,N), TSS, Chl, DO, Prim. Prod. & Resp., phytoplankton & zooplankton preserved samples	Semi-annual, high/ low discharge conditions	Licor, YSI sondes, autoanalyzer, UV & high temp oxidation, CHN, gravimetric, acetone/fluorescence, O ₂ , DIC, direct count, net tows
ESTUARY Parker River and Plum Island Sound. Three locations, oligohaline, brackish, marine (upper, mid, sound)	1, 2, 4	Temp, DO, conductivity and depth	0.25 hr and multi-day intervals	YSI water quality sondes
ESTUARY NOAA/NOS, Boston, MA	4	Sea level	Monthly	NOAA/NOS station
ESTUARY Parker River and Plum Island Sound	5	Phytoplankton	Semi-annual, high/ low discharge conditions	CHEM TAX, HPLC pigments
ESTUARY Parker River	3, 4	Benthic fluxes	Semi-annual	Core incubations

<p>ESTUARY & HIGHER TROPHIC LEVELS</p> <p>Ipswich, Parker & Rowley Rivers and Plum Island Sound</p>	2,3	Functional group representatives: Sediments, POM, microbes, macrophytes, benthic diatoms, zooplankton, <i>Geukensia</i> , <i>Mytilus</i> , <i>Mya</i> , <i>Crassostrea</i> , <i>Nereis</i> , <i>Fundulus</i> , <i>Menidia</i> , Striped bass	Yearly at locations along a transect from fresh to marine	C, N Stable isotopes – IRMS Sulfur and deuterium on select samples
<p>HIGHER TROPHIC LEVELS</p> <p>Ipswich, Parker & Rowley River marshes and Plum Island Sound</p>	5	Zooplankton	Semi-annual, high/ low discharge conditions	Net tows, size fractions, direct counts
<p>HIGHER TROPHIC LEVELS</p> <p>Ipswich, Parker & Rowley River marshes and Plum Island Sound</p>	5	Birds	Monthly (May – Oct) in conjunction with Audubon and USFWS -Parker River National Wildlife Refuge.	Direct counts Lag to clear final data to LTER posting through USFWS is 2 years.
<p>HIGHER TROPHIC LEVELS</p> <p>Parker & Rowley Rivers and Plum Island Sound</p>	2, 3, 5	Nekton (fish, crabs and shrimp)	Monthly May - October	Flume nets provide a more stable estimate of small nekton use of marsh habitats and will replace the seine surveys after intercalibration.
<p>HIGHER TROPHIC LEVELS</p> <p>Parker & Rowley Rivers and Plum Island Sound</p>	2,3,5	Marsh Invertebrates	Monthly June-October	Numbers and biomass of marsh invertebrates using clip plots.
<p>HIGHER TROPHIC LEVELS</p> <p>Watershed portion of Ipswich, Parker & Rowley Rivers</p>	5	Anadromous fish	Yearly	New work in Watershed. Using tags and direct counts in cooperation with local watershed association groups.

Table 2. Collaborating projects in effect 2010-2013.

Bold indicate that the PI is a member of the LTER team. Code names are provided simply for reference since they appear on some of the posters. These projects are broken down into three groups:

- 1) Closely collaborating projects – these are projects that heavily rely upon the PIE LTER facilities and personnel and are closely tied to ongoing PIE goals and data collection efforts.
- 2) Cross site and regional projects – both within the LTER network and outside of it.
- 3) Intellectually linked – these projects do not directly use PIE sites or resources but have a strong intellectual connection to current PIE research.

1) Closely Collaborating Projects

Funding	PIs	Code Name	Topic
NSF OCE	Fagherazzi, Deegan, Fulweiler, FitzGerald	LENS	ETBC Feedbacks between nutrient enrichment and intertidal sediments: Erosion, stabilization, and landscape evolution.
EXXON-MOBIL	Fagherazzi	Bars	Morphodynamics and sedimentology of tidal bars in Plum Island Sound.
NSF-DEB	Deegan, Peterson, Johnson, Mozdzer, Bowen, Giblin, Fagherazzi, Nelson, McCormick	TIDE III	Ecosystem evolution and sustainability of nutrient enriched coastal saltmarshes (2014-).
NSF-DEB	Deegan, Peterson, Warren, Fleeger	TIDE	Interacting controls on ecosystem function: Nutrient state and omnivory in salt marsh ecosystems.
USGS	Deegan, Neill	NE CSC	Northeast Climate Science Center – Coastal impacts of climate change
NSF-DEB	Sievert, Cardon, Giblin	SONiCC	The role of sulfide oxidizing bacteria in marsh C and N cycling – focus on plant rhizosphere.
NOAA Sea Grant, MA	Giblin, Vallino, Banta	N Path	Nitrate reduction pathways in salt marsh sediments: The controls on denitrification, anammox and DNRA.
NOAA Sea Grant, MA	Giblin, Vallino, Banta		How nitrogen inputs to coastal areas affect sediment accumulation and decomposition rates in marshes.
NSF	Giblin	FSML	Improving the lab space at the Marshview field station
Mass Bays Program (EPA-NEP)	Moore, Burdick, Buchsbaum		Effect of salinity on the recent spread of Phragmites in northern sections of Plum Island Sound.
Mass Bays Program (EPA-NEP)	Novak, Short		Developing a site selection model for eelgrass restoration in Plum Island Sound.
New England Biolab Foundation	Duff		Teaching about climate change in schools – closely associated with our Schoolyard program.
NASA NEWS	Wollheim, Salisbury, Aiken	NASA DOC	Quantify DOC and DOC character across land use and river size at PIE. Controls of DOC flux and aquatic transformations.
NSF-CNH	Polsky, Hopkinson, Pontius, Wollheim	CNH	Suburbanization, water-use, nitrogen cycling and eutrophication: Interactions, feedbacks and uncertainties in the Ipswich River watershed and Plum Island Sound estuary.
NSF-DEB	Wollheim, Peterson, Gooseff, Hopkinson, Vorosmarty	N Scaling	The role of transient storage zones in regulating nutrient fluxes across stream size.

Brown University	Tang, Deegan	TSA Phenology	Does nutrient enrichment alter the traits and flowing phenology of <i>Spartina alterniflora</i> ?
NSF (Bio Oce)	Stanley, Spivak		Eutrophication effects on sediment metabolism and benthic algal-bacterial coupling: An application of novel techniques in a LTER estuary.
EPA	Wigand, Deegan		Using CT scans to understand how eutrophication affects <i>Spartina</i> belowground biomass.
EPA	Ayvazian, Deegan		How does eutrophication affect the food source and growth?
University of Massachusetts/USGS	Mather, Deegan	Striped bass	Striped bass distribution and habitat use in Plum Island Sound estuary.
Northeast Climate Science Center	Deegan		Does eutrophication make saltmarshes more susceptible to climate change?
YSI Foundation	Hopkinson, Weston, Giblin, et al.		Determining the effects of land use and climate change on estuarine metabolism: Development of new methods for analyzing tidal coastal systems.
NH Water Resources Center	Lightbody, Kalnejais, Wollheim		Quantifying strength of linkages between advection dominated channels and fluvial wetlands, quantifying reaction rates using chambers

2) Cross-Site Regional

Funding	PIs	Code Name	Topic
NSF Macrobiology	Dodds, Bowden, Jones, Whiles, Ballantine, Rosemond, Wollheim	SCALER	Scaling aquatic ecosystem processes from reaches to river networks. Understanding patterns of dissolved oxygen.
NSF/USFS ULTRA-ex, plus recent NSF/EPA Supplement	Warren, Polsky, Wollheim	ULTRA-ex	Predicting impact of future land use scenarios on hydrology and nutrient fluxes.
NSF EaSM	Vorosmarty, Melillo, Duchin, Gonzalez, Wollheim	Northeast EaSM	Modeling interactions of energy, economy and ecosystems in the Northeast corridor.
NSF-EF	Groffman, Neill, Polsky	Ecological Homogenization of Urban America	Tests the hypothesis that urban development across the US is homogenizing ecosystem structure and function across North America.
USGS – CSC	Deegan, Neill	SLR & Birds	Predicting the effects of sea level rise on Atlantic coast wading bird habitat.
Hubbard Brook Research Foundation	Neill	Carbon Science Links	Compares carbon stocks and C storage options across multiple counties in NE US including PIE region.
NOAA-Mass CZM	Giblin, Vallino	CZM	Identifying at risk resources and supporting climate change adaptation responses
NSF-LTER	Pontius	Maps and Locals	Develops a quantitative framework and software to measure land change and integrates local ecological knowledge across LTER sites.

NSF-DEB	Morris	SC LTREB	LTREB: Long term studies of saltmarsh primary production-based in South Carolina.
UMASS Center for Agriculture	Polsky	Integrated Research and Extension Project	Understanding the factors that influence outdoor residential water conservation: A case study in suburban Boston.

3) Intellectually Linked

Funding	PIs	Code Name	Topic
Mass Bays Program (EPA-NEP)	Deegan , Logan (MASS Div. Mar. Fish)	Docks and Shading	Effects of dock shading on saltmarsh habitat
NSF-EAR	Horton, Kemp, Morris , et al.		Collaborative research: Sea-level rise and saltmarsh response: a paleo perspective.
NOAA	Hagen, Morris , et al.		Integrated modeling for the assessment of ecological impacts of sea level rise.
SC NOAA Sea Grant	Morris , et al.		The molecular basis of brown marsh.
NSF-OCE/DEB	Alber et al., and Hopkinson	GCE LTER	GA LTER – Incorporating C budgeting of coupled marsh-estuary into long-term program.
NASA IDS	Lohrenz et al. and Hopkinson		Assessing impacts of climate and land use change on terrestrial ocean fluxes of carbon and nutrients and their cycling in coastal ecosystems.
NSF-EF	Vallino , Huber	ATB-MEP	Part of the NSF Advancing Theory in Biology program examining the use maximum entropy production (MEP) to explain microbial biogeochemistry.
NOAA	Polsky	SARP	Integrated water and land planning as a climate adaptation strategy: Comparisons of Portland, Oregon and Phoenix, Arizona.
NSF DMUU	Polsky	Decision Center for a Desert City	Exploring how urbanization and planning interactions affect climate vulnerabilities.
NSF-OCE	Rich, Vallino , Giblin	Anammox	Examined controls on metabolic switch between denitrification, anammox and dissimilatory nitrate reduction to ammonium. Developed MEP-based model for anaerobic N processing.
NSF-EPSCOR	Nisbet, Gardner, Wake, Howarth, Wollheim	Ecosystems and Society	Characterizing ecosystem services of New England.
NOAA-Sea Grant	Wollheim , McDowell, Robinson, Peterson, Dailey, Toppin, Pellerin		Understanding the mechanisms controlling storm event nitrogen fluxes from the Lamprey River Watershed using continuous in situ sensors.

Table 3. Major Experiments at PIE LTER.

Purpose	Experiment Established	Ecosystem Type	Manipulation	Measurements
On-going experiments				
Test fundamental plant limiting nutrient and sediment and vegetation response.	N&P enrichments to marsh surface. 15 years — Established in 1998.	Marsh platform <i>S. alterniflora</i> , <i>S. patens</i> and <i>Typha latifolia</i>	Inorganic N and P addition to 1m ² plots.	Porewater nutrients, plant standing stocks and production, sediment deposition, marsh elevation.
Test the relative strength of top down (predator) and bottom up (nutrient) controls on multiple ecosystem functions of saltmarsh ecosystems.	TIDE 10 years — established in 2003; Nutrient enrichment 2004-2013; Crossed by predator removal 2004-2008.	8 salt marsh creek watersheds, 60,000 m ² each; benthic algae in creeks, creekbank <i>S. alterniflora</i> , high marsh dominated by <i>S. patens</i> , short form <i>S. alterniflora</i> on marsh platform	Enrichment of incoming tidal water with 70 μM nitrate and 5 μM P. Selective removal of meso-consumer fish that literature suggested was at top of tropic cascade.	N cycling, microbial and primary production, microbial, plant and animal community structure and abundance, marsh elevation and change in creekbank geomorphology.
Evaluation of a real-world nutrient enrichment of saltmarsh creek to determine the applicability of experimental manipulations and inform management.	Greenwood Creek Long-term enrichment by sewage outfall. 60 years - outfall started in 1950s. Monitoring began in 2000	Fresh to salt marsh creek 1km long	Town of Ipswich sewage effluent (~1000 μM total N in effluent).	Nutrients, isotopes, plant, animal and microbial community.
Test the impact of physical structure and habitat heterogeneity on biogeochemistry and community structure.	Dam removals – Human and beaver. Beaver dam removal planned in next 2 years.	Freshwater streams	Removal of beaver dams and human dam (timing in cooperation with state plan for dam removals).	Currently measuring biogeochemistry and community composition at locations of possible dam removals.
Experiments transitioned to periodic monitoring				
Test effect of a reduction in the availability of low quality organic matter	Detritus removal Saltmarsh. >25 years haying; evaluation of hypotheses began in 2000.	6 salt marsh creek watersheds, ~60,000 m ²	Experimental areas commercially hayed every 2 years – ongoing.	Biogeochemistry, plant and animal community, Intensive 2000-2004; ongoing periodic sampling.

Table 4. Education and Outreach 2010-2013: Education

Category	Institutions	Number of participants	Notes
K-12 Education	Various local schools	908 students and 28 teachers per year	Includes 225 students each year from a district with high percentage of minorities
K-12 Education	Governor's Academy	11 students	Summer research internships
K-12 Education	Triton Regional H.S.	35 students	Environmental science class does winter stream sampling for PIE
High School Education	Gulf of Maine Institute	Teams of 8 students and 2 mentors. Summer conclaves with ca. 50 students.	Giblin on Board of Directors, Duff regularly teaches at summer institute. Johnson, Deegan, Nelson, Buchsbaum gave presentations and led field trips on coastal eutrophication and climate change.
Undergraduate Education	Various colleges	11 REU's funded by LTER, 12 at Clark through HERO	Additional REU's have been funded by other universities
Undergraduate Education	U. New Hampshire	1 UNH Undergrad conducted senior year capstone project	Presented at the UNH Undergraduate Research Conference
Undergraduate Education	Various colleges	52 SES students	Deegan/Giblin/Vallino
Undergraduate Education	Boston Univ.	37 students	Estuaries and Nearshore Systems class at PIE, Fagherazzi
Graduate Education	Boston University	3 Ph.D.	Fagherazzi
Graduate Education	Brown	3 Ph. D.	Deegan
Graduate Education	Brown-MBL IGERT	12	Giblin
Graduate Education	Clark University	4 Ph.D. 11M.S.	Pontius, Polsky
Graduate Education	LSU	1 M.S.	Deegan/Johnson
Graduate Education	LSU	1 M.S.	Deegan/Fleeger
Graduate Education	LTER Coastal Course	140 participants	Morris and Fagherazzi
Graduate Education	U. Mass-Amherst	2 MS; 1 Ph.D.	Mather
Graduate Education	U. Mass-Boston	2 Ph.D.	Bowen
Graduate Education	U. Mass-Dartmouth	1 Ph.D.	Chen/ Vallino
Graduate Education	U. New Hampshire	2 MS; 1 Ph.D.	Wollheim
Graduate Education	U. New Hampshire	3 M.S.	Lightbody/Wollheim
Graduate Education	U. Rhode Island	1 M.S.	Deegan
Graduate Education	Yale	1 Ph.D.	Raymond
Graduate Education	LTER Coastal Course	140 participants	Morris and Fagherazzi
Postdoctoral Fellows	MBL	3	Deegan, Giblin
Postdoctoral Fellows	U. New Hampshire	2	Wollheim
Postdoctoral Fellows	Kansas State Univ.	1	Mather

Table 4 (continued) Education and Outreach 2010-2013: Outreach

Audience	Activities
Coordination with Parker River National Wildlife Refuge	<p>Buchsbaum- Presentation on climate change vulnerability at Refuge. Giblin and Buchsbaum advised and commented on Comprehensive Conservation Plan.</p> <p>Duff report on North Pool <i>Phragmites</i> issue</p> <p>Duff collaboration to control perennial pepperweed.</p> <p>Regular discussions on mutual bird research – shorebirds, salt marsh sparrows, data sharing</p>
Coordination with other Federal Agencies	<p>Deegan and Johnson have given several presentations to EPA on the impacts of eutrophication on saltmarshes.</p> <p>Buchsbaum serves on Management Council of Mass Bays Program (EPA, National Estuaries Program) and on the Ecosystem Indicator Partnership of the Gulf of Maine Council on the Marine Environment</p>
Climate change outreach – local impacts	<p>Presentations on potential impacts on Great Marsh region by Giblin, Buchsbaum, Duff, Deegan, Nelson to a variety of audiences.</p>
Climate change outreach – national policy	<p>Morris: NOAA Restoration Center Sea Level Rise Impacts on Tidal Wetland Restoration Projects Steering Committee 2011; Coastal Louisiana Science and Engineering Special Team (SEST) member 2011-2013; UNESCO Blue Carbon Working Group Member, 2011-pres; NCEAS carbon sequestration group, 2009-2012</p> <p>Deegan: DOI Northeast Climate Science Consortium, Member Executive Board 2012-present; Coastal Louisiana Science and Engineering Special Team (SEST) member 2011-2013; ICES Study Group on Designing Marine Protected Area Networks in a Changing Climate, Invited Member, 2010 - 2011.</p> <p>Buchsbaum: Invited presentation on Great Marsh vulnerability to climate change at 1st National Adaptation Forum (Denver 2013).</p>
Conservation and Watershed Associations	<p>Buchsbaum (CoPI) and Duff (Ed Coordinator) are on staff of Mass Audubon, New England’s largest conservation organization.</p> <p>Member of PIE-Rivers (local river restoration coalition). Giblin keynote speaker. Wolheim wrote letter of support for successful proposal and is on steering committee.</p> <p>Wollheim on Ipswich River Watershed Association advisory committee and presented on nutrient loading and dissolved oxygen issues at Technical Advisory Committee Meeting Recruit private citizens to help collect water sampled during winter. Two local residents, and one class at Triton regional HS.</p>

	<p>Buchsbaum and Giblin presented at Essex County Greenbelt Association (local land trust) annual meetings</p> <p>Great Marsh Symposium: Giblin keynote presentation on climate change. Buchsbaum presentation on marsh haying and poster on bird research.</p> <p>Deegan on the Massachusetts Nature Conservancy Board of Directors. 2011-2014</p>
Coordination with state agencies	<p>Partner with CZM on EPA funded grant on impact of SLR on coastal wetlands of the Parker River using LIDAR</p> <p>Buchsbaum participation in Great Marsh Revitalization Task Force and Mass Bays Program funded research. Vallino hydrology/hydrodynamic model was useful for plan development.</p> <p>Partner with Coastal Zone Management (CZM) in production of LIDAR map of southern New England. PIE LTER funded portion of flight to ensure entire PIE domain was flown with LiDAR</p>
Children's book on lawns	Polsky – part of LTER children's book series
New England Estuarine Research Society, Bird Conservation Conference	Buchsbaum, Duff, Johnson, REU presentations
Media	<p>15+ examples of articles in media highlighting PIE research. Includes articles in local and regional newspaper and journal.</p> <p>Neill organized workshops for science journalists.</p> <p>Johnson publishes Life in Science article "Weeds Making Waves" (Science 18 April 2014) about boats made from <i>Phragmites australis</i>. Johnson maintains a blog of PIE research and natural history.</p> <p>Duff and Buchsbaum co-starred in "Danger in the Reeds" video.</p>
Engaging citizens in our science	<p>Adopt a Herring Program – citizens "adopt" individual tagged river herring and follow their movements through a website.</p> <p>Adopt a Striped Bass website developed by Mather, Deegan and students to explain research on mobile species that link ecosystems and provide support for tagging program.</p> <p>Citizen Science - Volunteers have assisted the LTER project with bird surveys, water sampling, and controlling invasive species.</p>
Teacher Training	<p>Salt Marsh Science presented at Massachusetts Environmental Education Society.</p> <p>Duff developed "Inland Fish and Warming Waters" curriculum and presented it at the National Science Teachers Association's Conference in Boston April 2014</p>

Table 5. Senior Personnel of the PIE LTER

Anne Giblin - Marine Biological Laboratory – lead PI – biogeochemistry

Executive Committee

Robert Buchsbaum	Mass Audubon – group leader – outreach
Linda Deegan	Marine Biological Laboratory - group leader – consumers
Charles Hopkinson	University of Georgia - group leader – estuarine biogeochemistry
James Morris	University of South Carolina – group leader - marshes
Robert “Gil” Pontius	Clark University – group leader – human dimension
Wil Wollheim	University of New Hampshire - group leader – watershed research
Joseph Vallino	Marine Biological Laboratory - group leader – modeling

Other Senior Personnel

Jennifer Bowen	University of Massachusetts – microbes
Sergio Fagherazzi	Boston University – geomorphology
David Johnson	Marine Biological Laboratory – invertebrate biology and food webs
Colin Polsky	Clark University – geography
Peter Raymond	Yale University – estuarine and marine carbon cycling
Jeffrey Turner	University of Massachusetts Dartmouth – zooplankton (2010-2012)
Nathanial Weston	Villanova University – estuarine biogeochemistry

Other personnel

Robert “Hap” Garritt	Marine Biological Laboratory - Information Manager
Elizabeth B. Duff	Mass Audubon – Education Coordinator III

REFERENCES CITED

- Algar, C.K. and J.J. Vallino. 2014 Predicting microbial nitrate reduction pathways in coastal sediments. *Aquat. Microb.Ecol.* 71 (3): 223-238, doi: 10.3354/ame01678.
- Altieri, A. H., M. D. Bertness, T. C. Coverdale, N. C. Herrmann, and C. Angelini. 2012. A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. *Ecology* 93:1402-1410.
- Andersen, D.C. and P.B. Shafroth. 2010 Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona. *Ecohydrology* 3: 325-338.
- Bain, D. J., J. A. Arrigo, M. B. Green, B. A. Pellerin, and C. J. Vorosmarty. 2011. Historical legacies, information and contemporary water science and management. *Water* 3:566-575.
- Bain, D. J., R. L. Hale, and W. M. Wollheim. 2012. Hotbeds of biogeochemical diversity: Insights from urban Long-Term Ecological Research sites. *Elements* 8:435-438, doi: 410.2113/gselements.2118.2116.2435.
- Bain, D.J., M. B. Green, J. L. Campbell, J.F. Chamblee, S. Chaoka, J.M. Fraterrigo, S.S. Kaushal, S.L. Martin, T.E. Jordan, A.J. Parolari, W.V. Sobczak, D.E. Weller, W. M. Wollheim, E.R. Boose, J.M. Duncan, G.M. Gettel, B.R. Hall, P.Kumar, J.R. Thoompson, J.M. Vose, E.M. Elliott, and D.S. Leigh. 2012. Legacy effects in material flux: structural catchment changes predate long-term studies. *Bioscience* 62:575-584.
- Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: How channel networks structure riverine habitats. *Bioscience* 54:413-427.
- Bernhard, A. E., J. Tucker, A. E. Giblin & D. A. Stahl. 2007. Functionally distinct communities of ammonia-oxidizing bacteria along an estuarine salinity gradient. *Environmental Microbiology* 9:1439-1447.
- Briggs, M., M. Gooseff, C. Arp, and M. Baker. 2009. A method for estimating surface transient storage parameters for streams with concurrent hyporheic storage. *Water Resource Research* 45:W00D27.
- Briggs, M. A., M. Gooseff, B. J. Peterson, K. Morkeski, W. M. Wollheim, and C. S. Hopkinson. 2010. Surface and hyporheic transient storage dynamics throughout a coastal stream network. *Water Resource Research* 46:W06516, doi:06510.01029/02009WR008222.
- Buchsbaum, R. N., L. A. Deegan, J. Horowitz, R. H. Garritt, A. E. Giblin, J. P. Ludlam, and D. H. Shull. 2009. Effects of regular salt marsh haying on marsh plants, algae, invertebrates and birds at Plum Island Sound, Massachusetts. *Wetlands Ecology and Management* 17:469-487.
- Burchsted, D., M. Daniels, R. Thorson, and J. Vokoun. 2010. The river discontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. *BioScience* 60:908-922.
- Burgin, A. J. and S. K. Hamilton. 2007. Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways. *Frontiers in Ecology and the Environment* 5:89-96.
- Carpenter, S. R., M. L. Cole, M. Pace, M. Van de Bogert, D. L. Bade, D. Bastviken, J. R. Gille, J. F. Hodgson, and E. S. Kritzberg. 2005. Ecosystem subsidies: Terrestrial support of aquatic food web from ¹³C addition to contrasting lakes. *Ecology* 86:2737-2750.
- Casini, M., T. Blenckner, C. Möllmann, A. Gårdmark, M. Lindegren, M. Llope, G. Kornilovs, M. Plikshs, and N. C. Stenseth. 2012. Predator transitory spillover induces trophic cascades in ecological sinks. *Proceedings of the National Academy of Sciences* 109:8185-8189.

- Claessens, L., C. Hopkinson, E. Rastetter, and J. Vallino. 2006. Effect of historical changes in land use and climate on the water budget of an urbanizing watershed. *Water Resources Research* 42:W03426.
- Curtis, L. A., J.L. Kinley., and N.L. Tanner. 2000. Longevity of oversized individuals: growth, parasitism, and history in an estuarine snail population. *Journal of the Marine Biological Association of the UK* 80(05): 811-820.
- D'Alpaos, A., S. Lanzoni, S.M. Mudd, and S. Fagherazzi. 2006. Modeling the influence of hydroperiod and vegetation on the cross-sectional formation of tidal channels. *Estuarine, Coastal and Shelf Science* 69:311-324.
- Dalsgaard, T., B. Thamdrup, and D. E. Canfield. 2005. Anaerobic ammonium oxidation (anammox) in the marine environment. *Research in Microbiology* 156:457-464.
- Davis, J. M., A. D. Rosemond, S. L. Eggert, W. F. Cross, and J. B. Wallace. 2010. Long-term nutrient enrichment decouples predator and prey production. *Proceedings of the National Academy of Sciences* 107:121-126.
- Deegan, L. A. 1990. Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. *Marine Ecology Progress Series* 68:195-205.
- Deegan, L. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Sciences* 50:74-79.
- Deegan, L. A. and R. H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series* 147:31-47.
- Deegan, L. A., J. E. Hughes, and R. A. Rountree. 2000. Salt marsh ecosystem support of marine transient species. *In* M. Weinstein and D. A. Kreeger (Eds.). *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic, Dordrecht, The Netherlands. pp. 333-365.
- Deegan, L. A., J. L. Bowen, D. Drake, J. W. Fleeger, C. T. Friedrichs, K. Galvan, J. E. Hobbie, C. S. Hopkinson, D. S. Johnson, J. M. Johnson, L. E. Lemay, E. Miller, B. Peterson, C. Picard, S. Sheldon, J. J. Vallino, and R. S. Warren. 2007. Susceptibility of salt marshes to nutrient enrichment and predator removal. *Ecological Applications* 17:S42-S63.
- Deegan, L. A., D. S. Johnson, R. S. Warren, B. J. Peterson, J. W. Fleeger, S. Fagherazzi, and W. M. Wollheim. 2012. Coastal eutrophication as a driver of salt marsh loss. *Nature* 490:388-392.
- Dewar, R. 2003. Information theory explanation of the fluctuation theorem, maximum entropy production and self-organized criticality in non-equilibrium stationary states. *Journal of Physics A: Mathematical and General* 36:631-641.
- Dewar, R. C. 2005. Maximum entropy production and the fluctuation theorem. *Journal of Physics A: Mathematical and General* 38:L371-L381.
- Dodds, W. K., C. T. Robinson, E. E. Gaiser, G. J. Hansen, H. Powell, J. M. Smith, N. B. Morse, S. L. Johnson, S. V. Gregory, and T. Bell. 2012. Surprises and insights from long-term aquatic data sets and experiments. *Bioscience* 62:709-721.
- Dodds, W.K. (Eds.) 2009. *Laws, Theories and Patterns in Ecology*. University of California Press.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. *Science* 333:301-306.
- Eyre, B. D. and A. J. P. Ferguson. 2006. Impact of a flood event on benthic pelagic coupling in a subtropical east Australian estuary (Brunswick). *Estuarine, Coastal, and Shelf Science* 66:111-122.
- Fagherazzi, S. and D. J. Furbish. 2001. On the shape and widening of salt marsh creeks. *Journal of Geophysical Research* 106:991-1005.

- Fagherazzi, S., L. Carniello, L. D'Alpaos, and A. Defina. 2006. Critical bifurcation of shallow microtidal landforms in tidal flats and salt marshes. *Proceedings of the National Academy of Sciences* 103:8337-8341.
- Fagherazzi, S., C. Palermo, M. C. Rulli, L. Carniello, and A. Defina. 2007. Wind waves in shallow microtidal basins and the dynamic equilibrium of tidal flats. *Journal of Geophysical Research* 112:F02024, doi:10.1029/2006JF000572.
- Fagherazzi, S., M. L. Kirwan, S. M. Mudd, G. R. Guntenspergen, S. Temmerman, A. D'Alpaos, J. van de Koppel, J. M. Rybczyk, E. Reyes, C. Craft, and J. Clough. 2012. Numerical models of salt marsh evolution: Ecological and climatic factors. *Reviews of Geophysics* 50:1, doi:10.1029/2011RG000359.
- Fagherazzi S., D.M. FitzGerald, R.W. Fulweiler, Z. Hughes, P.L. Wiberg, K.J. McGlathery, J.T. Morris, T.J. Tolhurst, L.A. Deegan, and D.S. Johnson, D.S. 2013. Ecogeomorphology of Salt Marshes. *In: John F. Shroder (Ed.). Treatise on Geomorphology, Volume 12.* pp. 180-200.
- Ferry, K. H. and M. E. Mather. 2012. Spatial and temporal diet patterns of subadult and small adult striped bass in Massachusetts estuaries: Data, a synthesis, and trends across scales. *Marine and Coastal Fisheries* 4:30-45.
- Flecker, A. S., P. B. McIntyre, J. W. Moore, J. T. Anderson, B. W. Taylor, and R. O. Hall Jr. 2010. Migratory fishes as material and process subsidies in riverine ecosystems. *In Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques.* American Fisheries Society, Symposium, Vol. 73. pp. 559-592.
- Fleeger, J. W., D. S. Johnson, K. A. Galván, and L. A. Deegan. 2008. Top-down and bottom-up control of infauna varies across the saltmarsh landscape. *Journal of Experimental Marine Biology and Ecology* 357:20-34.
- Foo, K., D. Martin, C. Wool, C. Polsky. 2013. The production of urban vacant land: relational placemaking in Boston, MA neighborhoods. *Cities* 35:156-163.
- Fuller, M.R. and B.L. Peckarsky. 2011. Ecosystem engineering by beavers affects mayfly life history. *Freshwater Biology* 56: 969-979.
- Galván, K., J. W. Fleeger, and B. Fry. 2008. Stable isotope addition reveals dietary importance of phytoplankton and microphytobenthos to saltmarsh infauna. *Marine Ecology Progress Series* 359:37-49.
- Galván, K., J. W. Fleeger, B. Peterson, D. Drake, L. A. Deegan, and D. S. Johnson. 2011. Natural abundance stable isotopes and dual isotope tracer additions help to resolve resources supporting a saltmarsh food web. *Journal of Experimental Marine Biology and Ecology* 410:1-11.
- Gardner, L. R. and E. F. Gaines. 2008. A method for estimating pore water drainage from marsh soils using rainfall and well records. *Estuarine, Coastal and Shelf Science* 79:51-58.
- Giblin, A. E., N. B. Weston, G. T. Banta, J. Tucker, and C. S. Hopkinson. 2010. The effects of salinity on nitrogen losses from an oligohaline estuarine sediment. *Estuaries and Coasts* 33: 1054-1068.
- Giner, N.M., C. Polsky, R.G. Pontius Jr., D.M. Runfola. 2013. Understanding the social determinants of lawn landscapes: A fine-resolution spatial statistical analysis in suburban Boston, Massachusetts, USA. *Landscape and Urban Planning*. 111:25-33.
- Giner, N.M., C. Polsky, R.G. Pontius Jr., S. Ratick, and D.M. Runfola, accepted 3/2014. Spatial prediction of lawns in suburban Boston, Massachusetts, USA. *Cities and the Environment*.
- Gober, P., K.L. Larson, R. Quay, C. Polsky, H. Chang, V. Shandas. 2013. Why land planners and water managers don't talk to one another and why they should! *Society and Natural Resources* 26:356-364.
- Haas, H. L., C. J. Freeman, J. M. Logan, L. Deegan, and E. F. Gaines. 2009. Examining mummichog growth and movement: Are some individuals making intra-season migrations to optimize growth? *Journal of Experimental Marine Biology and Ecology* 369:8-16.

- Hartig, E. K., V. Gornitz, A. Kolker, A. F. Mushacke, and D. Fallon. . 2002. Anthropogenic and climate-change impacts on salt marshes of Jamaica Bay, New York City. *Wetlands* 22:71-89, doi:10.1672/0277-5212(2002)022[0071:AACCIO]2.0.CO.
- Harris EM, Martin DG, Polsky C, Denhardt L, Nehring A. 2012a. Beyond 'Lawn People': The role of emotions in suburban yard management practices. *The Professional Geographer*.
- Harris EM, Polsky C, Larson K, Garvoille R, Martin DG, Brumand J, Ogden L. 2012b. Heterogeneity in Residential Yard Care: Evidence from Boston, Miami, and Phoenix.. *Human Ecology*. 40:735-749.
- Hayden, B. and N. Hayden. 2003. Decadal and century-long changes in storminess at LTER sites. In D. Greenland, D. Goodin and R. Smith (Eds.). *Climate Variability and Ecosystem Response at LTER Sites*. Oxford University Press. pp. 262-285.
- Helton, A. M., G. C. Poole, J. L. Meyer, W. M. Wollheim, B. J. Peterson, P. J. Mulholland, E. S. Bernhardt, J. A. Stanford, C. Arango, L. R. Ashkenas, L. W. Cooper, W. K. Dodds, S. V. Gregory, R. O. Hall, S. K. Hamilton, S. L. Johnson, W. H. McDowell, J. D. Potter, J. L. Tank, S. M. Thomas, H. M. Valett, J. R. Webster, and L. Zeglin. 2011. Thinking outside the channel: Modeling nitrogen cycling in networked river ecosystems. *Frontiers in Ecology and the Environment* 9:229-238, doi:10.1890/080211.
- Hill, T. and C. Polsky. 2005. Suburbanization and adaptation to the effects of suburban drought in rainy central Massachusetts. *Geographical Bulletin* 47(2): 85-100.
- Hill, T. and C. Polsky. 2007. Suburbanization and drought: A mixed method vulnerability assessment in rainy Massachusetts. *Environmental Hazards* 7: 291-301.
- Holmes, R. M., B. J. Peterson, L. Deegan, J. Hughes and B. Fry. 2000. Nitrogen biogeochemistry in the oligohaline zone of a New England estuary. *Ecology* 81:416-432
- Hopkinson, C., A. Giblin, J. Tucker and H. Garritt. 1999. Benthic metabolism and nutrient cycling along an estuary salinity gradient. *Estuaries* 22: 863-881.
- Hughes, J. E., L. A. Deegan, B. J. Peterson, R. M. Holmes, and B. Fry. 2000. Nitrogen flow through the food web in the oligohaline zone of a New England estuary. *Ecology* 81:433-452.
- Huxel, G. R. and K. McCann. 1998. Food web stability: The influence of trophic flows across habitats. *American Naturalist* 152:460-469.
- Jelks H.L., S.J. Walsh, N.M. Burkhead, S. Contreras-Balderas , E. Diaz-Pardo , and D.A. Hendrickson . 2008. Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries* 33: 372–407.
- Johnson, D. S. and J. W. Fleeger. 2009. Weak response of saltmarsh infauna to ecosystem-wide nutrient enrichment and fish predator reduction: A four-year study. *Journal of Experimental Marine Biology and Ecology* 373:35-44.
- Johnson, D., J. Fleeger, and L. Deegan. 2009. Large-scale manipulations reveal that top-down and bottom-up controls interact to alter habitat utilization by saltmarsh fauna. *Marine Ecology Progress Series* 377:33-41.
- Johnson, D. S. and M. I. Short. 2013. Chronic nutrient enrichment increases the density and biomass of the mudsnail, *Nassarius obsoletus*. *Estuaries and Coasts* 36:28-35.
- Johnston, C. A., and R.J. Naiman, . 1990. Aquatic patch creation in relation to beaver population trends. *Ecology*, 1617-1621.
- Kathilankal, J. C., T. J. Mozdzer, J. D. Fuentes, P. D'Odorico, K. J. McGlathery & J. Zieman. 2008. Tidal influences on carbon assimilation by a salt marsh. *Environmental Research Letters* 3: 1-6.
- Kelaher, B. P. and J. S. Levinton. 2003. Variation in detrital enrichment causes spatio-temporal variation in soft-sediment assemblages. *Marine Ecology Progress Series* 261:85-97.
- Kemp P.S., T.A. Worthington ., T.E.L. Langford ., A.R.J. Tree and M.J. Gaywood . 2012. Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries* 13: 158–181.

- Kennedy, C. 2013. Habitat heterogeneity concentrates predators in the seascape: Linking intermediate-scale estuarine habitat to striped bass distribution. University of Massachusetts, Amherst. Masters Thesis.
- Kirwan, M. L., G. R. Guntenspergen, A. D'Alpaos, J. T. Morris, S. M. Mudd, and S. Temmerman. 2010. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37:L23401, doi:10.1029/2010GL045489.
- Kirwan M. L., R. R. Christian, L. K. Blum & M. M. Brinson. 2011. On the relationship between sea level and *Spartina alterniflora* production. *Ecosystems* 15: 140-147
- Koop-Jakobsen, K., and A. E. Giblin. 2009. Anammox in tidal marsh sediments: the role of salinity, nitrogen loading, and marsh vegetation. *Estuaries and Coasts* 32(2): 238-245.
- Kneib, R. T. 1997. The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology: An Annual Review* 35:163-220.
- Larson, K. L., D. D. White, P. Gober, C. W. Kirkwood, V. K. Smith, M. C. Nelson, C. L. Redman, and S. K. Wittlinger. 2013. "Advancing Science in Support of Water Policy and Urban Climate Change Adaptation at Arizona State University's Decision Center for a Desert City: A Synthesis of Interdisciplinary Research on Climate, Water, and Decision Making Under Uncertainty." Decision Center for a Desert City, Global Institute of Sustainability, Arizona State University. Technical Rpt. pp. 42.
- Lawrence, K. 2014. Effects of Discharge on Residence Time Distributions in a Small Headwater Wetland in the Ipswich River Watershed. University of New Hampshire. Masters Thesis.
- Leroux, S. J. and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147-1156.
- Lockfield, K. C. and J. W. Fleeger. 2013. Population-level responses by the mummichog, *Fundulus heteroclitus*, to chronic nutrient enrichment in a New England Salt Marsh. *Marine Ecology Progress Series*. *In press*.
- Lundberg, J. and F. Moberg. 2003. Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems* 6:0087-0098.
- Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall Jr. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* 92:1215-1225.
- Mariotti, G. and S. Fagherazzi. 2010. A numerical model for the coupled long-term evolution of salt marshes and tidal flats. *Journal of Geophysical Research* 115:F01004, doi:10.1029/2009JF001326.
- Mariotti G. and S. Fagherazzi. 2013. Critical width of tidal flats triggers marsh collapse in the absence of sea-level rise. *Proceedings of the National Academy of Sciences* 110:5352-5356, doi:10.1073/pnas.1219600110.
- Massol, F., D. Gravel, N. Mouquet, M. W. Cadotte, T. Fukami, and M. A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters* 14:313-323.
- Mather, M. E., J. T. Finn, K. H. Ferry, L. A. Deegan, and G. A. Nelson. 2009. Use of non-natal estuaries by migratory striped bass (*Morone saxatilis*) in summer. *Fisheries Bulletin* 107:329-338.
- Mather, M. E., J. T. Finn, S. M. Pautzke, D. Fox, T. Savoy, H. M. Brundage, L. A. Deegan, and R. M. Muth. 2010. Destinations, routes, and timing of adult striped bass on their southward fall migration: Implications for coastal movements. *Journal of Fish Biology* 77:2326-2337.
- Mather, M., J. Finn, C. Kennedy, L. A. Deegan, and J. M. Smith. 2013. What happens in an estuary doesn't stay there: Patterns of biotic connectivity resulting from long term ecological research. *Oceanography* 26:168-179.
- McCann, K. S. and N. Rooney. 2009. The more food webs change, the more they stay the same. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1789-1801.

- McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* 22:1711-1717.
- Mitwally H.M. and J.W. Fleeger . 2013. Long-term nutrient enrichment elicits a weak density response by saltmarsh meiofauna. *Hydrobiologia* 713:97-114.
- Morris, J. T. 1984. Effects of oxygen and salinity on ammonium uptake by *Spartina alterniflora* and *Spartina patens*. *Journal of Experimental Marine Biology and Ecology* 78:87-98.
- Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83:2869-2877.
- Morris, J. T., K. Sundberg, and C. S. Hopkinson. 2013. Salt marsh primary production and its responses to relative sea level and nutrients in estuaries at Plum Island, Massachusetts, and North Inlet, South Carolina, USA. *Oceanography* 26:78-84.
- Morris, J. T., G. P. Shaffer, and J. A. Nyman. 2013. Brinson Review: Perspectives on the influence of nutrients on the sustainability of coastal wetlands. *Wetlands*. 33:975-988.
- Morse, N. B. and W. M. Wollheim. In review. Climate variability masks the impacts of land use change on nutrient export in a suburbanizing watershed. *Biogeochemistry*.
- Mudd, S. M., S. Howell and J. T. Morris. 2009. Impact of the dynamic feedback between sedimentation, sea level rise, and biomass production on near surface marsh stratigraphy and carbon accumulation. *Estuarine, Coastal and Shelf Science* 82:377-389.
- Munguia, P., R.W. Osman, J. Hamilton, R. Whitlatch, and R. Zajac. 2011. Changes in habitat heterogeneity alter marine sessile benthic communities. *Ecological Applications* 21(3): 925-935.
- Naiman R.J., G. Pinay, C.A. Johnston and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* 75: 905-921.
- Nelson, J., C. Stallings, W. Landing, and J. Chanton. 2013. Biomass transfer subsidizes nitrogen to offshore food webs. *Ecosystems* 16:1130-1138.
- Pascal, P.-Y., J. W. Fleeger, H. T. Boschker, H. M. Mitwally, and D. S. Johnson. 2013. Response of the benthic food web to short-and long-term nutrient enrichment in saltmarsh mudflats. *Marine Ecology Progress Series* 474:27-41.
- Pascal P.-Y. and J.W. Fleeger. 2013. Diverse dietary responses by saltmarsh consumers to chronic nutrient enrichment. *Estuaries and Coasts*. 36: 1115-1124.
- Pautzke, S. M., M. E. Mather, J. T. Finn, L. A. Deegan, and R. M. Muth. 2010. Seasonal use of a New England estuary by foraging contingents of migratory striped bass. *Transactions of the American Fisheries Society* 139:257-269.
- Pennings, S. C. and B. R. Silliman. 2005. Linking biogeography and community ecology: Latitudinal variation in plant-herbivore interaction strength. *Ecology* 86: 2310-2319.
- Pittman, S., R. Kneib, C. Simenstad, and I. Nagelkerken. 2011. Seascape ecology: Application of landscape ecology to the marine environment. *Marine Ecology Progress Series* 427:187-302.
- Polis, G. A., M. E. Power, and G. R. Huxel (Eds). 2004. *Food Webs at the Landscape Level*. University of Chicago Press.
- Polsky, C., S. Assefa, K. Del Vecchio, T. Hill, L. Merner, I. Tercero and G. Pontius. 2009. The mounting risk of drought in a humid landscape: structure and agency in suburbanizing Massachusetts. *In* B. Yarnal, C. Polsky and J. O'Brien (Eds.). *Sustainable Communities on a Sustainable Planet: The Human-Environment Regional Observatory Project*. Cambridge University Press, New York.
- Polsky, C., R.G. Pontius, A. Decatur, N. Giner and D. Runfola. 2012. HERO Object-based Lawn Mapping Exploration of Suburbia: Rationale, Methods and Results for the NSF Plum Island Ecosystems Long-Term Ecological Research Site. Clark University George Perkins Marsh Institute Working Paper 2012-24. URL: <http://www.clarku.edu/departments/marsh/news/workingpapers.cfm>

- Polsky, C., J. M. Grove, C. Knudson, P. M. Groffman, N. Bettez, J. Cavender-Bares, S. Hall, J. Heffernan, S. Hobbie, K. Larson, J. Morse, C. Neill, K. Nelson, L. Ogden, J. O'Neill-Dunne, D. Pataki, M. Steele, and R.R. Chowdhury. 2014. Assessing the homogenization of urban land management with an application to US residential lawncare. *Proceedings, National Academy of Sciences* 111(12): 4432-4437. DOI:10.1073/pnas.1323995111
- Poole, G. C. 2002. Fluvial landscape ecology: Addressing uniqueness within the river discontinuum. *Freshwater Biology* 47:641-660.
- Poole, G. C. 2010. Stream hydrogeomorphology as a physical science basis for advances in stream ecology. *Journal of the North American Benthological Society* 29:12-25.
- Raymond, P. A. and C. S. Hopkins. 2003. Ecosystem modulation of dissolved carbon age in a temperate marsh-dominated estuary. *Ecosystems* 6: 694-705.
- Reiners, W. A. and K. L. Driese. 2001. The propagation of ecological influences through heterogeneous environmental space. *Bioscience* 51:939-950.
- Ritter, A. 2012. Effect of eutrophication on benthic microalgae. Senior Thesis. Middlebury College.
- Rosell, F., O. Bozser, P. Collen, and H. Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* 35(3-4): 248-276.
- Runfola, D.M., C. Polsky, C. Nicolson, N.M. Giner, R.G. Pontius, Jr., J. Krahe and A. Decatur. 2013. A growing concern? Examining the influence of lawn size on residential water use in suburban Boston, MA, USA *Landscape and Urban Planning* 119:113-123.
- Scheiner, S. M., and M.R. Willig. (Eds.). (2011). *The theory of ecology*. University of Chicago Press.
- Schneider, L., and R. G. Pontius. 2001. Modeling land-use change in the Ipswich watershed, Massachusetts, USA. *Agriculture, Ecosystems & Environment* 85:83-94.
- Shelford, V. E. 1931. Some concepts of bioecology. *Ecology* 12:455-467.
- Short, M.I. 2012. Nutrient effects on *Spartina patens* decomposition dynamics in a New England salt marsh. BS Brown University.
- Smith, J.M., and M.E. Mather. 2013. Beaver dams maintain native fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology* 58:1523-1538.
- Stewart, R. J., W. M. Wollheim, M. Gooseff, M. A. Briggs, J. M. Jacobs, B. J. Peterson, and C. S. Hopkins. 2011. Separation of river network scale nitrogen removal among main channel and two transient storage compartments. *Water Resource Research* 47:W00J10, doi:10.1029/2010WR009896.
- Thorp, J. H., M. C. Thoms, and M. D. DeLong. 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. *River Research and Applications* 22:123-147.
- Troxler, T. G., C. Coronado-Molina, D.N. Rondeau, S. Krupa, S. Newman, M. Manna, and F.H. Sklar. 2013. Interactions of local climatic, biotic and hydrogeochemical processes facilitate phosphorus dynamics along an Everglades forest-marsh gradient. *Biogeosciences Discussions* 10(6): 10287-10326.
- Turner, R. E. 2011. Beneath the salt marsh canopy: loss of soil strength with increasing nutrient loads. *Estuaries and Coasts* 34(5): 1084-1093.
- Vallino, J. J. and C. S. Hopkins, Jr. 1998. Estimation of dispersion and characteristic mixing times in Plum Island Sound Estuary. *Estuarine, Coastal, and Shelf Science* 46:33-350.
- Vallino, J. J. 2000. Improving marine ecosystem models: Use of data assimilation and mesocosm experiments. *Journal of Marine Research* 58:117-164.
- Vallino, J. J. 2003. Modeling microbial consortiums as distributed metabolic networks. *The Biological Bulletin* 204:174-179.
- Vallino, J. J. 2010. Ecosystem biogeochemistry considered as a distributed metabolic network ordered by maximum entropy production. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:1417-1427.

- Vallino, J. J. 2011. Differences and implications in biogeochemistry from maximizing entropy production locally versus globally. *Earth System Dynamics* 2:69-85.
- Vallino, J.J., Algar, C.K., Fernandez Gonzalez, N., Huber, J.A.. 2014. Use of receding horizon optimal control to solve MaxEP-based biogeochemistry problems. *In Beyond the Second Law: Entropy Production and Non-Equilibrium Systems*, Dewar, R.C., Lineweaver, C., Niven, R. and Regenauer-Lieb, K., (Eds), Springer, pp 337-359, doi: 10.1007/978-3-642-40154-1_18
- Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8:2-8.
- Weston, N. B., A. E. Giblin, G. Banta, C. S. Hopkinson and J. Tucker. 2010. The effects of varying salinity on ammonium exchange in estuarine sediments of the Parker River, Massachusetts. *Estuaries and Coasts* 33(4): 985-1003.
- Whittinghill, K. A., M. M. Mineau, W. M. Wollheim, R. B. Lammers, and R. J. Stewart. 2013. Modeling Nitrogen Processing in New England River Networks. Gordon Research Conference: Catchment Science: Interactions of Hydrology, Biology, and Geochemistry. Andover, NH.
- Winkel, A., Colmer, T. D., and O. Pedersen. 2011. Leaf gas films of *Spartina anglica* enhance rhizome and root oxygen during tidal submergence. *Plant, Cell and Environment* 34(12): 2083-2092.
- Winemiller, K. O., A. S. Flecker, and D. J. Hoeinghaus. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* 29:84-99.
- Wollheim, W. M., B. J. Peterson, C. J. Vorosmarty, C. Hopkinson, and S. A. Thomas. 2008. Dynamics of N removal over annual time scales in a suburban river network. *Journal of Geophysical Research - Biogeosciences* 113:G03038, doi:10.1029/2007JG000660.
- Wollheim, W. M., M. B. Green, C. Hopkinson, B. A. Pellerin, and N. Morse. 2013. Impacts of ecosystem service regionalization on a suburban New England watershed. *Estuaries and Coasts*, doi:10.1007/s12237-013-9646-8.
- Wollheim, W. M., T. K. Harms, B. J. Peterson, K. Morkeski, C. S. Hopkinson, R. J. Stewart, M. N. Gooseff, M. A. Briggs. In press. Nitrate uptake dynamics of surface transient storage in channels and fluvial wetlands. *Biogeochemistry*.
- Wu, J. and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. *The Quarterly Review of Biology* 70:439-466.