ABSTRACT

Title of Dissertation: EUTROPHICATION AND COASTAL WETLANDS:
LINKING NUTRIENT ENRICHMENT TO
TIDAL FRESHWATER MARSH ECOSYSTEM
STRUCTURE AND FUNCTION

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The Chesapeake Bay watershed has been affected by human activities for over

300 years, causing an increase in nutrients entering its coastal aquatic ecosystems. Yet

most of the efforts identifying the consequences of coastal eutrophication have not

observed its effects on the marginal tidal wetlands of the Bay. The tidal freshwater

marshes of Broad Creek and Marshyhope Creek, two tidal tributaries of the Nanticoke

River (Delmarva Peninsula, USA), have been exposed to different levels of nutrient

input, that appear to be adversely affecting Broad Creek. The Broad Creek watershed has

had historically higher fertilizer application rates and more animal production facilities

than Marshyhope Creek, both of which have been linked to increased availability of

nutrients in coastal ecosystems.

This study collected emergent macrophytes and aquatic macrofauna of tidal

freshwater marshes in these two creeks from 2000 through 2002. Analysis of plant

community composition indicated that Broad Creek had fewer plant species than Marshyhope Creek, yet greater overall plant biomass. Comparisons of nekton in the two creeks determined that there were more fish and macroinvertebrate species, individuals and biomass in Marshyhope Creek. Multivariate analysis identified strong seasonal patterns that extended across both creeks in floral and faunal distributions, but also suggested that animal abundance patterns were related to the creeks. Ecological network analysis suggested both creeks appear to be resistant to environmental stressors, but probably lack resilience. Broad Creek, however, had higher levels of total ecosystem activity than Marshyhope Creek, although ecosystem organization and development was similar between both creeks, suggesting nutrient enrichment in Broad Creek but not necessarily eutrophication. Stable isotope analysis indicated that the nitrogen circulating through Broad Creek is more enriched in ^{15}N than Marshyhope Creek, although both creeks have enriched nitrogen signatures. Nevertheless, the high $\delta^{15}N$ in Broad Creek is indicative of larger nitrogen inputs to the system originating from animal waste. These results, however, must be tempered by an acknowledgement of the effects of a severe drought that caused an increase in salinity from October 2001 through August 2002, affecting animal and plant abundance throughout 2002.

EUTROPHICATION AND COASTAL WETLANDS: LINKING NUTRIENT
ENRICHMENT TO TIDAL FRESHWATER MARSH ECOSYSTEM
STRUCTURE AND FUNCTION

By

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Dissertation submitted to the Faculty of the Graduate School of the
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DEDICATION

For my three girls,

Claudia, Sophie and Nathalie

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never have considered without his tutelage. His constant modesty in light of all he has accomplished has humbled me, and I owe to him much of my scientific and philosophical maturity.

If not for a chance invitation from Andrew Baldwin to come along on a research trip to the mangroves of Biscayne Bay National Park in 1997, I never would have found the complementary yin to Robert Ulanowicz's yang in my ecological education. Without my introduction to "brute force" ecology, I could never have tackled such an ambitious field research endeavor. Along the way, in the many river miles we have traveled together, our student-teacher relationship has evolved into a friendship, for which I am sincerely grateful.

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Finally, I must lay any success I have achieved could not have happened without my wife, Claudia Link. If not for her, I would have given up years ago, but she has unwaveringly supported me, encouraging me always to continue onward. I owe her everything.

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CHAPTER 1

COASTAL EUTROPHICATION AND THE TIDAL FRESHWATER MARSHES

OF THE NANTICOKE RIVER

INTRODUCTION

The coastal landscape of the Chesapeake Bay has been affected by human activity

for over three hundred years (Cooper 1995). Steadily increasing human populations

within coastal watersheds across the United States have caused changes in the patterns of

water, sediment and nutrient delivery in every major coastal system (Kiddon et al. 2003;

Boesch 1996). The Chesapeake Bay is uniquely vulnerable to changes in land-use within

its watershed, possessing the largest ratio of watershed land-surface area to water volume

of any estuary in the world (Horton 2003). Blue crab harvests, oyster yields and seagrass

density declines, to name several adverse outcomes, are all byproducts of human

activities (Ernst 2003). Annual inputs of nutrients and sediments are still well above

desired levels even after 30 years of active intervention, and most restoration efforts for

species recoveries remain below 50 percent of their desired outcomes (Chesapeake Bay

Program 2006; Chesapeake Bay Foundation 2005).

One of the most pressing problems facing coastal systems in developed regions of

the world are the effects of eutrophication (Nixon 1995; Cloern 2001). During 2005, the

Chesapeake Bay received an estimated 370 million pounds of nitrogen, nearly 200

million pounds above desired levels (Chesapeake Bay Program 2006). Typically, the

single largest source of excess nutrients comes from non-point sources within the watershed, with agricultural run-off often the largest source (Carpenter et al. 1998). This is the case in the Chesapeake Bay, where agricultural sources in recent years have been estimated to contribute 58 percent of the nitrogen and 82 percent of the phosphorus that enters the Bay through non-point pathways (Ernst 2003). The primary nitrogen sources on the Delmarva Peninsula are agricultural, with 35 and 59 percent coming from manure and commercial fertilizer applications, respectively (Denver et al. 2004).

The entire coastal landscape is affected by the presence of these excess nutrients, and the effects are particularly well documented for the open Bay. Coastal eutrophication has been linked to many issues in the Bay proper, including seagrass decline and deep water anoxia, which result in degraded habitat quality for important Bay animal species (Kemp et al. 1983; Kemp et al. 1992; Hagy et al. 2004; Chesapeake Bay Program 2006). Yet the effects of the nutrient enrichment on other sub-ecosystems in the Chesapeake Bay's watershed are not as well understood, particularly for tidal wetlands. These ecosystems are certainly not immune to the effects of eutrophication. They are routinely cited as ideal natural systems for removing excess nutrients from coastal waters, particularly nitrogen (Kadlec and Knight 1996). This constant pressure from anthropogenic stressors ought to heighten the curiosity of ecologists and conservationists and encourage further study of these wetlands. Bay-wide monitoring efforts, however, acknowledge that evaluating the health of coastal wetlands of the bay region will be extremely difficult given the financial limitations of the restoration plans (Chesapeake Bay Program 2006). Efforts are underway to better identify the services wetlands

provide, but these efforts focus more on their roles within the entire watershed landscape (Tiner 2005). Only one study ever directly examined the effects of elevated nutrient inputs in tidal freshwater marshes, but it has been over 25 years since it was published (Whigham et al. 1980). Nutrient enrichment in ecosystems results in complex system responses, where effects often propagate throughout the higher trophic levels as the system as the components compensate for these changing environmental conditions (Carpenter et al. 1985; Vanni et al. 1997; Schindler et al. 1997; Lavrentyev et al. 1997). There has never been a comprehensive effort, however, to assess the consequences of nutrient enrichment in multiple trophic levels in tidal freshwater wetlands.

This chapter will provide a basic description of the flora and aquatic fauna of tidal freshwater marshes typically found in the Nanticoke River and other Chesapeake tributaries. Following this, I will review nutrient enrichment in marsh ecosystems and how it may affect the resident organisms of the wetlands. Nitrogen is generally considered a more immediate nutrient threat to the Chesapeake Bay than phosphorus (Chesapeake Bay Program 2004c). It is also typically the limiting nutrient in freshwater wetlands (Bowden 1987), particularly so in freshwater marshes (Bedford et al. 1999). Therefore, this discussion will be framed around the role of this nutrient in the tidal marshes.

<u>Tidal Freshwater Marshes</u>

Tidal freshwater marshes are an often-overlooked ecosystem in the coastal landscape of the Chesapeake Bay. In the 1980's several reviews emerged that made serious attempts to summarize the scattered ecological knowledge of these wetlands (Simpson et al. 1983; Odum et al. 1984; Odum 1988). These summaries are notable for identifying as much that is unknown about tidal freshwater marshes as is actually understood. Plant communities have been the most studied component of tidal freshwater marshes (e.g., Flemer et al. 1978; Whigham and Simpson 1978; Doumlele 1981; Whigham and Simpson 1992; Leck and Simpson 1995; Neubauer et al. 2000; Field and Philipp 2000; Baldwin et al. 2001). Fish and macroinvertebrates have received some attention, with early studies identifying patterns in faunal distribution relative to general habitat characteristics (Rozas and Odum 1987; McIvor and Odum 1988; Rozas et al. 1988). Recent studies have been concerned with changes in animal distributions based on differences in the plant community composition (Yozzo and Smith 1998; Meyerson et al. 2000). It seems, however, that most interest in faunal uses of marshes is more commonly directed toward estuarine systems (Weinstein and Balletto 1999; Hanson et al. 2002; Posey et al. 2003).

Tidal freshwater marshes are defined by three primary characteristics: they usually have salinity below 0.5 ‰, the plant and animal communities are dominated by freshwater species, and they are exposed to water level fluctuations driven by lunar tides (Odum 1988). They occur most frequently in areas where there is a major influx of freshwater, tidal amplitudes exceed 0.5 m, and the regional geomorphology of the coastal

basin constricts and magnifies the tidal wave in the upstream portion of the estuaries (Odum et al. 1984). Tidal freshwater marshes reach their greatest extent in coastal rivers of the mid-Atlantic region, and cover approximately 164,000 hectares along the entire East Coast (Mitsch and Gosselink 2000). Interestingly, these wetlands do not receive unique categorization in the USGS national wetland classification system (Cowardin et al.). Instead, they appear to span several categories, based on differences in microhabitat and proximity to the tidal source (Odum et al. 1984; Dahl 2000).

Typically, tidal freshwater marshes can be subdivided into three zones: high, mid- and low marsh. These sub-communities are characterized by the frequency and duration of tidal flooding and, as a consequence of this tidal regime, by the vegetation present on the marsh surface. Zonation is not as straightforward in tidal freshwater marshes as it is in salt marshes, but the aforementioned zones are relatively distinct areas that support specific plant types (Odum 1988). Spatterdock (*Nuphar lutea*) is the dominant plant species in the low marsh, occupying the most frequently flooded parts of the intertidal zone. *Nuphar* is a perennial that has thick and extensive rhizomes below the sediment surface, and it is the only vascular plant that grows with any significant abundance in this location (Tiner 1993). Only *Polygonum punctatum* and *Zizania aquatica* seedlings occur with any other measurable frequency in the low marsh (M. Egnotovich, personal observation). As is the case with many emergent wetlands (Grace 2001), total biomass in this zone peaks in early summer and slowly declines as the growing season progresses.

The mid-marsh zone is typically characterized by the presence of *Pontederia cordata* and *Zizania aquatica*. *P. cordata*, or Pickerel weed (a perennial species), dominates in late spring through early summer (Whigham and Simpson 1982), while the rice abundance increases later in the growing season (August-September) (Whigham and Simpson 1992). Flooding occurs every tidal cycle, but duration and water depth is less than in the low marsh zone (Odum et al. 1984).

The high marsh is the least frequently flooded area of the three marsh types, and is where the majority of plant species associated with tidal freshwater marshes are found. For example, censuses of plant species abundance in 1 m x 2 m plots in high marshes along the Nanticoke River between 2000 and 2002 recorded more than 30 unique species each year (Baldwin et al., unpublished). Seed bank samples from these same plots showed similar richness, with 34 different species emerging from soil samples collected within the same plots (Peterson and Baldwin 2004b). In general, species density tends to be greatest closest to the channels in the high marsh (Leck and Simpson 1994), but richness is nonetheless much higher than in other coastal marshes (Odum 1988). The high marsh also demonstrates the greatest degree of seasonal variation, with aboveground plant dominance shifting from early season perennials to late season annuals (Whigham and Simpson 1992). In the early part of the growing season, *Peltandra virginica* and *Acorus calamus* dominate the marsh vegetation, but their abundance typically begins to decline by July as the annual species *Impatiens capensis*, *Polygonum* spp. and *Leersia oryzoides* begin to constitute a larger portion of marsh plant biomass (Doumlele 1981).

By September, the marsh is noticeably overgrown with the yellow flowers of *Bidens* spp.

as the other plants begin to senesce (Odum et al. 1984).

The marshes are considered a highly productive ecosystem and one of the most

productive wetland types (Mitsch and Gosselink 2000). Aboveground annual productivity

estimates range from 430 g dry weight m^{-2} y^{-1} in *Sagittaria latifolia* dominated marshes

to over 1850 g dry weight m^{-2} y^{-1} in Phragmites marshes (Whigham et al. 1978).

Estimates of total net community primary production in tidal freshwater marshes

suggested that annual production rates are probably closer to 800 g carbon m^{-2} y^{-1}, which

includes a sizeable fraction of production from benthic microflora (Anderson et al. 1998).

Contributions of phytoplankton to community production in tidal freshwater marshes is

almost entirely unknown (Odum et al. 1984). Plankton is routinely censused in every

major tributary in the Chesapeake Bay watershed, including tidal freshwater habitats, and

phytoplankton presence in the marshes can only be inferred from adjacent near-shore

waters (Marshall and Burchardt 2004; Chesapeake Bay Program 2005b).

Similarly to phytoplankton, very little is directly known about the microfauna

inhabiting tidal freshwater marshes, although there have been some basic descriptions of

community composition in these wetlands. Nematodes, ostracods, tardigrades,

oligochaetes, Harpacticoid and Cyclopoid copepods and the sabellid polychaete

Manayunkia spp. are the numerically dominant species found in the benthos of marshes

along the Hudson River (Yozzo and Smith 1995). Other research identifies Chironomids

as highly abundant benthic invertebrates in the Hudson River wetlands, although the

overall abundance of the benthic organisms is thought to be highly variable according to season (Findlay et al. 1989). These organisms are likely an important trophic link between the marsh surface and fish species that enter the marshes at high tide. Even less is understood about what role the zooplankton plays in the tidal freshwater marshes. Species presence and abundance can be inferred from open water plankton samples taken in tidal freshwater zones of the Chesapeake Bay tributaries (Stroup et al. 1991; Chesapeake Bay Program 2005b). But other than being a likely food source for small fish and macroinvertebrates, one can only speculate about the function of zooplankton in tidal freshwater marshes.

About 40 species of fishes and macroinvertebrates constitute the faunal community of tidal freshwater marshes (Odum et al. 1984). Commonly found fish species in these marshes include *Fundulus heteroclitus, Fundulus diaphanus, Notropis hudsonius, Gambusia affinis, Menidia beryllina, Gobiosoma bosc,* and *Etheostoma olmstedi* (Rozas and Odum 1987). Dominant macroinvertebrates typically include *Palaemonetes pugio*, *Gammarus* spp., and on occasion, *Calinectes sapidus* (Odum et al. 1984). None of these animals, however, are endemic to this specific ecosystem as most will thrive either in the non-tidal freshwater systems upstream or the estuarine conditions farther downstream. Nonetheless, this habitat apparently offers the aquatic macrofauna a wealth of habitat resources to exploit (McIvor and Odum 1988; Simpson et al. 1983).

Detailed studies of fauna of tidal freshwater marshes have been few since the late 1980's. The majority of this research focused on the fauna associated with tidal

freshwater marshes of the Chickahominy River, Virginia. William Odum and his associates looked at multiple environmental factors that affected aquatic macrofauna abundance in and around the marshes. They found higher fish densities in lower order headwaters where there was often higher density of submerged aquatic vegetation (SAV) (Rozas and Odum 1987). Manipulations of SAV density in tidal streams indicated that total abundance of animals declined in locations where SAV was removed (Rozas and Odum 1987b). Within these adjacent SAV beds, the small aquatic macrofauna probably are exposed to less predation and can forage in these areas while the marsh is not flooded (Rozas and Odum 1988; Yozzo and Smith 1998).

Marsh surface utilization by these animals depends, to a large degree, on the physical characteristics of the adjacent stream banks where the SAV grows. Nekton density seems to function independently of water depth in the marshes (Yozzo and Smith 1998). Instead, the characteristics of the mud banks of the lower intertidal zones influence animal abundance. Depositional banks consist of softly piled fine sediments and flood shallowly at high tide, while erosional banks are in deeper water and have firmer, coarser sediments (McIvor 1987). Abundance of aquatic macrofauna are greater over the depositional banks than the erosional banks, suggesting that smaller forage animals preferentially use shallower habitat as an additional source of refuge at low tide (McIvor and Odum 1988).

Nekton move from available low tide refugia into the more structurally complex marshes at high tide. There are high concentrations of fish in small creeklets that run

across the depositional banks from the marsh surface to the channels, but these constitute a very low amount of the total bank area. More fish migrate over open stream banks than through the rivulets, implying that fish will preferentially use the deeper passages to the marsh, but use is limited by the relatively small extent of the rivulets (Rozas et al. 1988). More than other factors, the presence of these shallow depositional banks positively influences the shape and size of the aquatic macrofauna community that can invade the marsh at high tide.

Tidal freshwater marshes are considered to be detritus-based systems, as most plant material does not appear to flow directly to consumer organisms in marshes (Page 1997). Most of the annual macrophyte production ends up as detritus at the end of the growing season (Whigham et al. 1978). The detritus tends to be recycled quickly, and by the onset of the next growing season the marsh surface is often bare, aside from the lesser amounts of refractory detritus (Whigham et al. 1980). Microfloral productivity is not well understood in these marshes, but may be an important pathway of energy and material flow to higher trophic levels (Odum et al. 1984). It is likely that higher trophic levels depend on a mixture of primary production sources, with macrophyte contributions mediated by detrital processes (Wainright et al. 2000)

Marsh Responses to Nutrient Enrichment

Prevailing thought in plant community ecology suggests that nutrient enrichment will lead to reductions in plant species diversity through the loss of rare species, replacements by exotics, and competitive exclusion as nutrients no longer limit plant

growth (Wisheu and Keddy 1996; Bedford et al. 1999). In addition to the decline in

species richness, there may be a concomitant increase in productivity in the community

(Grace 2001), possibly the result of dominant species experiencing increased growth rates

(Verhoeven et al. 1996). Yet productivity responses to changes in diversity are often

ambiguous (Johnson et al. 1996; Waide et al. 1999). High plant diversity is often

correlated with higher community productivity and stability, but individual population

dynamics ironically become less stable, reflected as reduced standing crop of specific

species (Tilman et al. 1997). Several studies identify shifts in wetland plant species

composition with increased nutrient load as invasive species experience higher growth

rates and suppress native species (Green and Galatowitsch 2002; Svengsouk and Mitsch

2001; Woo and Zedler 2002). Research in salt marshes in Narragansett Bay demonstrated

that increased human activity in close proximity to tidal salt marshes led to changes in

marsh soil salinity and nitrogen availability that likely encouraged plant community

composition changes (Silliman and Bertness 2004; Wigand et al. 2003; Bertness et al.

2002). The invasive species may alter ecosystem nitrogen dynamics, as the species that

typically succeed in the higher nutrient wetlands can sequester more nitrogen in plant

biomass and often reduce available nitrogen in the soils (Windham and Meyerson 2003;

Boyer and Zedler 1998).

Faunal responses to nutrient enrichment in marshes are not as clear as those seen

in the plant communities. Response largely depends on the animal community, as most

studies attempt to identify changes in animal abundance as the physical structure of the

marsh habitat changes with shifts in plant species composition and abundance. Several

studies have looked at fish response to *Phragmites* invasion with inconclusive results. The invasive plants do not appear to drastically alter total fish and macroinvertebrate abundance in tidal marshes (Osgood et al. 2003; Meyer et al. 2001; Weis and Weis 2000). There are species-specific shifts in numerical density of fish, however, as some species that were highly abundant in non-*Phragmites* marshes were much less abundant in marshes dominated by the invasive plant (Hanson et al. 2002; Able and Hagan 2000). Macroinvertebrates seem to be more responsive to the changes in plant community composition, as species richness and numerical density were lower in coastal New Jersey salt marshes where *Phragmites* replaces *Spartina* (Angradi et al. 2001). The *Phragmites* invasion ultimately alters marsh hydrology and flooding behavior, and this long-term effect may, in time, result in significant changes in nekton use as available non-*Phragmites* marsh disappears (Weinstein and Balletto 1999). This effect has been observed in marshes in New Jersey that had well-established *Phragmites* communities (Able et al. 2003).

Yet nutrient enrichment has had pronounced effects on marsh fauna abundance and diversity in other habitats. In the Everglades, locations receiving higher nutrient loads were observed to have significantly more macroinvertebrates than the pristine locations, although some species abundant in the pristine locations were less so in the enriched areas (Rader and Richardson 1994). In Delaware River salt marshes, pulse nitrogen enrichment studies indicated that not only did plant biomass increase with the additions, but terrestrial insect population abundances fluctuated in response, and the effects lingered for several years after the additions (Gratton and Denno 2003). Increases in

available nitrogen increased *Spartina foliosa* growth in marshes in San Diego Bay,

resulting in more vertical structure in the marshes that likely provided improved habitat

for nesting bird species (Boyer and Zedler 1998). Macroinvertebrate density and species

richness declines in brackish marshes have also been linked to increased nutrient loads

(Kerry et al. 2004).

The comparisons presented in the majority of these studies are between systems

that are quite different, often where the treatment sites have already experienced the plant

community transformations. Studies contrasting faunal use of *Phragmites* and *Spartina*

marshes, for example, did not observe any transitional stages of marsh plant community

before conversion to *Phragmites* was complete. In the salt marshes, it could be that the

low number of plant species limits the marsh's overall response to nutrient enrichment

with species replacement being the only possible outcome. In tidal freshwater systems,

the larger species pool may provide alternative end-points for community development

rather than monoculture species replacements (Perry and Hershner 1999). Are there

noticeable shifts in plant and animal species composition and abundance in the

intermediate stages of nutrient enrichment before these communities undergo dramatic

shifts? There is evidence that changes in plant stem density will affect predator foraging

success rates. In habitats with higher plant stem densities, prey species are more abundant

as capture rates decline for predatory fish (Harrison et al. 2005; Savino and Stein 1982),

and it appears that there may be a threshold stem density above which predator success

rates are significantly degraded, resulting in higher prey species abundance (Gotceitas

and Colgan 1989). Fish seeking refuge from predation may even have preferences for

specific vegetative cover in habitats with heterogeneous plant community composition

(Chick and McIvor 1997). But these trends do not appear to have been examined in

conjunction with the effects of nutrient enrichment on plant community composition in

any habitat, let alone tidal marshes.

<u>Nutrient Enrichment in the Nanticoke River</u>

Large-scale cultivation of nitrogen-fixing crop species, industrial conversions of

atmospheric nitrogen into ammonia and the consumption of fossil fuels have rapidly

increased the amount of nitrogen that circulates through pools outside of the atmosphere

(Vitousek et al. 1997). Since 1860, anthropogenic contributions to reactive nitrogen pools

(all the forms of nitrogen except N_2) have increased from 15 teragrams N y^{-1} to over 165

Tg y^{-1}, with most used in agricultural applications (Galloway et al. 2003). Nearly 40

percent of the world's human population owe their survival to this massive agricultural

nitrogen subsidy, as pre-industrial nitrogen yields per acre could never support the

current number of living people (Smil 2002).

Nearly half of the total land surface of the Eastern Shore is devoted to agricultural

uses (Delmarva Poultry Industry 2005). Most of the crop production directly supports a

large poultry industry, which yields huge numbers of chickens each year, over 600

million broiler chickens in 2000 alone (Denver et al. 2004). The chickens produce a

massive amount of waste – commercial layer hens alone produce upwards of 260 pounds

of waste per every 1000 birds every day (Collins et al. 1999). This waste is typically

applied to crop fields as fertilizer to produce feed for animal production. Poultry waste is

phosphorus rich, but phosphorus is not very mobile in soils, so it does not present the same sorts of problems that nitrogen does (Campbell and Edwards 2001). A large amount of the nitrogen contained in the waste is lost to the atmosphere via ammonia volatilization, but the residual pool is still very large (Wolf et al. 1988). The nitrogen not used by the crop plants typically escapes into surface and ground waters, cascading "downstream" to the next system (Galloway et al. 2003). In the Delmarva Peninsula, most of the groundwater ultimately ends up in coastal rivers and streams and finally the Bay itself (Phillips et al. 1999).

The extended Nanticoke River watershed, including the Marshyhope Creek, Broad Creek and Deep Creek sub-watersheds, covers 822 square miles on the lower Eastern Shore in Maryland and Delaware (Chesapeake Bay Program 2003a). The watershed has the highest percentage of wetlands associated with any Chesapeake tributary, and tidal freshwater wetlands make up a very large portion of the watershed's total wetland coverage (Tiner 2005). In 1991, the river system was identified as both a Last Great Place and a Bioreserve by The Nature Conservancy (The Nature Conservancy 1998). Yet the Nanticoke River is facing a number of environmental threats, ranging from shoreline erosion from boat traffic to increased nutrient loads from human activities. Given the aquatic nature of many of these problems, the river's tidal wetlands are one of the most endangered ecosystems in the watershed, and may be particularly threatened by the altered nutrient dynamics (The Nature Conservancy 1998).

Two major tributaries of the Nanticoke River are Marshyhope Creek and Broad Creek (Figure 1.1). The Marshyhope Creek watershed covers 221square miles in both Maryland and Delaware, while that of Broad Creek spans across 123 square miles in Delaware. Further differentiating these two sub-watersheds are their respective patterns of land cover and use. Wetlands cover about 18.6 percent of the Marshyhope landscape, while Broad Creek's watershed contains only 6.5 percent. Proportionally, Broad Creek also has more than twice as much developed land than Marshyhope, 2.4 percent versus 0.9 percent (Chesapeake Bay Program 2003a). Even more significantly, though, the smaller Broad Creek watershed contains over 280 animal production facilities, while Marshyhope Creek has only 60 within its landscape (Chesapeake Bay Foundation 1996). As a possible consequence of this agricultural activity, the Broad Creek watershed has averaged about 265 – 1040 lbs/acre/year of nitrogen input derived from animal waste. The average manure-based nitrogen load in the Marshyhope watershed appears to be somewhat lower, with most areas ranging between 170 – 265 lbs/acre/year (Chesapeake Bay Foundation 1996). These differences suggest that the tidal freshwater marshes, as well as the other ecosystem types found in Broad Creek, have potentially been exposed to substantially higher nutrient loads than those in Marshyhope Creek have.

With more urban and agricultural land use in a smaller space and with fewer wetlands serving as potential nutrient traps, there may be measurable signs of ecosystem distress (sensu Rapport and Whitford 1999) in Broad Creek, such as shortened food chains and declines of species diversity (Odum 1985). There were some preliminary

Figure 1.1. The Nanticoke River watershed within the Chesapeake Bay Region (from M. Weiner, Geography Department, University of Maryland).
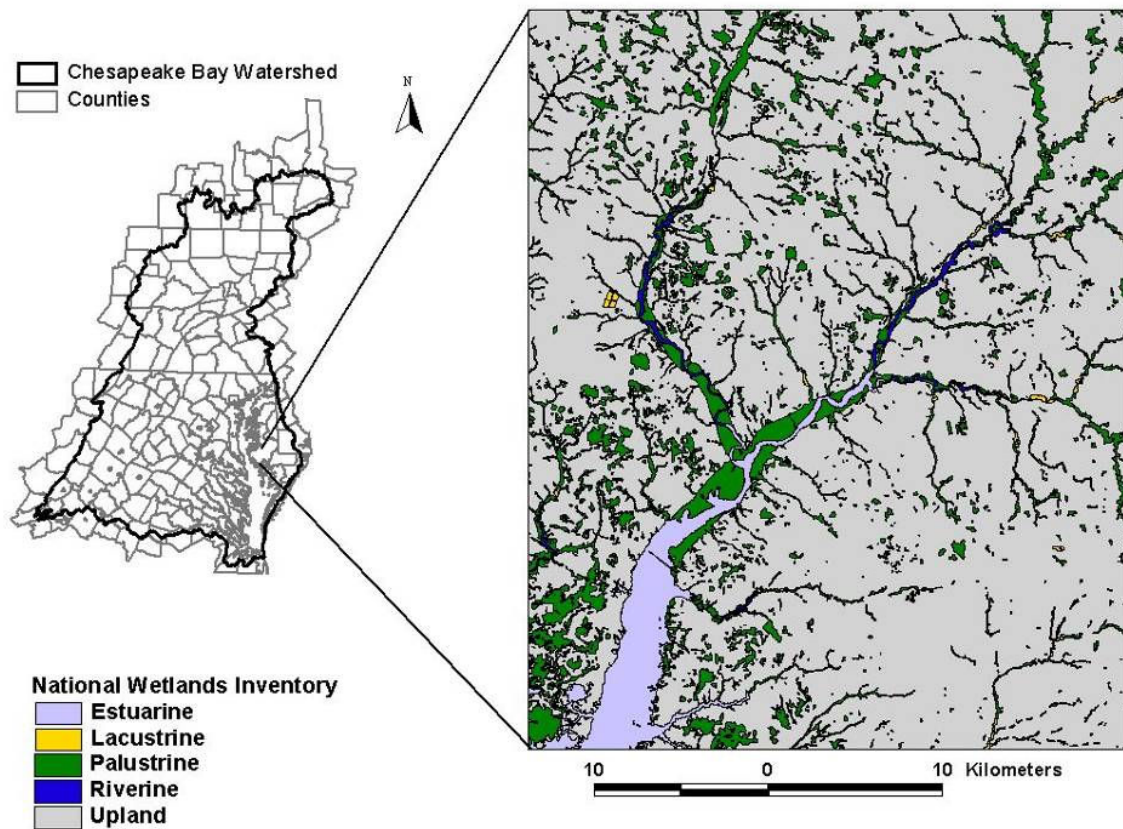
indications in the Nanticoke tidal freshwater marshes that nutrient enrichment may be altering plant composition (Baldwin et al.unpublished). Observational sites were established across the tidal freshwater region of the river to monitor plant species composition and abundance. Looking only at the data from Marshyhope Creek and Broad Creek in 2000, herbaceous plant species richness was lower in both tidal marshes and swamps in Broad Creek (Figure 1.2). Given the higher nitrogen loads in Broad Creek, this reduced species richness is evidence that nutrient enrichment is affecting these wetlands.

Complicating the overall threats facing the Nanticoke River is the fact that the watershed is split between two states. Maryland and Delaware have implemented different shoreline protection and land-use strategies and their respective levels of participation in the "Save the Bay" efforts have followed different courses. Maryland has been a full partner in the Chesapeake Bay Program (CBP) since its inception in 1983. Delaware has only recently become a Headwater State Partner in the CBP, even though 28% of the state's surface area drains into the Chesapeake Bay (Chesapeake Bay Program 2001). The states also differ in the type and scope of enforceable laws that could affect the Nanticoke River's tidal freshwater marshes. For example, Maryland implemented relatively strict guidelines in the Critical Areas Act (1984) for shoreline development, albeit with exemptions for farmland (Ernst 2003), while Delaware has left much of the interpretation of state law regarding coastal development up to local government (McElfish Jr. 1998). Delaware law has also exempted more potentially detrimental agricultural practices (fertilizer uses, sediment run-off, etc.) than has

Figure 1.2. Comparisons of soil nitrate content and plant species richness in Broad Creek and Marshyhope Creek. Soil samples were collected only on one date (August 2000), while the aboveground vegetation was censused twice during the growing season. All data presented are means compiled from sites located only on the two creeks; all other sites were filtered out (from Baldwin et al. unpublished).
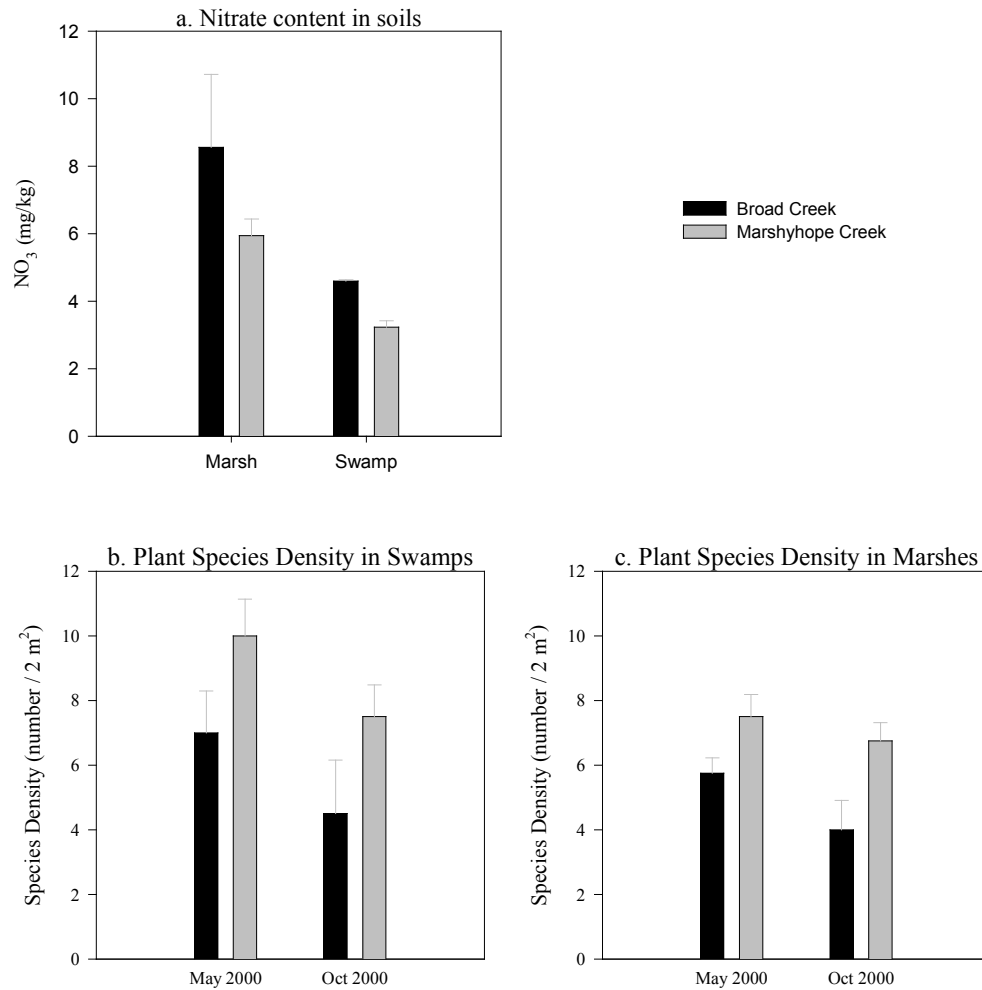
Maryland (McElfish Jr. 1998). Maryland, on the other hand, has recently required all farm operations to adopt strict nutrient control practices, although the success of this legislation, the Water Quality Improvement Act, is in doubt as compliance is rather low (Ernst 2003).

Research Goals

Given their respective differences in land use, nutrient inputs and observed differences in the plant community composition, the two tributaries of the Nanticoke, Broad and Marshyhope Creek, will serve as the primary point of comparison for this entire dissertation. Broad Creek will be hypothesized as the "impacted" system, while Marshyhope Creek will be considered the "pristine" system. The lack of truly pristine marsh sites on the Eastern Shore arguably complicates the comparisons. Yet the evidence thus far presented in this chapter suggests that the systems are reasonably different in both nitrogen sources and load, and may be responsible for reduction in plant species richness in Broad Creek. The similarity between the creeks necessitates a broad range of approaches to identify what probably are subtle compositional and functional differences between the creek systems. The chapters included in this dissertation assess these differences on multiple levels, from the elemental composition of the organisms up to ecosystem level processes, all in an attempt to identify how nutrient enrichment affects tidal freshwater marshes.

The next chapter seeks to identify whether there is a consistent pattern to the distribution and abundance of macrophytes, small fish and macroinvertebrates that

distinguishes the creeks from each other. The comparisons look at total community characteristics and selected dominant species to identify differences in numerical abundance and biomass, and whether any differences are likely the result of environmental factors not related to differences in nutrient regimes of the two creeks. The chapter hypothesizes that there are differences between the species assemblages and abundances of the two creeks. It further examines whether or not any differences in plant community composition or aboveground biomass result in corresponding differences in the nekton.

The third chapter recasts the fish and invertebrate data from chapter three in a multivariate analysis to identify any patterns that the community variables and individual species analyses may have overlooked. Ordination techniques are used to address the hypothesis that plant and animal community composition and structure is more dependent upon the longitudinal gradient of relative distance upstream than on other factors. It also readdresses a hypothesis from the previous chapter, by identifying any plant community characteristics that may be related to how the nekton community is structured across the entire landscape.

The fourth chapter looks beyond the comparisons of the stocks of animals and any correlation between individual populations and examines the implications of the interactions contained in trophic networks of the flora, fauna and detrital pools of the tidal freshwater marshes. Using a methodology called Ecological Network Analysis (Ulanowicz 2004), I examined whether the tidal freshwater marshes in Marshyhope

Creek and Broad Creek demonstrated any characteristics on the system level that corresponded with hypothesized trends resulting from nutrient enrichment. In this case, given the background information presented in this chapter, I hypothesize that the analysis will reveal that Broad Creek demonstrates more "symptoms" of the effects of eutrophication than Marshyhope Creek.

The fifth chapter examines some interesting trends in the isotopic signatures of nitrogen in the flora and fauna of the tidal freshwater marshes, investigating whether or not the isotope ratios of Broad Creek would suggest that it is receiving more animal-derived nitrogen than Marshyhope Creek. It also addresses how local land use and land cover may be responsible for the differences in the quality of nitrogen between the two creeks.

The final chapter presents a summary of the major findings of the entire dissertation and provides a synthesis of the entire scope of the work.

CHAPTER 2

COMPARISON OF AQUATIC MACROFAUNA AND MARSH VEGETATION BETWEEN TWO TIDAL FRESHWATER CREEK SYSTEMS OF THE NANTICOKE RIVER

INTRODUCTION

As in many other ecosystems, research in tidal freshwater wetlands demonstrates the historically common "either-or" divide in ecological interest between plants and animals. Studies that have focused on the plant community mention little if anything about the fauna that resides amidst the vegetation, with environmental gradients receiving most discussion about causality in plant community dynamics (e.g., Latham et al. 1994; Leck and Simpson 1994; Leck and Simpson 1995; Peterson and Baldwin 2004a). Conversely, studies of the fauna of these systems have generally neglected vegetation, in a quantitative sense. The ecological role of the plant community has often been limited to non-specific discussions of its structural contributions to the habitat or general descriptions of the plants near the sample stations (e.g., Hastings and Good 1977; Rozas and Odum 1987; Rozas and Odum 1987a; Rozas et al. 1988; McIvor and Odum 1988; Yozzo and Smith 1998).

Some recent studies of nekton use of tidal marshes have begun to qualitatively identify plant community composition. These, however, have been limited to estuarine systems and have concentrated on the effects of an invasive plant species, *Phragmites australis* (Cav.) Trin. ex Steud., whose presence is believed to adversely affect nekton

abundance (Weinstein and Balletto 1999; Weis and Weis 2000). There has also been some research that tracked nutrient and material flow from salt marsh vegetation into the surrounding aquatic environment, which quantitatively identified individual plant species (Heinle and Flemmer 1976; Wainright et al. 2000; Weinstein et al. 2000; Weis et al. 2002). Interactions between plants and animals in tidal freshwater marshes have received some investigation (Findlay et al. 1989; Baldwin and Pendleton 2003), but there has been no comprehensive study of the relationships between tidal freshwater marsh vegetation and the nekton that use these habitats at high tide.

About 40 species of fishes and macroinvertebrates are typically found in these tidal marshes (Odum et al. 1984; White 1989). None of these animals, however, are endemic to this specific ecosystem, which may be another reason for the relative lack of research centered on these marshes. Most of the organisms thrive either in the non-tidal freshwater systems upstream or the estuarine conditions farther downstream, yet members of both environments often overlap here, presumably utilizing the wealth of resources available in these tidally subsidized systems (Boesch and Turner 1984). Factors such as the presence of adjacent subtidal SAV beds, low stream order, and the presence of shallow sloped erosional mudbanks all positively affect the densities of aquatic animals that utilize tidal marsh surfaces (Rozas and Odum 1987a; Rozas et al. 1988; McIvor and Odum 1988).

Marshes most likely offer the small aquatic macrofauna resources to exploit and refuges from aquatic and terrestrial predators (Kneib 1997; Kneib 1987; Rozas and

Hackney 1983). In non-tidal habitats, increases in emergent plant stem density can be strongly correlated with increases in abundance of small aquatic organisms (Savino and Stein 1982). Beds of submerged aquatic vegetation also have been observed to foster high densities of small aquatic animals as compared to nearby unvegetated habitat (Sheridan 1997; Lazzari 2002). Yet the nature of tidal freshwater marsh utilization by animals is highly seasonal, with the highest levels typically occurring in the summer months when marsh plant community development is at its most complex (Yozzo and Smith 1998). While researchers have investigated the subtidal habitats adjacent to the tidal freshwater marshes (Rozas and Odum 1988; Rozas and Odum 1987a; Rozas and Odum 1987b), they did not look at how the composition and structure of the emergent marsh vegetation was related to the nekton community.

This chapter examines patterns in the distribution and abundance of nekton and herbaceous vegetation found in the tidal freshwater marshes of the Nanticoke River. Unlike in salt marshes where researchers have looked at the relationship between plants and animals, there are few obvious contrasts in the vegetation of the Nanticoke River's tidal wetlands. There are no widespread areas of plant species invasion in these wetlands offering clear comparisons between impacted and unimpacted sites (Weinstein and Balletto 1999). Nor is there excessive, localized herbivorous activity from animals like the nutria (*Myocastor coypus*), abundant in the nearby Blackwater National Wildlife Refuge, that would offer a comparison between impacted and undisturbed habitats (Ford and Grace 1998). The marshes of the Nanticoke superficially appear very similar across the tidal freshwater region. Yet the entire watershed spans a large area with diverse land

cover, and also stretches across two states with differing regulations and practices. Given the variation in land-use in the surrounding watershed, these wetlands may possess more subtle differences in plant community composition and structure throughout the extent of the tidal freshwater portion of the watershed (The Nature Conservancy 1998). As mentioned previously, there is evidence that Broad Creek and Marshyhope Creek have differing nutrient loading rates, and this may be reflected in the plant communities of their wetlands as lower plant species richness appears to be associated with higher levels of nitrate in the wetland soils (Figure 1.2).

This chapter will explore how the abundance of fish and macroinvertebrates varies with the composition of the marsh vegetation between two major tributaries of the Nanticoke River. More specifically, it asks the following question: do subtle differences in the plant community composition of apparently similar marshes correspond with any differences in the abundance of the nekton? Since there is evidence that these two creeks differ with respect to their plant community composition, then it is possible that these differences may lead to changes in the composition of the nekton.

STUDY SITES

The Nanticoke River (Delmarva Peninsula, Maryland and Delaware) possesses large areas of tidal freshwater wetlands. The majority of these wetlands are tidal freshwater swamps, but there are also expansive areas of tidal freshwater marshes located along the river. In contrast, the majority of other studies investigating the nekton in tidal freshwater ecosystems were situated in the vast tidal marshes of the lower Chickahominy

River, on the western shore of the Chesapeake Bay (Virginia, USA). These marshes, unlike those of the Nanticoke, often span upward of 1 km between the surrounding uplands and the main river channel (Rozas and Odum 1987a). In the Nanticoke, however, the majority of marshes are on the fringes of the river itself and often less than 100 m wide.

The Nanticoke River system contains two major tributaries located in the tidal freshwater portion of the Nanticoke watershed. Broad Creek enters the Nanticoke River in Delaware approximately five miles upstream from Marshyhope Creek and reaches toward the southeast across lower Sussex County, Delaware. Marshyhope Creek runs north from the Nanticoke River through Dorchester and Caroline Counties, Maryland. The creek's upper reaches cross into Delaware near Smithville, Maryland, extending northward into Kent County, Delaware (Figure 1.1). I chose to locate my sample sites on the two creeks expecting that local land use differences between the creeks would result in distinctly observable differences in the plant community composition.

I selected three marshes on each creek as the study sites (Figure 2.2). These six were chosen from a larger group of marshes I identified that would be able to support my research activities. The eligible marshes were all at least 2 acres in area and possessed well-developed high and low marsh vegetation structure. The area requirement eliminated all the narrow strip marshes that are situated between much of the river and

Figure 2.2. Map of the Nanticoke River, Marhsyhope Creek and Broad Creek identifying locations of sample sites and collection stations.
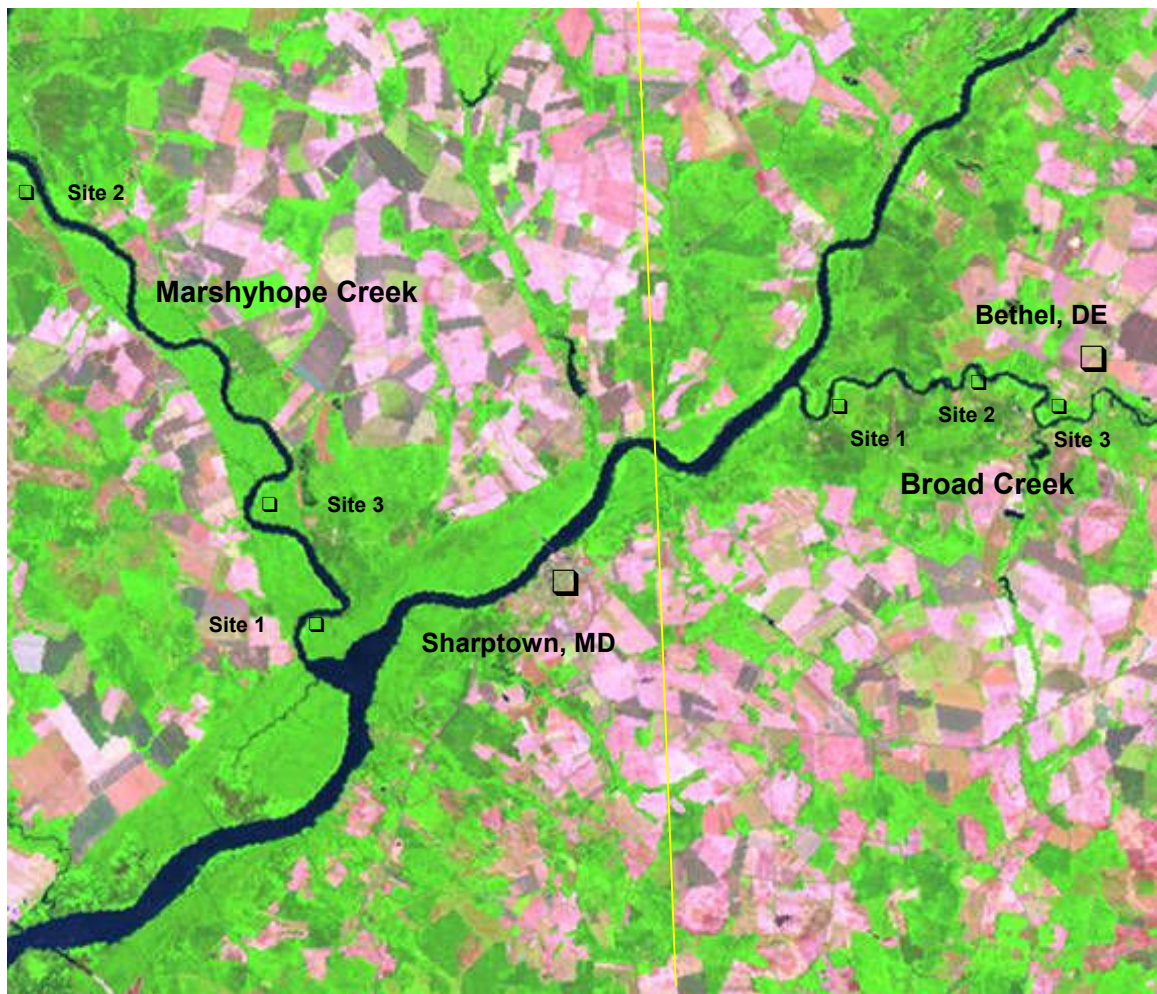
the adjacent tidal freshwater swamps. I identified eight marshes on Marshyhope Creek and five on Broad Creek that met my selection criteria, and then the study sites were randomly selected from these two groups. The precise locations of the six selected marshes were recorded using GPS (Table 2.1).

RESEARCH METHODS

I collected soil, plant, macroinvertebrate and small fish samples from the study sites in August 2000, October 2000, May 2001, August 2001, October 2001, May 2002 and August 2002. Only the throw trap, water quality and low marsh vegetation data were collected in 2000. From May 2001 until the conclusion of field activities in August 2002, all sampling protocols described hereafter were performed at each site. Sampling activities were confined to the growing season since these months are when animal species richness is at its maximum and aboveground vegetation is at its most complex levels of development. Detailed descriptions of the sampling protocols are in Appendix I.

Herbaceous Vegetation

In both high and low marsh habitats, a 0.25 m^2 PVC square quadrat was used to define an area of aboveground biomass that was harvested by cutting the plant stems at ground level with a knife. High marsh vegetation was sampled haphazardly by tossing the quadrat into a designated sampling area of the marsh. The aboveground vegetation that was rooted within the square was removed and returned to the University of Maryland Wetland Ecology and Engineering Laboratory for subsequent sorting and identification. The same local area of each marsh site was sampled repeatedly on each collection date.

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Table 2.1. Locations of sample sites on Broad Creek and Marshyhope Creek.
Latitude and longitude of sites and description of site's relative location.

Site locations	Latitude	Longitude
Broad Creek Marsh 1	38.56578N	75.63109W
Broad Creek Marsh 2	38.56998N	75.63844W
Broad Creek Marsh 3	38.56973N	75.66492W
Maryshope Marsh 1	38.53375N	75.76457W
Maryshope Marsh 2	38.59863N	75.81700W
Maryshope Marsh 3	38.55313N	75.77311W

BC1: Extensive marsh 0.3 mi upstream from Phillips Landing.
BC2: Located on south side of creek, 0.5 mi downstream from Bethel, DE
BC3: Located on north side of creek, 0.1 mi downstream from Bethel, DE
MC1: On east side of creek, 0.2 mi upstream from Marshyhope / Nanticoke
      confluence, on Camp Nanticoke, BSA
MC2: West side of river, 5 mi upstream of Eldorado, MD
MC3: On east side of creek, 3 mi upstream from Marshyhope / Nanticoke
      confluence, on Camp Nanticoke, BSA

For the low marsh vegetation samples, the quadrat was placed in a randomly chosen corner of the throw trap after it was deployed. Samples were harvested similarly to the high marsh plots. All samples were sorted down to the species level, and placed into a drying oven at 80° C for 48 hours and then weighed to determine dry mass.

<u>Throw Traps</u>

A 1 m x 1 m rigid aluminum throw trap was used to collect samples of small fish and macroinvertebrates from the marsh sites (Figure 2.3). This active trap design has been frequently used in shallow water vegetated habitats for more than twenty years (Kushlan 1981) and its effectiveness has been well documented (Chick et al. 1992). The traps were deployed haphazardly along the low water edge of the low marsh habitat in water of depths between 5 cm and 45 cm. In order to minimize the effects of tidal stage on faunal distributions, I only collected samples as the tide was falling. This was also a logistical necessity, as this was a window period, when the passive traps were collecting specimens. In addition to the collection of the aquatic macrofauna, vegetation samples from one corner of the trap were collected. Additionally, water depth within the trap, dissolved oxygen, temperature, salinity and conductivity were measured. Conductivity was not recorded before 2001, but the other variables were measured from the beginning of the study. Specimens were euthanized in the field and returned to the Wetland Ecology and Engineering Laboratory at the University of Maryland for identification. All fish were identified to species level, while invertebrates were identified to the lowest determinable taxonomic resolution. I collected a total of 245 throw trap samples over the duration of the study, approximately six traps per marsh site per collection date.

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Figure 2.3. Diagram of the throw trap. These are the specifications for the design of the throw trap used to sample aquatic macrofauna in the tidal freshwater marshes of the Nanticoke River from May 2000 through August 2002. The walls were made of two pieces of two 2 m by 0.6 m 1/8-inch thick aluminum sheets that were both folded to form L-shaped halves of the trap. The ends of the "L" were welded together, while aluminum angle was riveted to the top and to the welds to stabilize the frame. A second strip of angle was riveted to the frame about 20 cm from the bottom for additional stability.
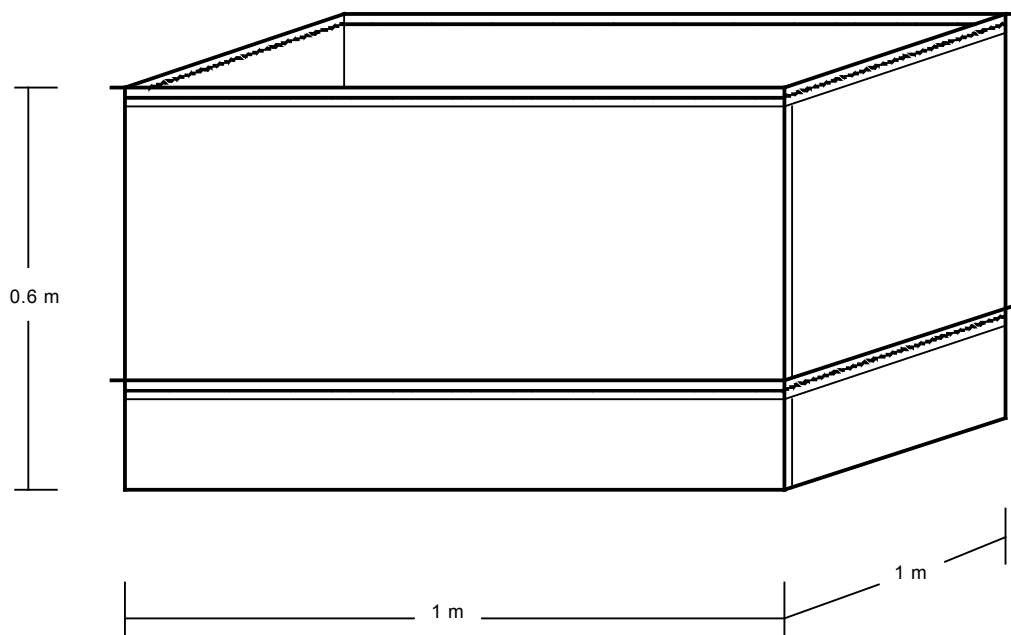
<u>Flume Traps</u>

I used my own variation of the flume trap along the high marsh/low marsh transition areas based on the classic design of the same name (McIvor and Odum 1985). Fish are more mobile than the macroinvertebrates in these marsh communities, and this method offered an additional measure of fish abundance that might identify any biases in the throw trap. It should also help identify any larger fish moving into the shallower waters of the low marsh / high marsh transition zone that the throw trap was missing. This trap consists of two components: a permanent set of parallel barrier nets positioned across the marsh surface perpendicular to the waters edge (Figure 2.4), and a collection net attached to the mouth of the barrier nets that was deployed only when I was actively trapping animals (Figure 2.5). When the collection net was not deployed, the trap could not capture any animals. Two permanent stations (i.e., the barrier nets) were located at each of the six sites. I constructed six of these trap nets for this study, which enabled me to sample all six stations on either creek simultaneously.

The collection nets were deployed at slack high tide. Any animals that entered the space between the barriers were trapped in the collection net as the tidal water receded. The traps were cleared once the water levels receded below the mouth of the barrier nets. Specimens were sorted and identified in the same manner as described for the throw traps. I attempted to collect three samples per station per collection date. This would ideally produce six samples per marsh site per trip, or 18 samples per creek per trip. Across all dates, I collected 136 flume samples; equipment failures on all but one date prevented me from collecting the maximum number of possible samples.

Figure 2.4. Diagram of flume trap barrier nets. The barrier nets were permanently installed at 12 sampling stations, two at each marsh site. The barriers were 12 m long and were 1.5 m apart, made of 1/8-inch plastic netting. Half of the barriers were in the high marsh, while the other half extended into the low marsh. Barrier height gradually increased from about 0.8 m in the high marsh to 1.4 m at the opposite end in the low marsh, ensuring that the top was always above the high water mark. 1-inch PVC poles anchored the barrier nets, and 3-inch PVC guide posts were attached at the low marsh end where the flume nets were attached during collection periods.
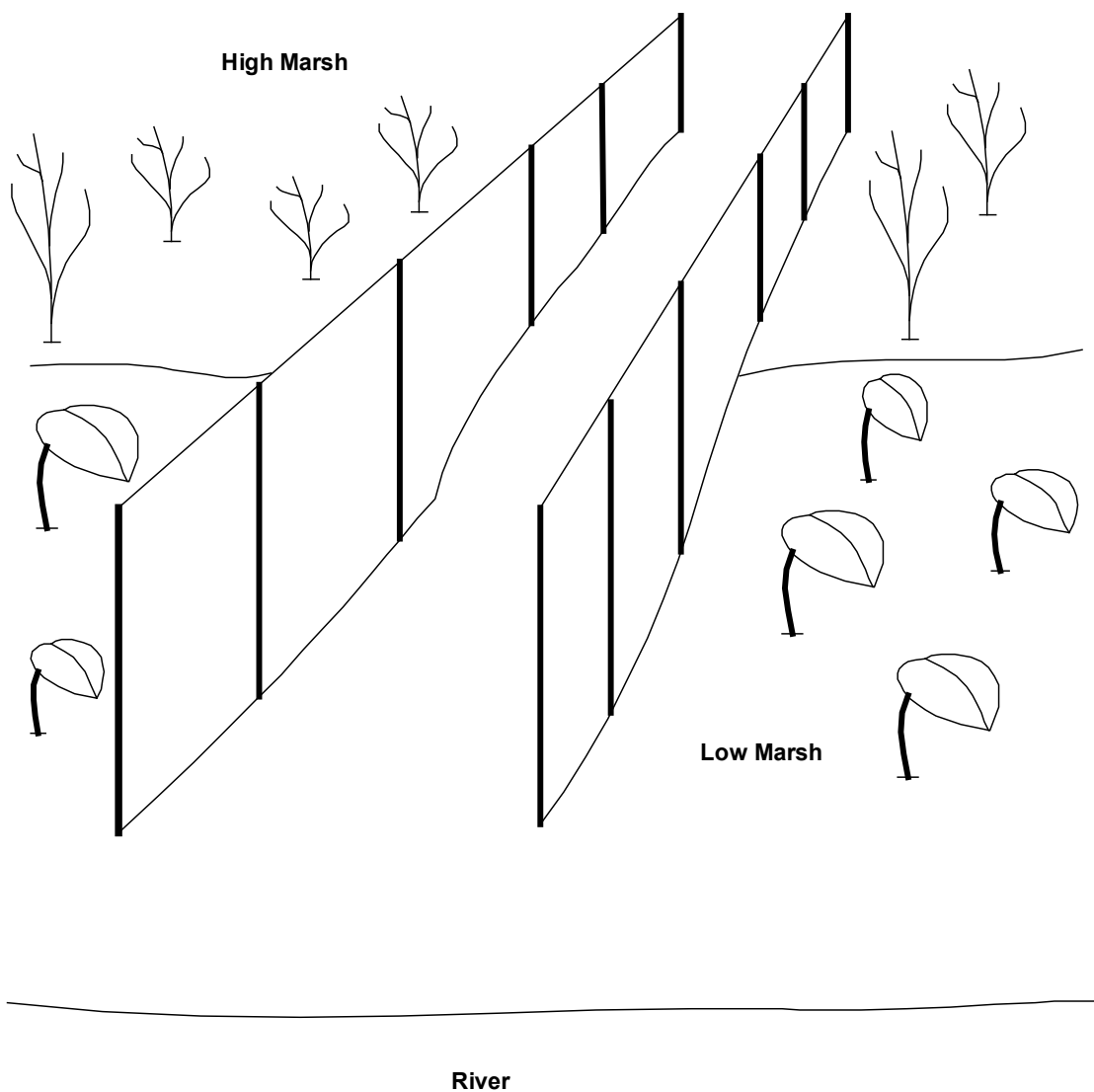
Figure 2.5. Diagram of the flume trap collection net. This is the net that attaches to the low marsh end of the barrier nets during sample collections. The perspective is as if the viewer were standing inside the barrier nets looking at the collection net deployed. The upper 2/3 of the collection net consisted of only a sheet of 1/32-inch knotless netting, while the lower third of the trap contained the mini-trawl net that captured the animals. The clear floating bar on the right side indicate the metal stripping used to anchor net material to the frame, while the darker bar indicates the position of the guide pole that would slide inside the guide-post of the barrier nets.
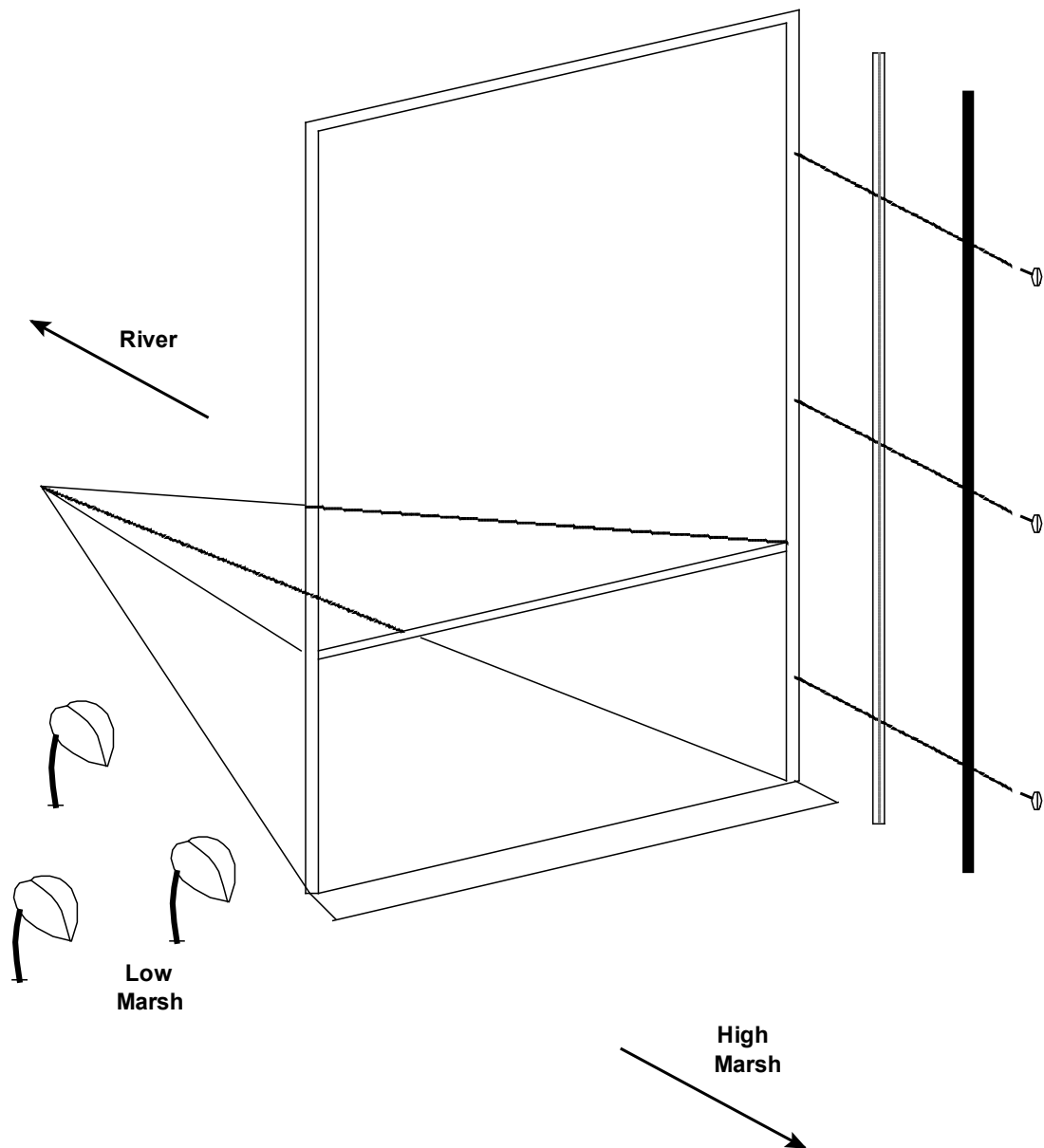
<u>Data Analysis</u>

When it was deemed necessary, data were transformed (ln (x+1)) to minimize any issues with non-normality in order to proceed with parametric statistical evaluations. All transformations were done before any data reductions were performed (i.e., transformations occurred before any site means were calculated). Means and upper and lower measures of significance were back transformed for the presentation of the data.

Comparison of Animal Trapping Methods

The two different trapping techniques were used determine if there were any unexpected biases in either of the trapping methods. It was impossible to compare directly the numerical or biomass catches of each trap since the resultant units of measurement are not compatible. The data, however, were relativized to the proportion each species contributes to the total abundance, permitting a comparison between the yields from each trapping technique.

I compared these proportions using a paired sample t-test for each species using SPSS 10 to compute the test statistics examining mean site biomass and numerical abundance (SPSS Inc. 1999). The proportion for each species found in the throw and flume traps were paired based on sample date and creek, producing 28 comparisons for each species. I looked at the 12 most abundant animal species across the five sample dates, omitting those that occurred in less than 5% of the samples. To evaluate the significance of the t-test results, I used the Hochberg experimental-wise error to test significance of each comparison. This sequential method is considered more powerful

than other Bonferoni experiment-wise tests of significance (Quinn and Keough 2002).

After the t-tests were performed, the p-values are ranked from greatest to smallest. The

largest p-value was compared to α, the second largest to $\alpha/2$, the third largest to $\alpha/3$, and

so on (in these analyses, $\alpha = 0.05$). Whenever a calculated p-value was less than its

paired critical value, it and all other p-values less than or equal to that value were

considered to be significant (Hochberg 1988).

Correlation Analysis

The throw trap data set has habitat data (e.g., salinity, water temperature, and

dissolved oxygen) directly associated with each sample unit. Therefore, it was possible to

examine these data to identify if any of the measured water quality and associated

vegetation variables were correlated with the fish and invertebrate assemblages. Pearson

correlation coefficients are present in three matrices, one for all samples combined and

then one for each creek. The correlation matrices present the strength of the relationship,

direction of the relationship and the statistical significance of the relationship. SPSS was

used to calculate the Pearson correlation coefficients (SPSS Inc. 1999).

Analysis of Variance

Analysis of Variance (ANOVA) was performed on all the community level

variables and for density and biomass of selected dominant species. Site means for each

sample date were compiled from each of the original data sets consisting of the individual

samples. The replicate cases in this study are the sites, where each collection (i.e.,

individual throw trap deployment, flume trap collection, high marsh plant quadrat, etc.) represents a subsample within each site on each date.

Creek, date and their interaction were used as independent factors to identify differences between the two creeks. I used a repeated measures analysis since the sites were sampled repeatedly over time, which introduced the likelihood that the data were temporally correlated. Different covariance matrix structures were evaluated to produce the model with the best fit for each dependent variable, altering assumptions about the heterogeneity of variance. The ANOVA model with the best fit (i.e., the one that produced the lowest Bayesian Information Criterion (BIC) score for model fit) was chosen in each case (Larry Douglass, Biometrics Program, University of Maryland, personal communication). Examples of the SAS programs are presented in Appendix II.

Six covariates (salinity, conductivity, water temperature, water depth, dissolved oxygen and plant stem density) were also included in the ANOVA of the throw trap data sets. This was the only data set where each sample unit had corresponding estimates of environmental parameters. Higher-order interactions among covariates and factors, however, were not considered in the models, as inclusion of these interactions consumed too many degrees of freedom to perform meaningful ANOVA. PROC MIXED was used for all ANOVA (SAS Institute 2003). PROC MIXED incorporates these variables in the model statement and apportions residual variance to the various covariates, often improving the results of the overall design. Non-significant covariates ($p > 0.10$) that did not improve the model were removed.

Sørensen's Similarity Index

I used Sørensen's Similarity Index to to determine how different the species pools of the two creeks were. The index uses presence and absence of species to calculate a value between 0 and 1 that measures similarity between communities (Sørensen 1948). A similarity of one indicates that the two sets are identical, while a score of zero indicates that there are no common species. The data were compiled in two different ways to look at the patterns in similarity over time. First, vegetation and animal species present in each creek were tallied to develop a comprehensive list of species occurring in each creek on each date. Thus, each species was reduced to simple measure of presence or absence in the two creeks. These two lists were used for the unweighted index. The weighted index accounted for species presence in each site. This second index incorporates a measure of frequency into its calculation. Both creeks, for example, may have *Schoenoplectus tabernaemontani* (softstem bulrush) present, but in one creek it may have only been found in one site, while the other creek had the plant in all three sites. The latter calculation considers these differences, while the former does not.

RESULTS

Nekton Community Summary

The throw traps collected a total of 37 different animal species across both creeks (Tables 2.2 for Broad Creek and 2.3 for Marshyhope Creek). The flume traps collected 19 species, although most invertebrates were not counted with this method (Tables 2.4

Table 2.2. Summary of throw trap collections from August 2000 through August 2002 for Broad Creek. Species are ranked in order of decreasing numerical abundance and have been split into two groups: fish and invertebrates. Length measurements for invertebrates are either carapace widths (crab species) or rostrum length (crayfish and shrimps). Biomass is the total sum of wet weights for all individuals collected.

Broad Creek

Species	Total Number	Biomass g wet wt.	Median g wet wt.	Median TL (mm)	Length Range TL (mm)
Fundulus diaphanus	615	354.3341	0.2462	30	5 - 86
Notropis hudsonius	62	2.1525	0.0026	14	6 - 32
Gambusia holbrooki	48	10.1200	0.1050	21.5	8 - 45
Trinectes maculatus	45	22.5449	0.4801	32	14 - 46
Morone americana	33	5.5414	0.1434	24	18 - 44
Etheostoma olmstedi	30	11.1025	0.0301	16.5	8 - 74
Lepomis macrochirus	20	46.3940	1.0742	40	21 - 106
Fundulus heteroclitus	19	40.2087	1.9260	52	40 - 70
Alosa psuedoharengus	11	17.6660	1.5155	57	56 - 62
Cyprinella analostana	2	2.3968	1.1984	51.5	43 - 60
Anguilla rostrata	1	0.0081	1.2019	93	58 - 163
FISH	886	512.4690			
Corixia sp.	1695	7.4202	0.0036	--	--
Gammarus sp.	191	1.4609	0.0048	--	--
Corbicula fluminea	77	2.8982	0.0189	--	--
Coenagrionidae	30	0.2277	0.0039	--	--
Physia gyrina	21	1.3059	0.0324	--	--
Cordulidae	12	0.3810	0.0230	--	--
Unknown Dipteran Larvae	11	0.2430	--	--	--
Lethrocercus sp.	7	0.6661	0.0543	--	--
Palaemonetes pugio	6	0.4376	0.0727	--	--
Sphaerium sp.	3	0.1760	0.0667	--	--
Neoephemeridae	3	0.0131	0.0025	--	--
Gomphidae	1	0.0531	0.0500	--	--
Hirudinea	1	0.0180	0.0180	--	--
Cyathura polita	1	0.0006	0.0006	--	--
INVERTEBRATES	2059	15.3014			
TOTAL ANIMALS	2945	527.7705			

Table 2.3. Summary of throw trap collections from August 2000 through August 2002 for Marshyhope Creek. Species are ranked in order of decreasing numerical abundance and have been split into two groups: fish and invertebrates. Length measurements for invertebrates are either carapace widths (crab species) or rostrum length (crayfish and shrimps). Biomass is the total sum of wet weights for all individuals collected.

Marshyhope Creek

Species	Total Number	Biomass g wet wt.	Median g wet wt.	TL (mm)	Length Range TL (mm)
Fundulus diaphanus	480	369.0660	0.4238	35	3 - 85
Gambusia holbrooki	213	33.1780	0.0761	20	9 - 76
Fundulus heteroclitus	132	419.1339	3.1503	61	19 - 89
Anchoa mitchilli	83	19.5445	0.1787	32	19 - 47
Notropis hudsonius	68	19.0535	0.0810	22	8 - 82
Etheostoma olmstedi	30	15.2693	0.1349	25.5	11 - 72
Morone americana	21	89.6013	0.1705	25	20 - 149
Gobiosoma bosc	14	3.7137	0.2243	26.5	12 - 35
Trinectes maculatus	11	2.2173	0.2118	19	14 - 32
Lepomis macrochirus	3	7.5331	0.8411	50	35 - 68
Anguilla rostrata	2	1.7185	0.8593	78	62 - 94
Micropterus salmoides	1	16.6425	16.6425	107	107
FISH	1058	996.6716			
Corixia sp.	20210	11.8936	0.0031	--	--
Gammarus sp.	308	1.8513	0.0052	--	--
Palaemonetes pugio	115	15.2138	0.1096	--	--
Corbicula fluminea	112	2.2759	0.0095	--	--
Unknown Dipteran Larvae	34	0.3288	--	--	--
Coenagrionidae	24	0.1905	0.0083	--	--
Physia gyrina	19	1.1077	0.0374	--	--
Chaoboridae	15	0.0686	0.0049	--	--
Simuliidae	9	0.0191	0.0017	--	--
Cordulidae	7	0.2962	0.0350	--	--
Caenidae	5	0.0145	0.0038	--	--
mud shrimp, Mysid	3	1.0210	0.0013	--	--
Uca minax	3	0.5466	0.1205	--	--
Belostoma sp.	2	0.1562	0.0781	--	--
Calinectes sapidus	2	1.3789	0.6895	--	--
Ranatra sp.	2	0.3245	0.1623	--	--
Orconectes limosus	1	0.0527	0.0527	--	--
Cyathura polita	1	0.0070	0.0070	--	--
INVERTEBRATES	20872	36.7469			
TOTAL ANIMALS	21930	1033.42			

Table 2.4. Summary of flume trap collections from May 2001 through August 2002 for Broad Creek. Species are ranked in order of decreasing numerical abundance and have been split into two groups: fish and invertebrates. Length measurements for invertebrates are either carapace widths (crab species) or rostrum length (crayfish and shrimps). Biomass is the total sum of wet weights for all individuals collected.

Broad Creek

Species	Total Number	Biomass g wet wt.	Median g wet wt.	Median TL (mm)	Length Range TL (mm)
Fundulus diaphanus	320	289.5519	0.2993	32	4 - 95
Fundulus heteroclitus	86	146.8756	1.4929	48	12 - 71
Gambusia holbrooki	50	8.2374	0.0841	20.5	11 - 41
Anchoa mitchilli	29	12.5784	0.4402	40	28 - 48
Lepomis macrochirus	20	324.8259	7.5837	75.5	20 - 183
Notropis hudsonius	14	33.1459	1.7058	50.5	20 - 97
Alosa psuedoharengus	7	13.0979	1.4599	57	55 - 80
Etheostoma olmstedi	2	1.6980	0.8490	44	30 - 58
Morone americana	2	52.1386	26.0693	119.5	100- 139
FISH	530	882.1496			
Palaemonetes pugio	3	0.1520	0.0644	8	6 - 8
Orconectes limosus	1	11.0094	11.0094	39	39
INVERTEBRATES	4	11.1614			
TOTAL ANIMALS	534	893.311			

Table 2.5. Summary of flume trap collections from May 2001 through August 2002 for Marshyhope Creek. Species are ranked in order of decreasing numerical abundance and have been split into two groups: fish and invertebrates. Length measurements for invertebrates are either carapace widths (crab species) or rostrum length (crayfish and shrimps). Biomass is the total sum of wet weights for all individuals collected.

Marshyhope Creek

Species	Total Number	Biomass g wet wt.	Median g wet wt.	Median TL (mm)	Length Range TL (mm)
Fundulus diaphanus	444	401.0478	0.4432	35	7 - 90
Fundulus heteroclitus	275	537.7719	1.4797	50	20 - 89
Anchoa mitchilli	160	28.3227	0.1557	31	18 - 42
Gambusia holbrooki	132	23.7874	0.1025	21.5	8 - 46
Morone americana	33	211.4052	0.1224	24	18 - 142
Notropis hudsonius	32	166.2843	4.4081	86.5	17 - 211
Gobiosoma bosc	16	4.9126	0.2733	28.5	33328
Etheostoma olmstedi	12	34.6617	2.9385	72.5	25 - 89
Trinectes maculatus	6	3.0532	0.5238	33.5	26 - 35
Menidia beryllina	6	2.5428	0.4723	42.5	19 - 50
Micropterus salmoides	1	16.1235	16.1235	108	108
Anguilla rostrata	1	0.2319	0.2319	61	61
Ameiurus nebulosus	1	23.3208	23.3208	128	128
FISH	1119	1453.4658			
Palaemonetes pugio	89	11.6494	0.1024	10	4 - 19
Calinectes sapidus	17	331.8129	1.1507	26	18 - 142
Uca minax	1	0.3220	0.322	9	9
INVERTEBRATES	107	343.7843			
TOTAL ANIMALS	1226	1797.2501			

for Broad Creek and 2.5 for Marshyhope Creek). Only two of 15 fish species trapped in the flumes were not found in the throw traps (*Menidia beryllina* and *Ameiurus nebulosus*). The throw trap samples contained 14 fish species, and only one species was not captured in the flumes (*Cyprinella analostana*). For these three species, however, only one or two individuals were caught over the duration of the study, suggesting that they are rarely found in the flooded emergent vegetation of the tidal freshwater wetlands.

The throw traps on both creeks collected 24,785 individuals, of which 21,905 were water boatmen (hemipterans in the Corixidae family). The flumes captured a combined 1,760 fish and invertebrates. *Fundulus diaphanus* (the banded killifish) was the most abundant fish collected in the throw traps (1,094 total individuals, 56% of all fish collected), with more than four times the number of individuals than the next most abundant species, *Gambusia holbrooki*, the mosquitofish (261 total individuals, 13%). Similarly, the flume trap collections were also dominated by *F. diaphanus* (764 total individuals, 46%), although *Fundulus heteroclitus* (mummichog) was the second most abundant species in this sampling method (361 total individuals, 22%). Only eight percent of the total fish caught in the throw traps were *F. heteroclitus*.

The proportional representation of each species in the total measures of animal abundance collected did not differ between trapping methods. For both density and biomass, the p-values for each species were never less than their corresponding Hochberg critical values, which implies that the relative proportions of each species collected in both traps are statistically the same (Table 2.6). These results suggest that the two

Table 2.6. Results of comparison of fish population proportions of the two trapping techniques. For each species mean proportions of the total catch are presented for both throw and flume trap. P-values calculated by paired sample t-tests and their corresponding Hochberg experiment-wise critical values are presented for each pair of means. Species are ranked in order of descending p-value. If a p-value is less than its corresponding critical value, it and all other pairs of means less than or equal to that p-value are significantly different. None of these values were significant.

Biomass Species	Population Proportions Throw	Flume	p-value	critical value
Morone americana	0.0664	0.0667	0.9924	0.0500
Anchoa mitchili	0.0170	0.0133	0.8075	0.0250
Fundulus heteroclitus	0.2275	0.2796	0.3359	0.0167
Gambusia holbrooki	0.0342	0.0200	0.2829	0.0125
Lepomis machrchirus	0.0663	0.1123	0.2533	0.0100
Gobiosoma bosc	0.0038	0.0004	0.1927	0.0083
Fundulus diaphanus	0.4360	0.3522	0.1634	0.0071
Palaemonetes pugio	0.0149	0.0028	0.1599	0.0063
Etheostoma olmstedi	0.0266	0.0081	0.1172	0.0056
Trinectes maculatus	0.0187	0.0008	0.0962	0.0050
Notropis hudsonius	0.0138	0.0687	0.0821	0.0045
Anguilla rostrata	0.0227	0.0000	0.0339	0.0042

Density Species	Population Proportions Throw	Flume	p-value	critical value
Lepomis machrchirus	0.0110	0.0105	0.9408	0.0500
Gobiosoma bosc	0.0021	0.0012	0.6068	0.0250
Anchoa mitchili	0.0136	0.0316	0.4005	0.0167
Morone americana	0.0152	0.0068	0.3567	0.0125
Palaemonetes pugio	0.0220	0.0115	0.2895	0.0100
Notropis hudsonius	0.0383	0.0173	0.2409	0.0083
Gambusia holbrooki	0.0279	0.0515	0.1746	0.0071
Trinectes maculatus	0.0151	0.0010	0.1078	0.0063
Etheostoma olmstedi	0.0158	0.0042	0.0361	0.0056
Anguilla rostrata	0.0035	0.0002	0.0204	0.0050
Fundulus diaphanus	0.1822	0.3123	0.0150	0.0045
Fundulus heteroclitus	0.0479	0.1427	0.0069	0.0042

trapping techniques are similarly effective at sampling the more mobile aquatic animals entering the marshes.

About 150 more fish were collected in throw traps in Marshyhope Creek than Broad Creek (Tables 2.2 and 2.3). The flume traps also collected more fish in Marshyhope Creek (589 more individuals) (Tables 2.4 and 2.5). *F. diaphanus* was the dominant species across both creeks and both trapping methods. Of the fish collected in throw traps in Marshyhope Creek, 69 percent were *F. diaphanus*, but this species comprised only 45 percent of the fish collected in Broad Creek. The percent composition was reversed in the flume traps, however, with *F. diaphanus* accounting for 60 percent and 40 percent of the fish collected in Broad Creek (BC) and Marshyhope Creek (MC), respectively. *Fundulus heteroclitus* was the next most dominant fish in both creeks in the flume traps (16 % in BC and 22 % in MC). In the throw traps, however, *F. heteroclitus* was the third most abundant fish after *Gambusia holbrooki* in Marshyhope Creek and was only the eighth most common fish species in Broad Creek (2.4% of all individuals). In Marshyhope throw traps, 12 fish species were captured while 11 species were found in those from Broad Creek collections. *Micropterus salmoides* (largemouth bass) and *Gobiosoma bosc* (naked goby) were not found in Broad Creek, while *Cyprinella analostana* (satinfin shiner) was not found in Marshyhope. The flumes captured members of 11 species in Broad Creek, and 13 species were taken in the flumes in Marshyhope Creek. Oligohaline species, *Menidia beryllina* (inland silverside) and *Gobiosoma bosc,* largely accounted for this difference, found only in Marshyhope Creek. *M. salmoides* was

also taken in Marshyhope Creek but absent from Broad Creek in the flumes, while *Alosa pseudoharengus* (alewife) was captured in Broad Creek but not Marshyhope.

The macroinvertebrate totals also differed between the creeks (see Tables 2.2 and 2.3). Throw trap collections from Marshyhope Creek had eight more invertebrate taxa than did Broad Creek (22 and 14, respectively). There were also more crustacean species in the Marshyhope flumes than in Broad Creek. *Calinectes sapidus, Uca minax* and *Palaemonetes pugio* were found in Marshyhope Creek's flumes, while only *P. pugio* and *Orconectes limosus* were found in Broad Creek. The most outstanding difference between the creeks regarding invertebrates is the massive numbers of Corixid waterboatmen caught in Marshyhope Creek. Nearly 18,000 Corixids collected were from one site in October 2001, and approximately 16,000 were found in one trap. *Gammarus* spp. (probably all *G. fasciatus*) was the second most abundant invertebrate in both creeks, with *Corbicula fluminea*, *P. pugio*, narrow-winged damselfly larvae (Coenagrionidae) and *Physia gyrina* accounting for the remainder of the majority of invertebrate animals collected in both creeks.

Plant Community Summary

I identified 30 different plant species in the high and low marshes from August 2000 through August 2002 (Table 2.7 and 2.8, respectively). *Acorus calamus* (sweetflag) was the dominant plant species collected, with over 12 kg dry weight collected over the two years of high marsh sampling. In the low marsh, the dominant *Nuphar lutea* (spatterdock) yielded almost 8 kg of dry biomass over three years of sampling in that

Table 2.7. List of high marsh plant species collected at both creeks, 2000-2002. Species ordered alphabetically, biomass (g dry weight collected) is total yield over the span of study. Bold font indicates the five most dominant species in the high marsh. Superscripts indicate order of abundance for dominant species. "Dead" refers to non-living plant biomass that was still standing.

Species	Broad Creek	Marshyhope Creek
Acorus calamus (L.)	**6603.9[1]**	**5637.9[1]**
Amaranthus cannabinus (L.) Sauer	31.3	10.7
Aster sp.	0.0	10.0
Bidens laevis (L.) B.S.P.	**1132.2[3]**	19.7
Bidens sp.	29.2	1.3
Boehmeria cylindrica (L.) Sw.	0.0	13.9
Calystegia sepium (L.) R.Br. ssp. Sepium	88.9	27.6
Cuscuta gronovii Willd. Ex J.A. Schultes	30.2	66.1
Dulichium arundinaceum (L.) Britt.	0.0	8.9
Galium tinctorium L.	121.5	55.0
Impatiens capensis Meerb.	331.1	**472.5[5]**
Iris versicolor L.	90.7	102.9
Leersia oryzoides (L.) Sw.	394.1	309.7
Mentha arvensis L.	6.3	2.0
Mikania scandens (l.) Willd.	0.0	5.6
Murdannia keisak (Hassk.) Hand.-Mas.	2.6	0.0
Nuphar lutea (L.)	52.5	0.0
Peltandra virginica (L.) Schott	**825.7[4]**	**842.4[3]**
Poaceae (unidentified species)	5.5	6.9
Polygonum arifolium L.	**1565.4[2]**	**666.5[4]**
Polygonum punctatum Ell.	76.9	3.1
Polygonum sagittatum L.	57.7	60.7
Sagittaria latifolia Willd.	19.4	8.4
Schoenoplectus fluviatilis (Torr.) M.T. Strong	**530.4[5]**	**1063.6[2]**
S. tabernaemontani (K.C. Gmel.) Palla	0.0	12.7
Sparganium americanum Nutt.	0.0	12.9
Typha angustifolia L.	0.0	18.2
Typha latifolia L.	0.0	254.5
Zizania aquatica L.	289.8	14.9
Dead	3126.2	3110.4
Total High Marsh	15411.7	12819.2
Number of Species	21	27

Table 2.8. List of low marsh plant species collected at both creeks, 2000-2002. Species ordered alphabetically, biomass (g dry weight collected) is total yield over the span of study. Bold font indicates the three most dominant species in the low marsh. Superscripts indicate order of abundance for dominant species. "Dead" refers to non-living plant biomass that was still standing.

Species	Broad Creek	Marshyhope Creek
Nuphar lutea (L.)	**3833.2[1]**	**3189.0[1]**
Peltandra virginica (L.) Schott	**59.4[3]**	**53.2[3]**
Polygonum punctatum Ell.	30.5	13.1
Pontederia cordata L.	15.6	38.7
Zizania aquatica L.	**61.5[2]**	**242.9[2]**
Dead	117.2	225.3
Total Low Marsh	4117.4	3762.2

marsh zone. The top seven most abundant species in the high marsh (i.e., those with more than 0.5 kg of total dry biomass) accounted for 92 percent of the total living biomass collected. In the low marshes, 93 percent of the total biomass was comprised of one species, *Nuphar lutea*. In each collection period, there was dead plant material in most quadrats, especially those in the high marsh. This material was also collected, although it was not identified to the species level. Dead plant material accounted for more than six kg of the total dry biomass in the high marsh and about 0.3 kg of the total low marsh biomass.

Of the eight most abundant plant species (those with more than a total of 500 g collected) across both low and high marsh habitats, five have greater biomass in Broad Creek. Only *Schoenoplectus fluviatilis* (river bulrush) had substantially more biomass on Marshyhope Creek. In the low marsh, *N. lutea* biomass collected on Broad Creek was over 600 g greater than that in taken Marshyhope Creek. *Zizania aquatica* (wild rice) had higher low marsh biomass in Marshyhope Creek, but in the high marsh zones, it was more abundant in Broad Creek. Overall, there was approximately 15.5 kg of total plant biomass collected from the high marshes in Broad Creek, while only 12.8 kg was collected from Marshyhope Creek. The same pattern is seen in the low marsh, with 4.1 kg and 3.8 kg of biomass harvested from Broad Creek and Marshyhope Creek, respectively.

Correlation Analysis

The environmental and habitat variables associated with the throw traps were plotted out over time to see if there were any apparent differences between the two

creeks. Water depth, water temperature, and dissolved oxygen suggested little difference between the creeks (Figures 2.6a-c). Total low marsh vegetation biomass was also considered a habitat variable as it provided a measure of physical structure in the marshes. This variable also revealed no distinct contrast between the creeks (Figure 2.7c). Salinity and conductivity plots, however, show the beginning of a change in the salinity regime of some of the Marshyhope sites. Salinity in Marshyhope Creek rose from a mean of 0.1 ‰ to almost 0.4 ‰ (Figure 2.7a). The most downstream site on Marshyhope Creek had individual salinity measures as high as 1.4 ‰ by August 2002. While the overall mean increase is still within the bounds defined as freshwater (<0.5 ‰), the downstream-most site definitely began to take on some of the characteristics of oligohaline waters. Over the two years conductivity was measured, mean conductivity in Broad Creek increased from 123 μS cm^{-1} to 208 μS cm^{-1}, while in Marshyhope, it increased to a larger degree from 127 μS cm^{-1} to 834 μS cm^{-1} (Figure 2.7b). Neither variable differed statistically between the creeks, but their impact does appear in the biological data as estuarine species such as *Calinectes sapidus* (blue crab) and *Menidia beryllina* appeared in the animal collections while freshwater species abundance declined or disappeared (e.g., *Gammarus* spp (amphipods) were absent in all sites by August 2002).

Correlations (reported as Pearson correlation coefficients) among all possible pair-wise combinations of the 16 throw trap variables were used to identify relationships between the environmental variables and the estimates of animal abundance. Of these variables, nine measure biological characteristics of the aquatic macrofauna. The three

Figure 2.6 a – c. Environmental characteristics of Marshyhope Creek and Broad Creek throw trap samples, 2000 through 2002, a. dissolved oxygen, b. water temperature and c. water depth in throw traps. Symbols represent arithmetic site means for each sample period, error bars are ± one standard error of the mean.
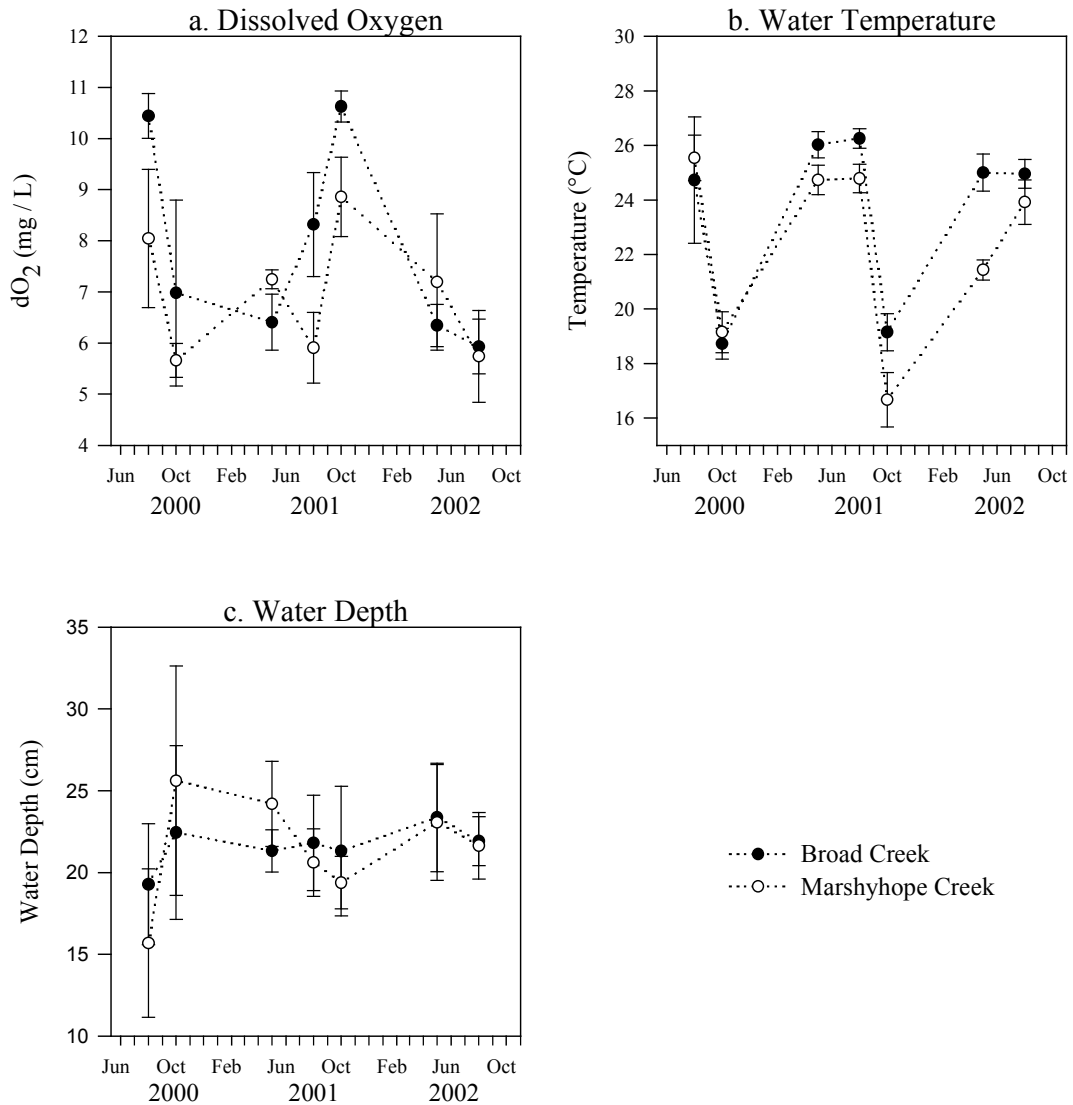
Figure 2.7 a – c. Environmental characteristics of Marshyhope Creek and Broad Creek throw trap samples, 2000 through 2002. a. Total plant biomass in low marsh, b. salinity and c. conductivity. Conductivity was not measured in 2000. Symbols represent arithmetic means for each creek on each collection date, and error bars are ± one standard error of the mean. Total plant biomass means and standard errors have been detransformed from the log transformed values.
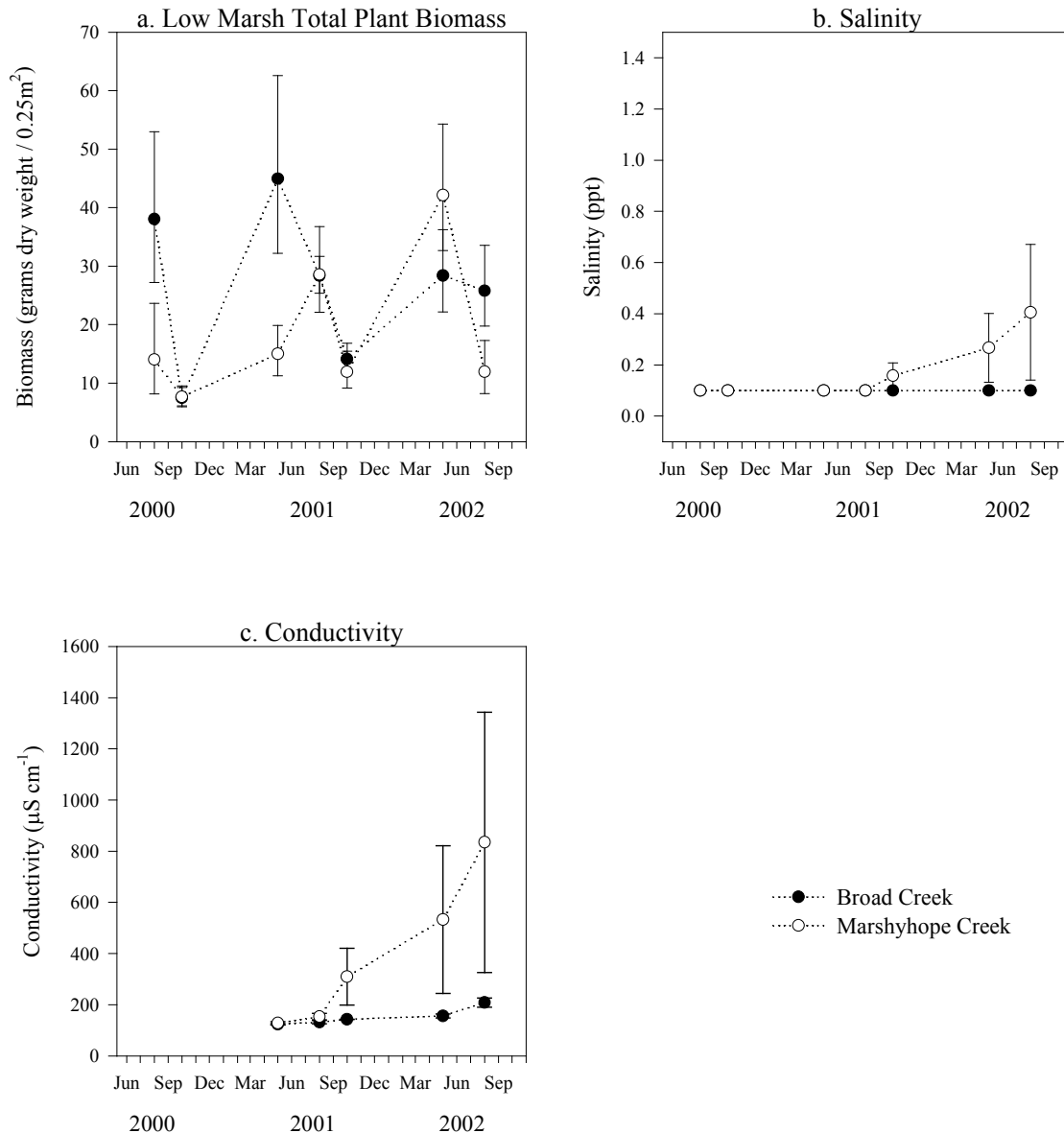
species density measures all indicate the number of species per sample (species richness m^{-2}), while the other variables are self-explanatory (numbers or grams m^{-2}).

The first table presents correlations across the entire data set (Table 2.9), while the other two matrices present the correlations within Broad and Marshyhope Creeks, individually (Table 2.10 and 2.11, respectively). Significant correlations (r values) between biological and physical variables were never of greater magnitude than ±0.266 in the aggregate matrix between fish species density and water temperature (Table 2.9). Fish species density and water temperature had the strongest significant relationship in Broad Creek (r = 0.365), while fish species density and water conductivity had the strongest correlation in Marshyhope Creek (r = 0.359). In the latter creek, changes in ionic concentrations in the water (i.e., salinity and conductivity) show the largest correlations, with biological variables positively related to fish species density and abundance, but negatively correlated to invertebrate species density and abundance (Table 2.11). At the combined level biological variables tended correlate with two environmental factors, dissolved oxygen and water temperature (Table 2.9). Invertebrate abundance was most highly correlated with dissolved oxygen (r = 0.232), and the other two invertebrate metrics, species density and biomass also had a positive relationship (r = 0.205 and 0.189, respectively). Community-level estimates for the fish had smaller correlations with dissolved oxygen, but were nonetheless significant. In these cases, however, the fish metrics were negatively related to oxygen content in the water. Broad Creek appears to account for most of the relationship between the estimates of animal abundance, as most of the correlations between the variables were highly significant

Table 2.9. Correlation matrix for combined creek data of community level and environmental variables for throw traps. Data presented are Pearson correlation coefficients (r values). Statistically significant relationships are denoted by asterisks, p < 0.05 = *, p < 0.01 = **, p < 0.001 = ***.

	Species Density	Total Abundance	Total Biomass	Fish Sp. Density	Fish Abundance	Fish Biomass	Invert. Sp. Density	Invert. Abundance
Species Density	1.0	0.462***	0.344***	0.477***	0.388***	0.344***	0.753***	0.362***
Tot. Abundance	0.462	1.0	0.398***	0.140*	0.396****	0.263**	0.414***	0.817***
Tot. Biomass	0.344	0.398	1.0	0.533***	0.729****	0.961***	-0.084	0.021
Fish Sp. Density	0.477	0.140	0.533	1.0	0.585****	0.563****	-0.093	-0.190**
Fish Abundance	0.388	0.396	0.729	0.585	1.0	0.773***	-0.093	-0.086
Fish Biomass	0.344	0.263	0.961	0.563	0.773	1.0	-0.134	-0.137
Invert. Sp. Density	0.753	0.414	-0.084	-0.093	-0.093	-0.134	1.0	0.600***
Invert. Abundance	0.362	0.817	0.021	-0.190	-0.086	-0.137	0.600	1.0
Invert. Biomass	0.147	0.595	0.199	-0.053	-0.064	-0.053	0.236	0.639
Trap Water Depth	0.149	0.090	0.027	0.074	0.108	0.096	0.109	0.129
dO₂	0.057	0.201	-0.097	-0.172	-0.178	-0.155	0.205	0.232
Temperature	0.091	-0.113	0.083	0.266	0.144	0.141	-0.124	-0.202
Conductivity	-0.053	-0.136	0.030	0.047	-0.074	0.014	-0.082	-0.071
Salinity	0.047	-0.118	0.069	0.106	-0.056	0.026	-0.008	-0.052
Stem Density	-0.057	-0.066	-0.196	-0.179	-0.167	-0.183	0.109	0.021
Plant Biomass	0.023	-0.046	-0.042	-0.034	-0.026	0.011	0.094	-0.054

Table 2.9 continued.

	Invert. Biomass	Water Depth	Dissolved Oxygen	Water Temp.	Water Conductivty	Salinity	Stem Density	Plant Biomass
Species Density	0.147*	0.149*	0.057	0.091	-0.053	0.047	-0.057	0.023
Tot. Abundance	0.595***	0.090	0.201**	-0.113	-0.136	-0.118	-0.066	-0.046
Tot. Biomass	0.199**	0.027	-0.097	0.083	0.030	0.069	-0.196	-0.042
Fish Sp. Density	-0.053	0.074	-0.172*	0.266**	0.047	0.106	-0.179**	-0.034
Fish Abundance	-0.064	0.108	-0.178*	0.144*	-0.074	-0.056	-0.167*	-0.026
Fish Biomass	-0.053	0.096	-0.155*	0.141*	0.014	0.026	-0.183**	0.011
Invert. Sp. Density	0.236***	0.109	0.205**	-0.124	-0.082	-0.008	0.109	0.094
Invert. Abundance	0.639***	0.129	0.232***	-0.202**	-0.071	-0.052	0.021	-0.054
Invert. Biomass	1.0	-0.020	0.189**	-0.117	0.152*	0.159*	-0.117	-0.071
Trap Water Depth	-0.020	1.0	0.074	-0.101	-0.063	-0.029	-0.074	-0.027
dO_2	0.189	0.074	1.0	-0.224***	-0.182*	-0.150*	-0.144*	-0.150*
Temperature	-0.117	-0.101	-0.224	1.0	-0.105	-0.026	0.072	0.223***
Conductivity	0.152	-0.063	-0.182	-0.105	1.0	0.989***	-0.166*	0.000
Salinity	0.159	-0.029	-0.150	-0.026	0.989	1.0	-0.204*	0.039
Stem Density	-0.117	-0.074	-0.144	0.072	-0.166	-0.204	1.0	0.497***
Plant Biomass	-0.071	-0.027	-0.150	0.223	0.000	0.039	0.497	1.0

Table 2.10. Correlation matrix for Broad Creek community level and environmental variables. Data presented are Pearson correlation coefficients (r values). Statistically significant relationships are denoted by asterisks. $p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$.

	Species Density	Total Abundance	Total Biomass	Fish Sp. Density	Fish Abundance	Fish Biomass	Invert. Sp. Density	Invert. Abundance
Species Density	1.0	0.467***	0.295***	0.411***	0.387***	0.313**	0.804***	0.438***
Tot. Abundance	0.467	1.0	0.351***	0.032	0.259**	0.139	0.529***	0.886***
Tot. Biomass	0.295	0.351	1.0	0.399***	0.665***	0.933***	-0.038	0.063
Fish Sp. Density	0.411	0.032	0.399	1.0	0.480***	0.455***	-0.028	-0.163
Fish Abundance	0.387	0.259	0.665	0.480	1.0	0.746***	-0.016	-0.096
Fish Biomass	0.313	0.139	0.933	0.455	0.746	1.0	-0.104	-0.162
Invert. Sp. Density	0.804	0.529	-0.038	-0.028	-0.016	-0.104	1.0	0.645***
Invert. Abundance	0.438	0.886	0.063	-0.163	-0.096	-0.162	0.645	1.0
Invert. Biomass	0.139	0.624	0.220	-0.084	-0.137	-0.114	0.242	0.665
Trap Water Depth	0.170	0.009	0.001	0.129	0.042	0.065	0.116	0.076
dO₂	0.070	0.207	-0.174	-0.197	-0.320	-0.339	0.234	0.394
Temperature	0.118	-0.113	0.092	0.365	0.230	0.188	-0.112	-0.181
Conductivity	-0.135	-0.265	-0.062	-0.041	-0.191	-0.056	-0.114	-0.155
Salinity	-0.013	-0.140	0.013	0.049	-0.127	-0.032	-0.040	-0.060
Stem Density	-0.082	-0.128	-0.207	-0.135	-0.142	-0.128	0.018	-0.102
Plant Biomass	0.028	-0.089	-0.060	-0.040	-0.058	0.034	0.113	-0.029

Table 2.10 continued.

	Invert. Biomass	Water Depth	Dissolved Oxygen	Water Temp.	Water Conductivty	Salinity	Stem Density	Plant Biomass
Species Density	0.139	0.170	0.070	0.118	-0.135	-0.013	-0.082	0.028
Tot. Abundance	0.624***	0.009	0.207***	-0.113	-0.265*	-0.140	-0.128	-0.089
Tot. Biomass	0.220*	0.001	-0.174	0.092	-0.062	0.013	-0.207*	-0.060
Fish Sp. Density	-0.084	0.129	-0.197	0.365***	-0.041	0.049	-0.135	-0.040
Fish Abundance	-0.137	0.042	-0.320**	0.230*	-0.191	-0.127	-0.142	-0.058
Fish Biomass	-0.114	0.065	-0.339***	0.188	-0.056	-0.032	-0.128	0.034
Invert. Sp. Density	0.242*	0.116	0.234*	-0.112	-0.114	-0.040	0.018	0.113
Invert. Abundance	0.665***	0.076	0.394***	-0.181	-0.155	-0.060	-0.102	-0.029
Invert. Biomass	1.0	-0.067	0.310**	-0.080	0.073	0.129	-0.176	-0.055
Trap Water Depth	-0.067	1.0	-0.133	-0.135	-0.084	-0.048	-0.127	-0.010
dO_2	0.310	-0.133	1.0	-0.193*	-0.221*	-0.163	-0.188*	-0.246
Temperature	-0.080	-0.135	-0.193	1.0	-0.005	-0.050	0.028	0.174
Conductivity	0.073	-0.084	-0.221	-0.005	1.0	0.991***	-0.192	0.043
Salinity	0.129	-0.048	-0.163	-0.050	0.991	1.0	-0.240**	0.042
Stem Density	-0.176	-0.127	-0.188	0.028	-0.192	-0.240	1.0	0.598
Plant Biomass	-0.055	-0.010	-0.246	0.174	0.043	0.042	0.598	1.0

Table 2.11. Correlation matrix for Marshyhope Creek community level and environmental variables. Data presented are Pearson correlation coefficients (r values). Statistically significant relationships are denoted by asterisks. $p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$.

	Species Density	Total Abundance	Total Biomass	Fish Sp. Density	Fish Abundance	Fish Biomass	Invert. Sp. Density	Invert. Abundance
Species Density	1	0.435***	0.374***	0.550***	0.379***	0.362***	0.667***	0.179
Tot. Abundance	0.435	1.0	0.446***	0.271**	0.603***	0.445***	0.173	0.645***
Tot. Biomass	0.374	0.446	1.0	0.663***	0.790***	0.995***	-0.175	-0.095
Fish Sp. Density	0.550	0.271	0.663	1.0	0.688***	0.673***	-0.215*	-0.302**
Fish Abundance	0.379	0.603	0.790	0.688	1.0	0.797***	-0.208*	-0.106
Fish Biomass	0.362	0.445	0.995	0.673	0.797	1.0	-0.197*	-0.141
Invert. Sp. Density	0.667	0.173	-0.175	-0.215	-0.208	-0.197	1.0	0.508***
Invert. Abundance	0.179	0.645	-0.095	-0.302	-0.106	-0.141	0.508	1.0
Invert. Biomass	0.083	0.524	0.065	-0.184	0.007	-0.022	0.279	0.652
Trap Water Depth	0.128	0.208	0.058	0.002	0.171	0.127	0.099	0.218
dO$_2$	0.109	0.269	-0.006	-0.124	-0.066	0.008	0.219	0.135
Temperature	0.128	-0.081	0.137	0.273	0.122	0.163	-0.114	-0.196
Conductivity	0.039	-0.025	0.194	0.359	0.231	0.199	-0.278	-0.349
Salinity	0.214	-0.325	0.134	0.235	-0.002	0.115	0.159	-0.332
Stem Density	-0.009	0.023	-0.165	-0.203	-0.174	-0.219	0.230	0.208
Plant Biomass	0.033	0.037	0.001	0.003	0.026	0.006	0.074	-0.080

Table 2.11 continued.

	Invert. Biomass	Water Depth	Dissolved Oxygen	Water Temp.	Water Conductivty	Salinity	Stem Density	Plant Biomass
Species Density	0.083	0.128	0.109	0.128	0.039	0.214*	-0.009	0.033
Tot. Abundance	0.524***	0.208***	0.269	-0.081	-0.025	-0.325***	0.023	0.037
Tot. Biomass	0.065	0.058	-0.006	0.137	0.194	0.134	-0.165	0.001
Fish Sp. Density	-0.184	0.002	-0.124	0.273**	0.359***	0.235*	-0.203*	0.003
Fish Abundance	0.007	0.171	-0.066	0.122	0.231*	-0.002	-0.174	0.026
Fish Biomass	-0.022	0.127	0.008	0.163	0.199	0.115	-0.219*	0.006
Invert. Sp. Density	0.279***	0.099	0.219*	-0.114	-0.278**	0.159	0.230*	0.074
Invert. Abundance	0.652***	0.218*	0.135	-0.196*	-0.349**	-0.332***	0.208*	-0.080
Invert. Biomass	1.0	0.109	0.221*	-0.104	-0.154	-0.225*	0.038	-0.091
Trap Water Depth	0.109	1.0	0.199*	-0.075	-0.017	0.053	-0.025	-0.049
dO$_2$	0.221	0.199	1.0	-0.285**	-0.342**	-0.160	-0.145	-0.097
Temperature	-0.104	-0.075	-0.285	1.0	-0.029	0.259**	0.086	0.283**
Conductivity	-0.154	-0.017	-0.342	-0.029	1.0	0.031	-0.197	-0.148
Salinity	-0.225	0.053	-0.160	0.259	0.031	1.0	-0.175	0.161
Stem Density	0.038	-0.025	-0.145	0.086	-0.197	-0.175	1.0	0.391***
Plant Biomass	-0.091	-0.049	-0.097	0.283	-0.148	0.161	0.391	1.0

(Table 2.10), while those in Marshyhope Creek were either not meaningful, or significant at a less rigorous level (Table 2.11). All three fish and one invertebrate (abundance) metrics were correlated with water temperature. The fish community variables were positively related to water temperature, while invertebrate abundance tended to decline as temperature increased (Table 2.9). Fish species density in both creeks was positively correlated with water temperature ($r = 0.365$ for BC, $r = 0.273$ for MC), while it appears that only in Marshyhope Creek was invertebrate abundance related to water temperature ($r = -0.196$).

Two other variables also were frequently correlated with community level properties. Salinity at the combined level was not significantly correlated to any of the biological variables (Table 2.9), but correlated with total species density, total animal abundance, fish species density, invertebrate abundance and invertebrate species density in Marshyhope Creek (Table 2.11). Numerical abundance estimates tended to decline as salinity increased, while species density tended to increase with the rising salinity. The categorical variable, stem density, showed negative correlations with fish metrics at the combined level (Table 2.9), and both fish and invertebrate metrics in Marshyhope Creek (Table 2.11). In Broad Creek, only the measure of total animal biomass was weakly correlated with stem density.

The relationships among the biological variables themselves are generally stronger, but their interpretation is either intuitive or more complicated. The three main community level variables, total species density, total biomass and total abundance, are all

significantly correlated in all three matrices, but many of the relationships are not very strong. After the invertebrates and fish were considered separately, however, the correlations among the fish-only community variables increased substantially. In Broad Creek for example, fish species density and fish abundance were the most highly correlated variables ($r = 0.69$). Causality in many of these relationships is often unclear as I did not attempt to experimentally evaluate their relationship. Some of these relationships, while highly significant and apparently strong, may only be reflecting life cycles in fish (e.g., fish abundance and fish biomass) or are highly redundant (species richness and fish species richness).

Analysis of Variance

In most cases, the community level variables presented did minimal relationships between the community variables and the environmental variables, which suggested that if there are differences in the resident aquatic macrofauna between the creeks, they are likely not due to the habitat variables that were measured. Preliminary data suggested that there were differences between the plant communities of the two creeks (see Figure 1.2), so I first determined whether the vegetation collections for this study revealed a similar trend.

Plant Community

The differences in the plant community offer some of the more pronounced contrasts between the two creeks. Throughout the duration of this study, Broad Creek appeared to have a higher total community biomass than Marshyhope Creek, but conversely, Marshyhope Creek tended to have greater species density (Figure 2.8). Aside

from August 2001, Broad Creek always had higher biomass, and only in August 2002 did

Broad Creek ever surpass the measured species density of Marshyhope Creek. Overall,

Broad Creek had significantly greater mean plant biomass than Marshyhope Creek – 5.05

g dry wt 0.25 m^{-2} in BC versus 4.85 g dry wt 0.25 m^{-2} in Marshyhope (Means and

standard errors for all variables on each collection date are presented in Appendix II).

While the ANOVA results suggest that season and creek are demonstrating an interaction

effect ($F_{4,5.14} = 8.271$, $p = 0.0182$) (Table 2.12), this is most likely due to the two

occasions where the means in Broad Creek and Marshyhope Creek have different

trajectories in October 2001 and August 2002 (Figure 2.8b). Plant species density differs

statistically at a less rigorous level ($F_{1,7.78} = 3.613$, $p = 0.0949$), but nonetheless still

supports the graphical inference that on average Marshyhope Creek, with 6.42 species

0.25 m^{-2}, is more species rich than Broad Creek at 5.80 species 0.25 m^{-2}.

In the low marsh, the community variables of species richness and total biomass

do not suggest any creek-level contrasts. The analysis of the dominant low marsh plant

Nuphar lutea by itself, however, indicates that Broad Creek had significantly greater

biomass than Marshyhope Creek (Table 2.12). This plant was generally more abundant in

Broad Creek than in Marshyhope, where May 2002 was the only occasion across all

seven sampling dates when more *N. lutea* was collected from Marshyhope Creek (Figure

2.9).

Figures 2.8 a and b. Characteristics of high marsh vegetation in Broad Creek and Marshyhope Creek: a. presents mean plant species density from May 2000 through August 2001, and b. shows mean total biomass over the same time span. Error bars are ± one standard error of the mean.
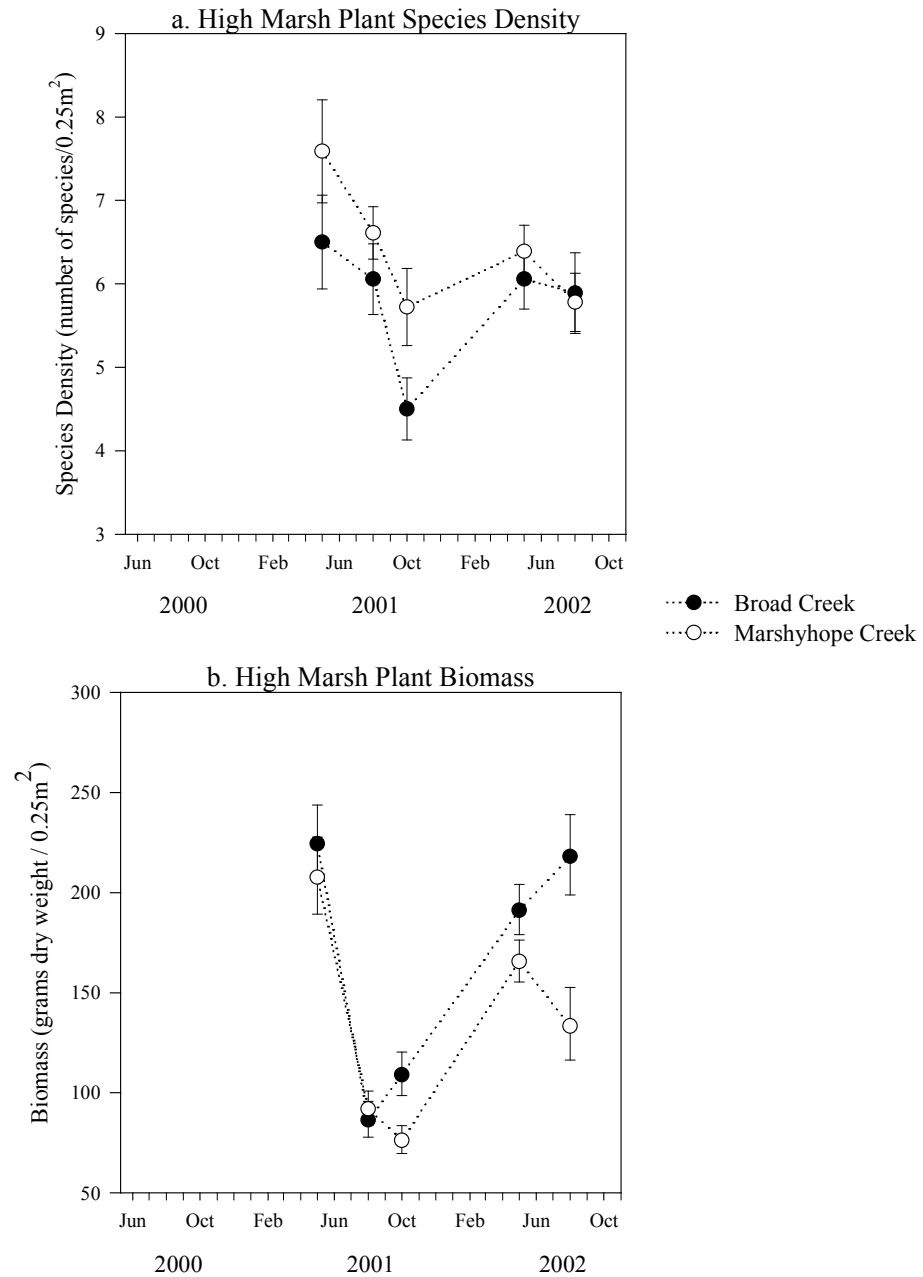
Table 2.12. Results of analysis of variance for vegetation variables. Statistically significant results are in bold type. Asterisks indicate the magnitude of the p value: * $p <$ 0.05, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$. HM = High Marsh, LM = Low Marsh.

Parameter **High Marsh Vegetation**	*Creek* *F Score*	*Date* *F Score*	*Creek*Date* *F Score*
Total Plant Biomass (HM)	**19.314***	**11.697****	**8.271***
Plant Species Density (HM)	3.613	**5.470***	0.491
Acorus calamus (HM)	0.161	**50.676*****	0.953
Impatiens capensis (HM)	0.509	**9.162***	0.916
Polygonum arifolium (HM)	2.056	**12.541*****	2.045
Petlandra virginica (HM)	0.006	**23.919*****	1.103
Low Marsh Vegetation			
Total Biomass (LM)	1.691	**4.853****	1.374
Species Density (LM)	0.415	1.492	1.247
Nuphar lutea (LM)	**4.457***	**7.694******	0.965
Zizania aquatica (LM)	0.254	1.797	2.600

Figure 2.9. Mean *Nuphar lutea* biomass collected in low marsh habitats in Marshyhope Creek and Broad Creek, August 2000 through August 2002. Symbols represent the mean value and error bars are presented as ± one standard error of the mean. Means and errors are detransformed values from their natural log equivalents.

Broad Creek
Marshyhope Creek
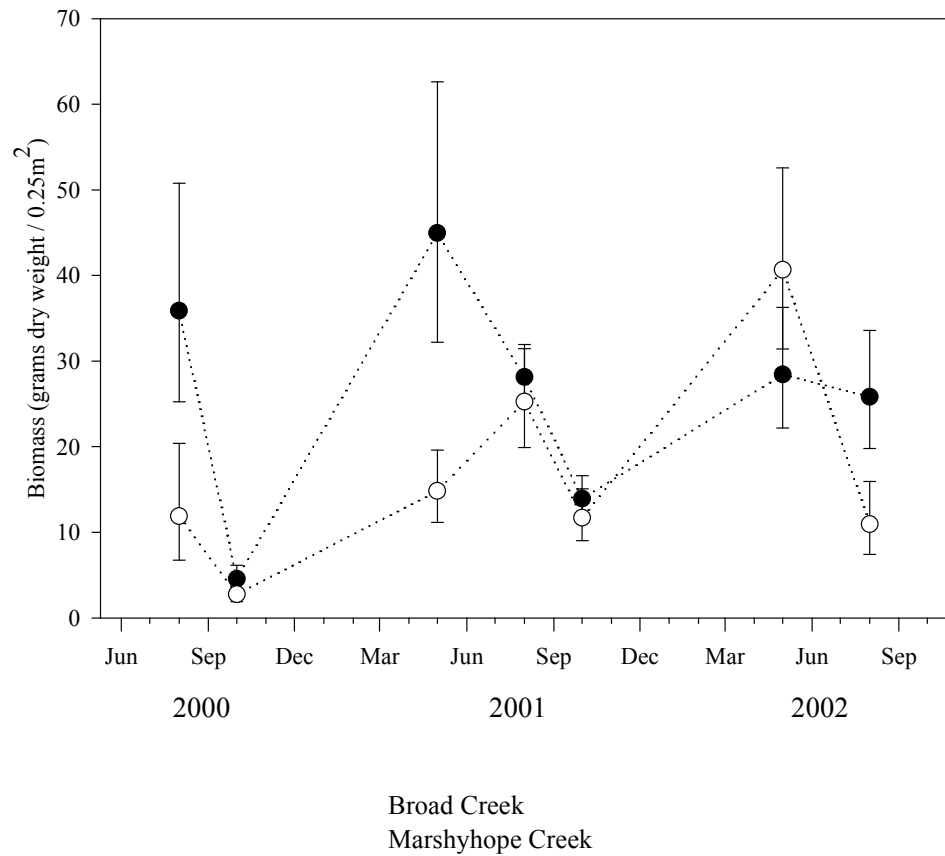
The effect of date was the most frequently significant result across all the plant community variables, but this reflects the extreme seasonal changes in plant community composition and abundance that occur in tidal freshwater marshes (Doumlele 1981; Whigham and Simpson 1992). No other variables in the low marsh vegetation indicated differences between the creeks.

Throw Traps

In the community variables for the throw traps, total biomass, total fish biomass, total invertebrate biomass and total fish species density all significantly differ between the creeks (Table 2.13). Of the nine community-level variables compared between the creeks, six models were improved by the inclusion of the covariates (ANCOVA). In all cases, only one covariate, either water temperature or dissolved oxygen, significantly improved the model. The covariates were also species pool specific: temperature was a significant covariate for all the fish community variables, while dissolved oxygen helped to better explain the variability in the invertebrates. There were no significant covariates for any of the combined total community-level variables.

Overall, mean total biomass in Marshyhope Creek was more than 2.0 g m^{-2} greater than that in Broad Creek (3.65 g m^{-2} and 1.57 g m^{-2}, respectively, Table A2.1). Mean total fish biomass and mean total invertebrate biomass (the components of mean total biomass) were both greater in Marshyhope Creek than in Broad Creek. Fish comprised the majority of the total biomass and the two variables, fish biomass and total

Table 2.13. Results of <u>Analysis of Co-Variance</u> for community-level animal variables in throw traps and <u>Analysis of Variance</u> for community animal variables flume traps. Statistically significant results are in bold type. Asterisks indicate the magnitude of the p value: * p < 0.05, ** p < 0.01, *** p < 0.001, **** p < 0.0001. Covariates without asterisks are p < 0.1. Only what were deemed significant covariates are included (p < 0.1) in the upper table. Covariates are: TEMP = water temperature, DO2 = dissolved oxygen. The flume trap sampling protocol did not directly include any measures of environmental variables as covariates, hence their absence from this table (See Chapter 3 for discussion of relationship between covariates and flume data).

Parameter **Throw Traps**	*Creek* *F Score*	*Date* *F Score*	*Creek*Date* *F Score*	*Covariate* *F Score*
Total Biomass	**10.990****	1.565	0.616	**3.20 (TEMP)**
Total Fish Biomass	**10.703****	1.558	0.743	**4.92 (TEMP)***
Total Invertebrate Biomass	**5.780***	0.846	1.373	**4.41 (DO2)**
Total Abundance	0.318	1.084	1.159	
Total Fish Abundance	0.407	1.769	2.335	
Total Invertebrate Abundance	1.121	1.802	1.183	**6.51 (DO2)***
Total Species Density	1.499	1.995	0.86	
Total Fish Species Density	**25.961*****	**6.768*****	**2.960***	**7.06 (TEMP)***
Total Invertebrate Species Density	1.121	1.802	1.183	**6.51 (DO2)***

Flume Traps	*Creek* *F Score*	*Date* *F Score*	*Creek*Date* *F Score*
Total Biomass	2.356	**3.350***	**4.385***
Total Fish Biomass	2.087	2.361	**4.256***
Total Abundance	2.662	**8.888****	**5.837***
Total Fish Abundance	1.997	**6.527****	**5.852***
Total Species Density	**8.638***	**10.571*****	**9.820*****
Total Fish Species Density	2.191	**5.640****	**6.274****

biomass, track almost identically over time (Figure 2.10 a and b). Animal biomass was greater in Marshyhope Creek than in Broad Creek on most sample dates. The only instance when fish and total biomass were greater in Broad Creek occurred in May 2002. Invertebrate biomass was always greater in Marshyhope Creek after 2000, but since this biomass is about an order of magnitude lower than that for the fish, they exert little influence on total biomass (Figure 2.10 a and c).

Total fish species density found in the throw traps differed significantly between the creeks (Table 2.13). Marshyhope Creek averaged 1.7 fish species m^{-2} while Broad Creek only had 1.1 fish species m^{-2} (Table A2.1). Fish species density had a noteworthy interaction effect ($F_{6,18.35} = 2.96$, $p = 0.0337$), but this relationship is fairly weak compared to that of creek effect alone ($F_{1,14.14} = 25.96$, $p = 0.0001$). Total species density and fish species density were greater on Broad Creek on only one occasion from 2000 through 2002 (Figure 2.11b). In October 2001, the spike in invertebrate species density contributed to greater total species density in Broad Creek (Figure 2.11b). May 2002 was the only occasion when Broad Creek had higher fish species density than Marshyhope Creek (Figure 2.11c).

The third community variable, total animal abundance, did not differ nor did its constituent elements, total fish or total invertebrate abundance. Looking at these data over time also does not reveal any similar patterns to the biomass or species density (Figure 2.12 a – c). Separately, fish and invertebrate abundance do not present any clear patterns, but total abundance reveals an interesting pattern. Before 2001, animal abundance was

Figures 2.10 a – c. Biomass observed in throw traps on Broad Creek and Marshyhope Creek, 2000-2002. 2.10a. Total biomass of all fish and macroinvertebrates, 2.10b. Total fish biomass only, and 2.10c. Total macroinvertebrate biomass only. Symbols represent means for each date and the error bars are ± one standard error of the mean. Means and errors are detransformed values from their natural log equivalents.

a. Total Biomass

b. Fish Biomass

c. Invertebrate Biomass

···●··· Broad Creek
···○··· Marshyhope Creek
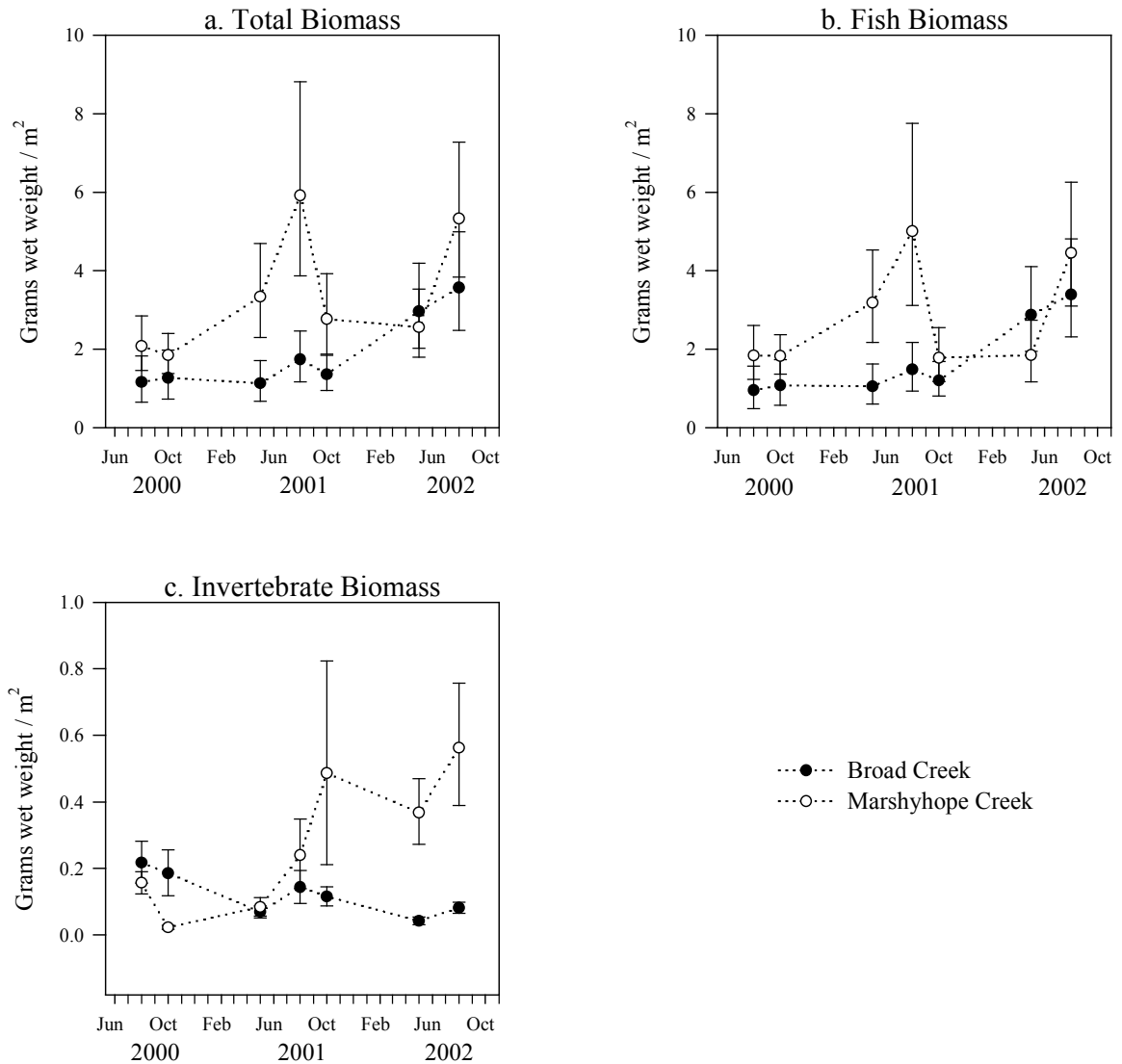
Figures 2.11 a – c. Mean species density observed in throw traps on Broad Creek and Marshyhope Creek, 2000-2002. 2.11a. Total species density of fish and macroinvertebrates. 2.11b. Total fish species density only, and 2.11c. Total macroinvertebrate species density only. Symbols represent means for each date and the error bars are ± one standard error of the mean.
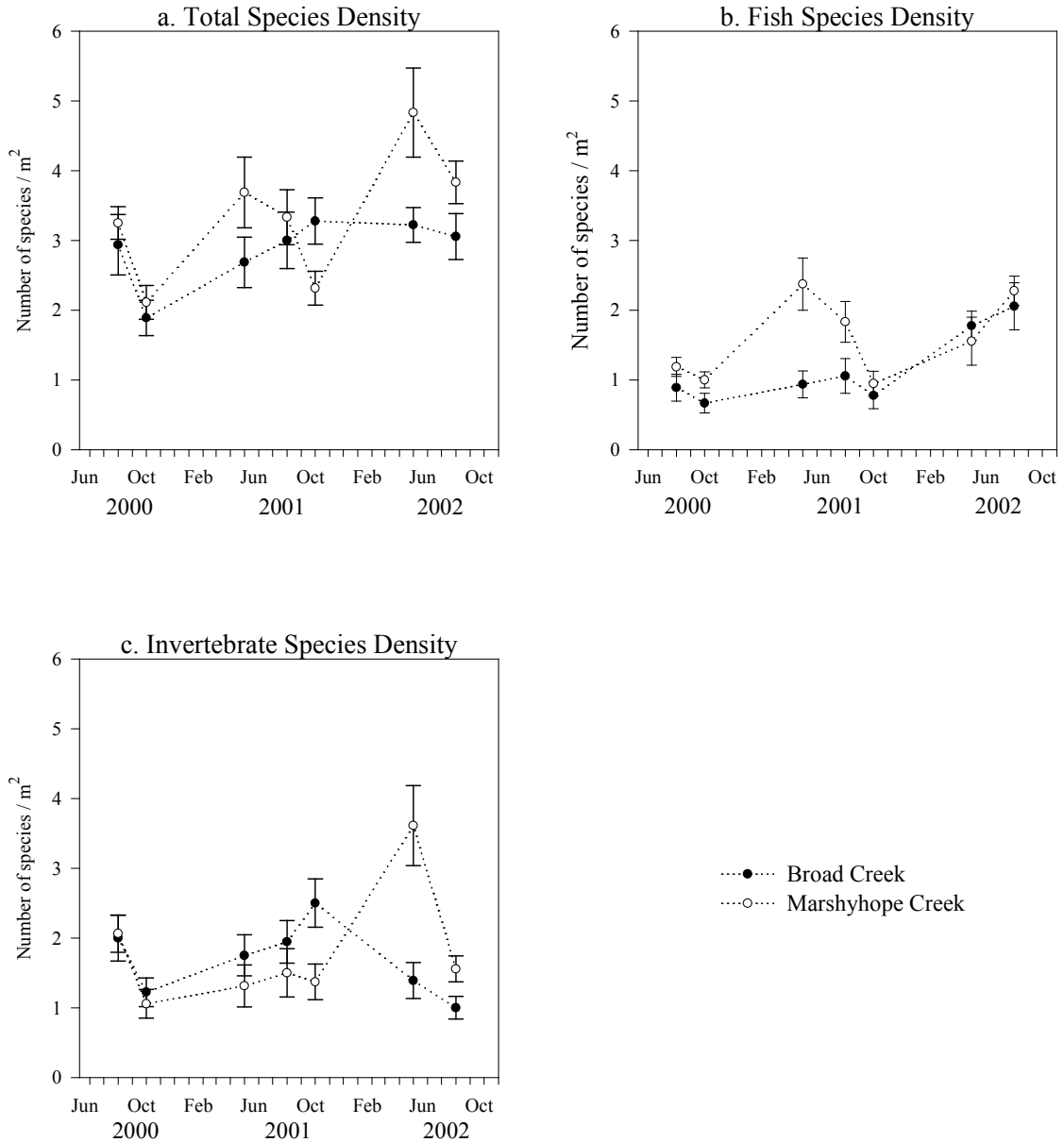
Figures 2.12 a – c. Animal abundances observed in throw traps on Broad Creek and Marshyhope Creek, 2000-2002. 2.12a. Total animal abundance of fish and macroinvertebrates, 2.12b. Total fish abundance only, and 2.12c. Total macroinvertebrate abundance only. Symbols represent means for each date and the error bars are ± one standard error of the mean. Means and errors are detransformed values from their natural log equivalents.
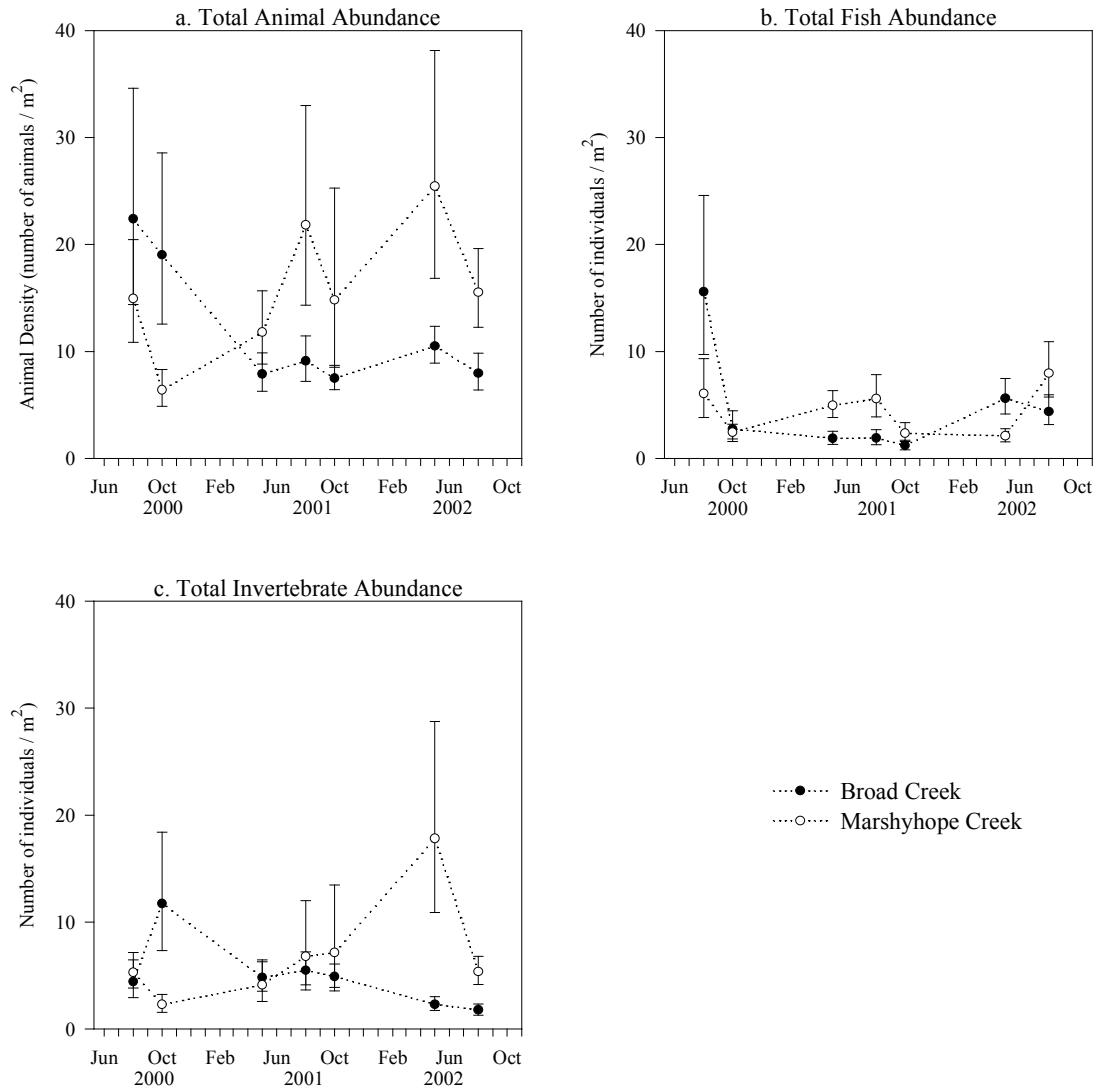
greater in Broad Creek, but at all sample dates after 2000 Marshyhope Creek had greater numerical abundance.

Among the dominant individual species from the throw traps, only *Gambusia holbrooki* density significantly differed between the creeks (grand means of 0.39 ind m^{-2} in MC, and 0.03 ind m^{-2} in BC) (Table 2.14). Five environmental factors acted as covariates for several of the individual species variables: low marsh plant biomass, salinity, water depth, water temperature and dissolved oxygen. Low marsh plant biomass was a significant covariate for banded killifish and mosquitofish density and also for spottail shiner biomass. Especially for the highly killifish, this would suggest that the presence of these small fish in the marshes is dependent to a certain extent upon the amount of vegetation present in the low marsh. The abundance of another dominant species, the mummichog, did not seem to be in anyway related to the biomass of vegetation in the marshes. For the killifish, salinity explained a significant amount of the residual variance. In the case of the mosquitofish, three other variables, water depth, temperature and salinity also accounted improved the ANCOVA model, although a lack of degrees of freedom prevented a serious examination of whether or not there were higher order interactions among these variables. *Gammarus* spp. density was related to water depth, while some amphipod biomass residual variance was accounted for by dissolved oxygen.

Looking at the results over time does not identify distinctions between the two creeks. The two dominant invertebrate taxa, Corixids and *Gammarus* spp., saw temporary

Table 2.14. Results of <u>ANCOVA</u> for abundant individual species in throw traps and <u>ANOVA</u> for abundant individual species flume traps. Statistically significant results are in bold type. Asterisks indicate the magnitude of the p value: * p < 0.05, ** p < 0.01, *** p < 0.001, **** p < 0.0001. Covariates without asterisks are p < 0.1. Covariates are: VEGBIO = low marsh plant biomass, SAL = salinity, DEPTH = water depth in trap, DO2 = dissolved oxygen, TEMP = water temperature. The flume trap sampling protocol did not directly include any measures of environmental variables as covariates, hence their absence from this table (See Chapter 3 for discussion of relationship between covariates and flume data).

Throw Traps	Creek F Score	Date F Score	Creek*Date F Score	Covariate F Score
Corixidae Biomass	0.264	0.364	0.677	
Corixidae Density	0.004	**5.396***	**5.035***	
Fundulus diaphanus Biomass	0.514	2.178	0.418	
Fundulus diaphanus Density	1.528	**12.828***	1.109	**5.67 (VEGBIO)*** **5.66 (SAL)***
Fundulus heteroclitus Biomass	4.866	2.38	2.009	
Fundulus heteroclitus Density	3.989	1.937	1.37	
Gambusia holbrooki Biomass	3.358	1.042	1.025	
Gambusia holbrooki Density	**8.546***	2.054	1.084	**5.88 (DEPTH)*** **3.56 (VEGBIO)** **10.48 (TEMP)**** **6.40 (DO2)***
Gammarus spp. Biomass	1.4	**8.050***	1.966	**6.40 (DO2)**
Gammarus spp. Density	0.105	**9.585****	**2.577***	**3.76 (DEPTH)**
Notropis hudsonius Biomass	1.889	1.095	1.145	**3.20 (VEGBIO)**
Notropis hudsonius Density	0.994	**6.253***	**6.491***	

Flume Traps	Creek F Score	Date F Score	Creek*Date F Score
Fundulus diaphanus Biomass	0.515	0.556	1.473
Fundulus diaphanus Density	0.29	**3.760***	2.829
Fundulus heteroclitus Biomass	2.605	**10.307***	1.289
Fundulus heteroclitus Density	1.554	**9.851****	**3.991***
Gambusia holbrooki Biomass	3.12	**4.531***	1.575
Gambusia holbrooki Density	1.361	**5.351***	1.128
Notropis hudsonius Biomass	0.299	0.121	2.162
Notropis hudsonius Density	0.423	0.309	1.845

spikes in abundance but nothing emerges that would indicate that the populations on the two creeks are existing at consistently different levels. For instance, Corixidae abundance generally declined over time in Broad Creek, while in Marshyhope Creek it appeared to be increasing, but then the abundance fell to near zero in both creeks by August 2002 (Figure 2.13 a and b). In the case of *Gammarus* spp., there were very similar levels of biomass and density in both creeks, but values spiked upward in Marshyhope Creek in May 2002. But similar to the Corixids, the amphipods also were nearly absent by August 2002 (Figure 2.13 c and d). All individual species data are presented in Appendix II.

Flume Traps

The flumes present a more complicated picture of the creeks (Table 2.13). Nearly every community level variable demonstrated both significant date and interaction effects. Species density was the only variable that resulted in a significant result in the creek effect ($F_{1,8.21} = 8.638$, p = 0.0267), but the magnitude of the interaction effect was just as large. The statistical evaluation of the data appears inconclusive, but as with the throw traps, there are trends in the data that appear over time. For the three community variables, biomass, abundance and species density, Marshyhope Creek always has larger means than Broad Creek except for one sample period. Total biomass was greater than 12 g m^{-2} in Marshyhope Creek on all dates except in October 2001, when it fell to less than 4 g m^{-2} (Figure 2.14a). Animal abundance and species richness also declined in October 2001. Abundance fell substantially from its previous measure in Marshyhope Creek during this sample period (Figure 2.15a). The number of species captured in Marshyhope Creek dropped below two species per trap in October 2001, but

Figure 2.14 a and b. Mean biomass in flume traps on Broad Creek and Marshyhope Creek, 2000 through 2002. Figure a. Total biomass of fish and invertebrates, Figure b. Total fish biomass only. Symbols represent means for each date and the error bars are ± one standard error of the mean. Means and errors are presented in equivalent natural log values.
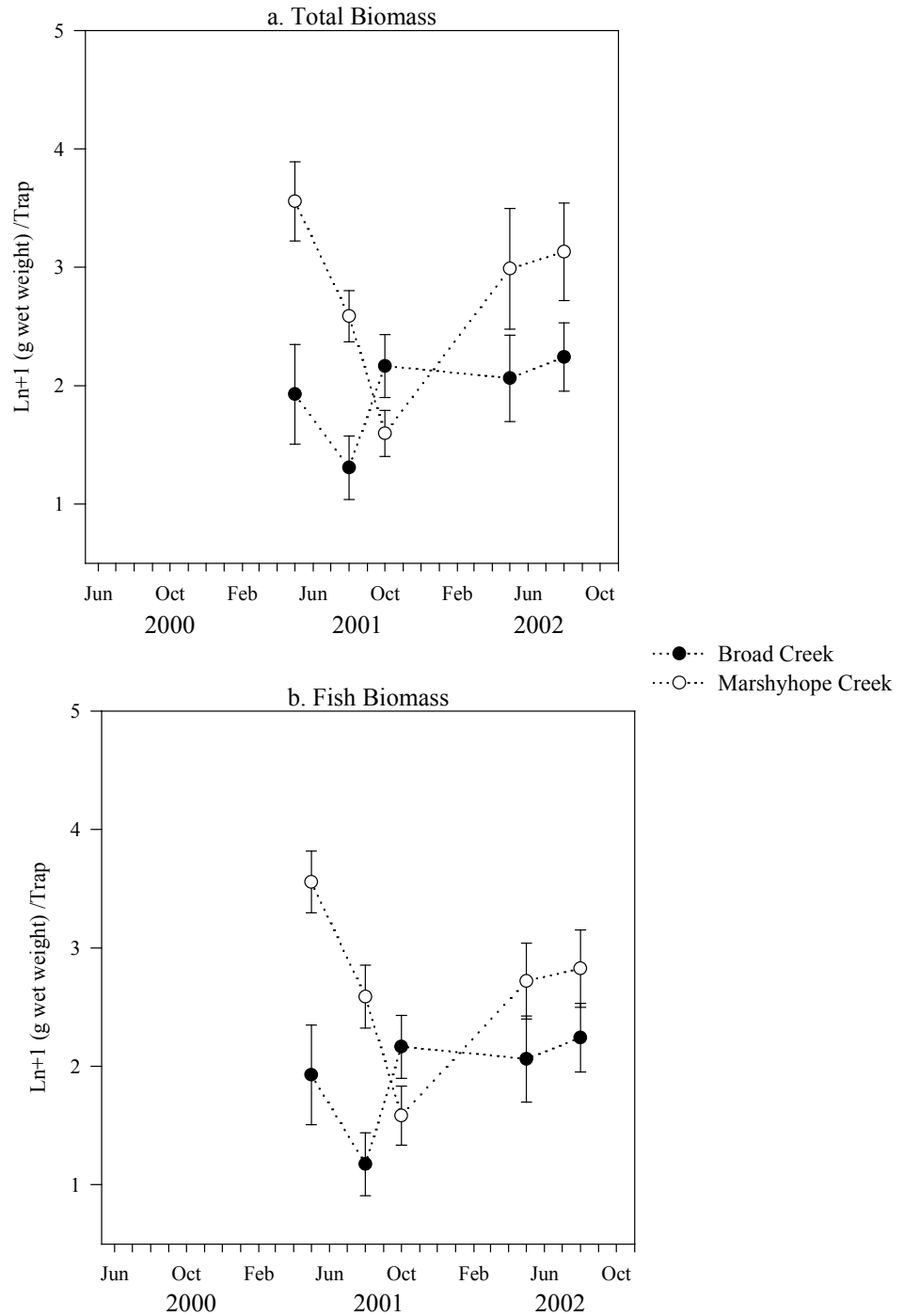
Figure 2.15 a and b. Mean animal abundances in flume traps on Broad Creek and Marshyhope Creek, 2000 through 2002. Figure a. Total animal abundance including fish and invertebrates, Figure b. Total fish abundance only. Symbols represent means for each date and the error bars are ± one standard error of the mean. Means and errors are presented in equivalent natural log values.
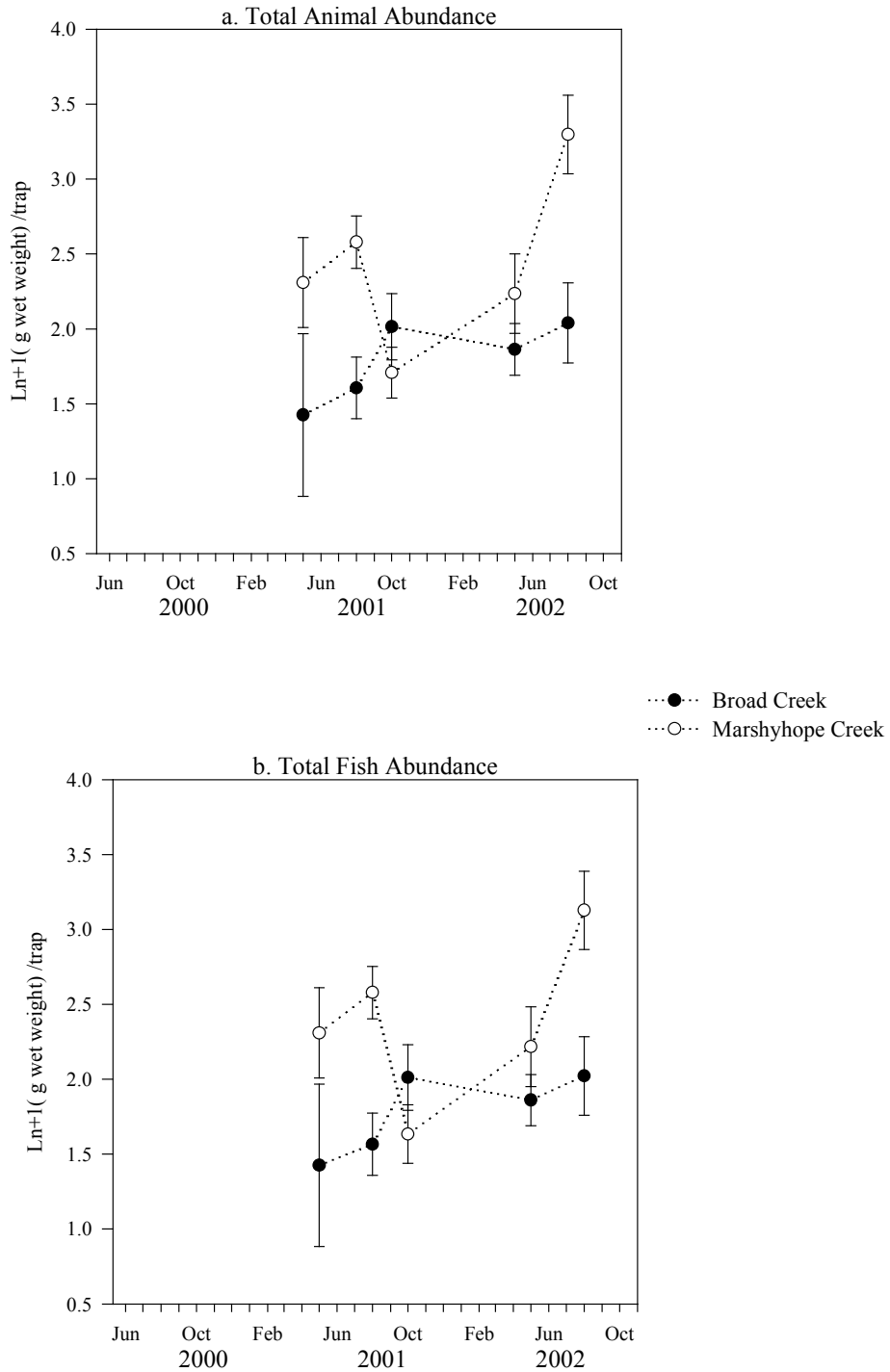
rebounded by the following May and increased again in August 2002 (Figure 2.16a). In October 2001 for every community variable, the means for animals in Broad Creek increased while those in Marshyhope decreased, resulting in the only instance when measured biomass, abundance and species richness were greater in Broad Creek than Marshyhope Creek.

The individual species again do not yield any meaningful results for the flume traps. Not one of the four most abundant species significantly differ in their numerical or biomass abundance between Broad Creek and Marshyhope Creek (Table 2.14). Nor does a visual inspection of the means of each creek on each date reveal any emerging patterns. Date effect appears to have the most impact on the abundance of individual species, which may be expected in such a seasonally variable environment. Individual species data are presented in Appendix II.

Sørensen's Similarity Index

For the site-weighted index, the similarity of the creeks ranges from 0.66 in May 2001 to 0.58 in August 2002 (Figure 2.17). The inclusion of the effect of site on the index introduces an estimate of abundance into the index, magnifying differences. It is possible that variability among the marshes within each creek generates this difference and influences the index values. Comparing only presence and absence based on creek should, therefore, increase similarity since imbalances in species presence in the marsh sites will be minimized. Looking at the data in this manner results in a similarity range from a high of 0.82 in May 2002 to a low of 0.59 by August 2002. Similarity by both

Figure 2.16 a and b. Species density of all animals and fish only in flume traps in Broad Creek and Marshyhope Creek, 2000 through 2002. Figure a. Total species density including fish and invertebrates, Figure b. Total fish species density only. Symbols represent means for each date and the error bars are ± one standard error of the mean.
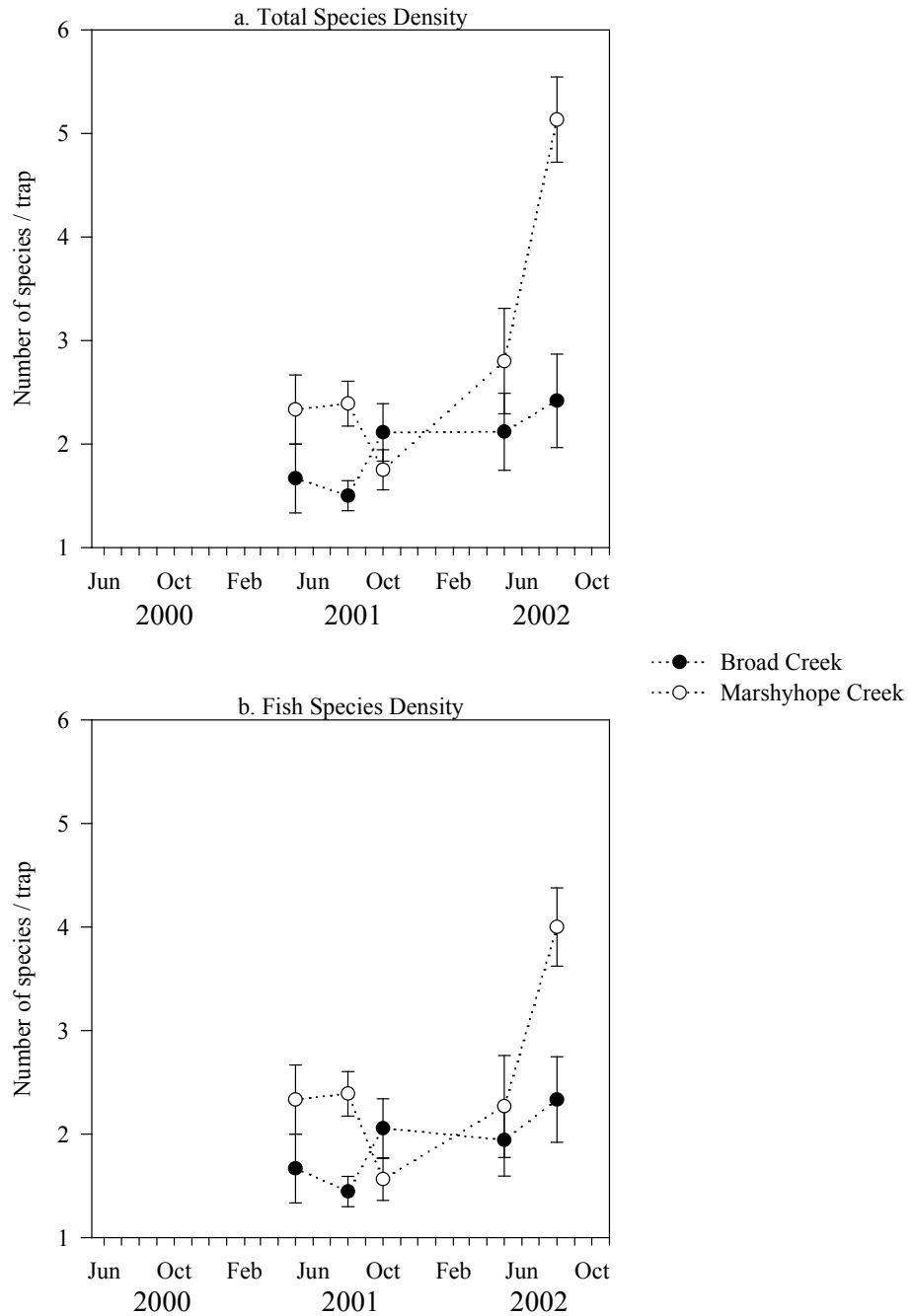
Figure 2.17. Sørensen's Similarity Index comparing Broad Creek to Marshyhope Creek from May 2001 through August 2002. The unweighted index considers only the presence or absence of each species in each creek, while the site-weighted index adds the presence or absence of each species in each site before calculating similarity. The inclusion of site in the second metric incorporates frequency of occurrence for each species in calculating the similarity, while the former method merely assesses similarity based on comparative species lists from each date.
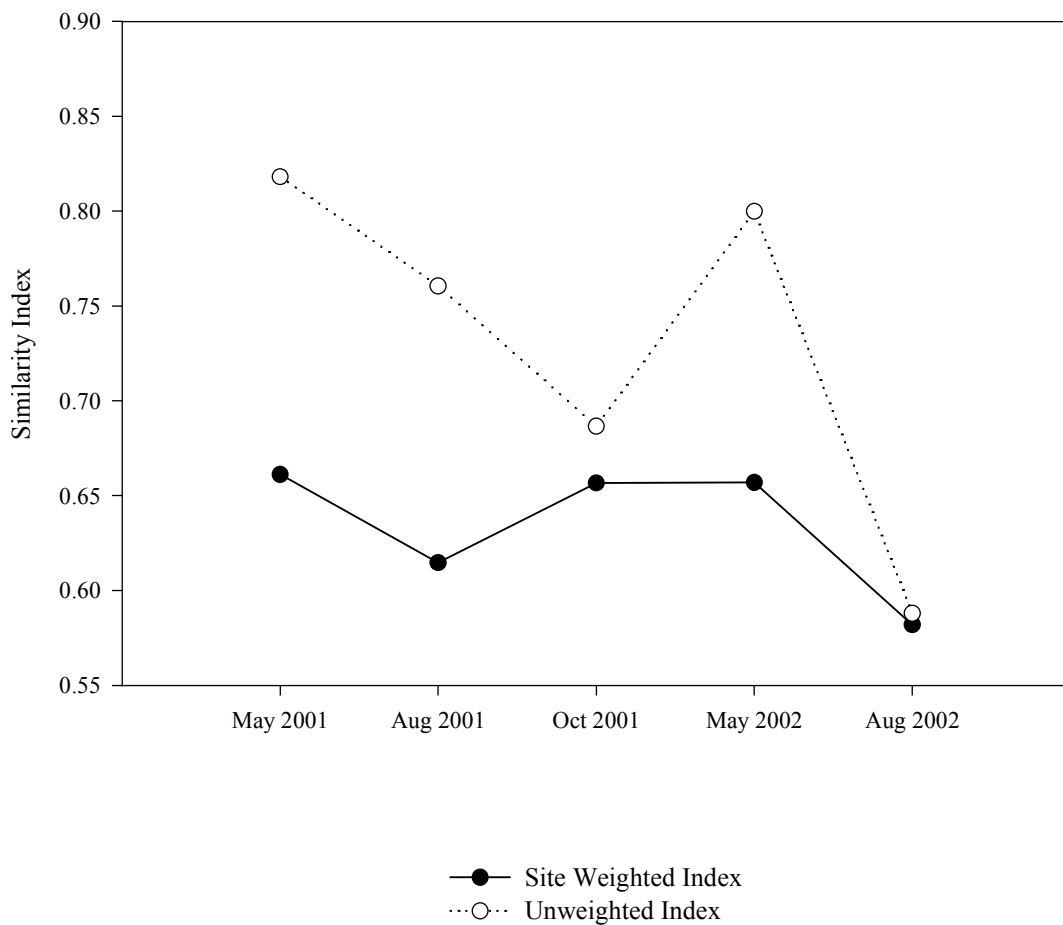
measures seems to imply that there is either a gradual decrease overall of similarity between creeks (site-weighted index), or that there is a potential seasonal decline in similarity from high values in the spring to lower values at the height of the growing season (unweighted index).

DISCUSSION

Several distinct differences emerged from this study that distinguish the creeks from each other. The differences in the plant community strongly suggest that there is a response to nutrient enrichment in Broad Creek, with more macrophyte biomass production than Marshyhope Creek yet fewer species per unit area (Figure 2.8). The difference in total species richness within the two creeks indicating fewer species in Broad Creek also corroborates the species density data (Table 2.7). Total nekton biomass was typically greater in Marshyhope, as was total animal density and species density in both trapping methods (Figures 2.10-2.12 and 2.14-2.16). These results combine to suggest that prolonged increases in the density of emergent marsh vegetation may lead to decreased aquatic macrofauna abundance. Given the fact that Broad Creek has a historically higher nitrogen load than Marshyhope Creek, the differences in nekton abundance may be an indirect consequence of this nutrient enrichment.

Yet this conclusion is by no means overwhelmingly supported by the results. The plant and animal communities offered some tempting differences, but the statistical comparisons generally did not support widespread differences between the two creeks. I hypothesized that differences in plant species biomass and composition would result in an

alteration of aquatic macrofauna abundance between the creeks. These mixed results corroborate similar research that looked at how aquatic animals were responding as plant community composition is changed. These studies suggested that plant species invasions in tidal marshes, particularly that of *Phragmites australis*, would create a less beneficial physical environment for nekton (Weinstein and Balletto 1999). My study approached this question from a different perspective. Species invasions resulting in complete species replacement are not the only way marsh vegetation can be affected by external events. Other more subtle changes can alter the characteristics of a plant assembly, the effects of which could cascade into the consumer organisms that depend on the structural benefits of the vegetation (Livingston 1984). Therefore, I wanted to identify if differences existed between presumably similar plant communities and, if they existed, to see if they were related to differences in aquatic macrofauna densities.

Any conclusions drawn by this study, however, are complicated by uncontrollable environmental factors that had far-ranging effects on the flora and fauna tidal freshwater marshes. Beginning in October 2001, a prolonged drought began in the mid-Atlantic region and persisted until the following September (National Drought Mitigation Center 2002). The consequence of the drought was a steady increase in the salinity of the river waters that flooded the marshes. Salinity changes likely explain why some differences appeared to not be significant, particularly in regard to animal abundance.

The premise that framed the study was that Marshyhope Creek and Broad Creek have observable differences in their plant communities. The species pools were quite similar, particularly among the dominant species, and a quick inspection of the two creek systems would lead most individuals to believe they are fairly similar. The tidal freshwater wetlands of the Nanticoke River consists of swamps filled with *Acre rurbrum* (red maple), *Fraxinus pensylvanica* (green ash) and *Nyssa sylvatica* (black gum) abutted by marshes that are dominated by *Acorus calamus* (sweetflag) in the early growing season and late emerging annuals in the high summer (Odum et al. 1984). Given the ubiquity of these dominant species, that quantifiable differences do exist is quite interesting.

In the parallel study that investigated the effect of nutrient enrichment and sedimentation on tidal freshwater vegetation I became aware that plant species density differed between the creeks (Figure 1.2 b and c). The initial trend in species density that indicated Marshyhope Creek had greater species density declined in magnitude after 2000, but nonetheless persisted for the duration of that study (Figure 2.18). My research echoed these findings. I found more plant species in Marshyhope Creek, yet total biomass collected during the study was greater in Broad Creek (Table 2.7). In each sampling period, plant species density in the high marsh of Broad Creek was always less than that in Marshyhope Creek aside from August 2002 (Figure 2.8a). I also discovered that on every sample date except August 2001 Broad Creek had greater plant biomass than Marshyhope Creek (Figure 2.8b). This biomass pattern extended to the low marsh where

Table 2.18. Comparison of mean plant species density between tidal freshwater marshes of Broad Creek and Marshyhope Creek. Symbols represent means for each date and the error bars are ± one standard error of the mean. Data from unpublished research of A.H. Baldwin.
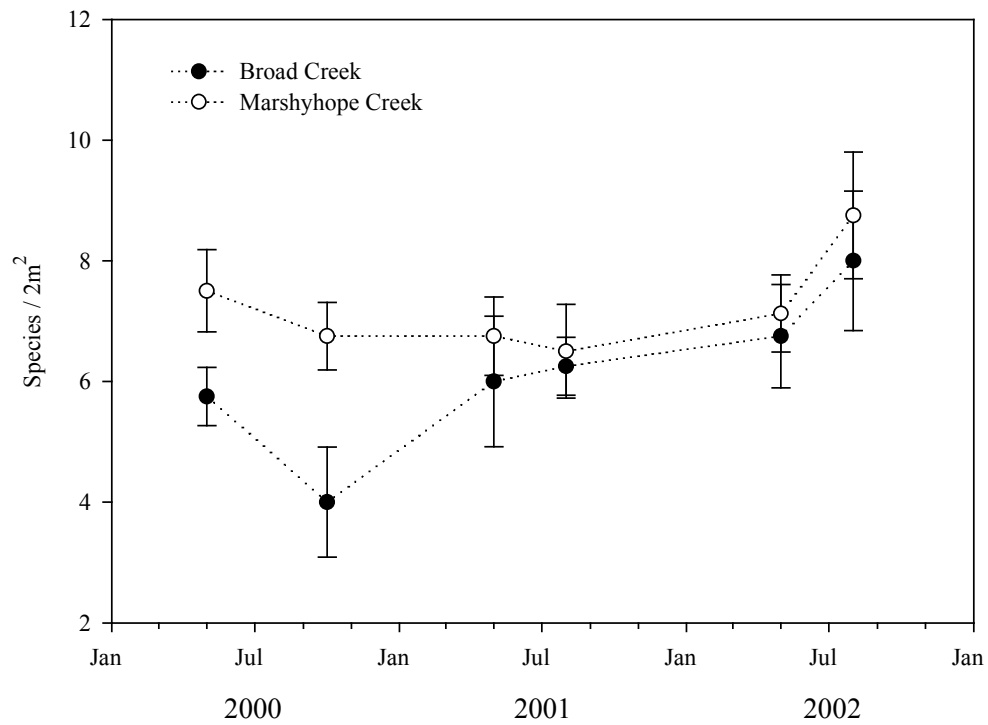
the dominant plant species, *Nuphar lutea*, had typically greater biomass density in Broad

Creek than in Marshyhope Creek. Nutrient enrichment can result in loss of species

diversity and increases in biomass production (Bedford et al. 1999; Grace 2001).

Dominant plant species may increase their biomass production in response to the

increased nutrients (Verhoeven et al. 1996), which may result in species loss as less

dominant plant species decline as other resources (e.g., sunlight) become less available

with the increased productivity (Tilman 1986). With over 300 animal production facilities

located within the two watersheds, and the high proportion of land surface dedicated to

agricultural activity, nutrient enrichment is a real source of concern in these habitats

(Chesapeake Bay Program 2004c).

Aquatic Macrofauna

In both collection methods I found more total fish and invertebrates in

Marshyhope Creek. In the throw traps, Marshyhope had about 20 percent more fish than

Broad Creek (Tables 2.2 and 2.3). The same trend appeared in the flume trap data, where

there were more than twice as many fish captured in Marshyhope Creek (Tables 2.4 and

2.5). The invertebrates also followed this pattern, yet the statistical comparisons

suggested the differences were not significant on almost every level. The obvious culprit

for this was the increase in salinity, as aquatic macrofauna will rapidly respond to any

sort of osmotic stress imposed by changing ionic concentrations in the water. Salinity

increases led to the introduction of species typically associated with oligohaline

environments from October 2001 through August 2002, which affected the comparisons

of the two creeks. Before the salinity change, for example, the largest invertebrates

collected were *Palaemonetes pugio*, whose mean body mass was approximately 0.13 g. By the end of the study, total invertebrate biomass rose dramatically as male blue crabs began to be captured with an average body mass of 19.1 g.

The throw trap biomass significantly differed between the creeks, and this was a trend that continued over the entire study aside from May 2002 (Figure 2.10a). The same pattern holds in the flume data, except for October 2001 (Figure 2.14a). I will refer to these instances where Broad Creek values exceed Marshyhope Creek as inversions, suggesting that something happened that depressed measures of animal abundance in Marshyhope Creek. Both of these inversions in each trapping method took place after the drought began. The throw traps showed pronounced declines in Marshyhope Creek fish biomass and a large increase in the variability of invertebrate abundance in October 2001 (Figure 2.10 b and c). After the inversions, however, Marshyhope Creek biomass returned to levels seen before the drought began. It appears as if the animal community, initially responding to an environmental stress with a decline in total biomass decline, rebounds to pre-stress biomass levels. In this case, however, the stress was not a pulse event, as salinity and conductivity continued to rise over the latter half of the study. The rebound in biomass numbers reflects species replacements, where *Gobiosoma bosc*, *Menidia beryllina*, large numbers of *Palaemonetes pugio* and *Calinectes sapidus* replaced the decline in *Fundulus diaphanus*, *Gambusia holbrooki*, *Notropis hudsonius*, *Gammarus* spp., and Corixidae biomass. This shift is reflected in the similarity index, where by August 2002 the similarity between the two creeks fell to its lowest measured level in the study as the changes in species composition of the aquatic macrofauna were most

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pronounced (Figure 2.17). This decline in similarity was probably magnified by the changes in the plant community as the prolonged effects of the drought seem to result in declines in species density and biomass in Marshyhope Creek by August 2002 (Figure 2.8 a and b).

Plant and Animal Relationships

Despite these differences that appear related to the change in salinity, the question still remains, are any characteristics of aquatic macrofauna related to characteristics of the plant community? In the salt marsh studies comparing *Phragmites* and *Spartina*, the marshes overrun by the invasive species generally had greater plant stem densities that ultimately may lead to altered hydrology and hydroperiod, degrading the habitat quality from a small aquatic macrofaunal perspective (Able et al. 2003). These changes in the plant community could impede access to the relative safety of the marsh surface and increase predatory pressures on the animals that rely on the high tide refuge (Weinstein and Balletto 1999). The correlation analysis suggested that there was no relationship between plant biomass and animal abundance. Given the impact salinity changes appeared to have on most comparisons, however, it is worthwhile to look for any potential trends linking plant community structure to faunal abundance that were not strong enough for the statistical analysis to detect.

Since animal biomass seems to be the only community nekton-related variable that differed between these two creek systems, I simultaneously plotted mean low marsh plant biomass and mean animal biomass to see if there was any sort of visible pattern to

their respective biomass abundance. In Marshyhope Creek, there seems to be an increase in animal biomass when plant biomass rises, the trend most evident in 2001 (Figure 2.19). In May 2002, however, fish biomass remains low even though Marshyhope Creek had its greatest mean *Nuphar* biomass at this time. Broad Creek demonstrates a similar pattern in the relationship between animal and plant biomass. Early season fish biomass is generally lower than that found in high summer, although in October 2000 it increased slightly from August 2000 levels (Figure 2.20). Any relationship with plant biomass is even less apparent than was seen in Marshyhope Creek. In October 2000, August 2001 and August 2002, animal biomass increases as plant biomass declines from their previous measures. The measured correlation between total fish biomass and low marsh plant biomass was

-0.06 in Broad Creek and 0.001 in Marshyhope Creek, confirming the lack of a relationship between the variables over time (Tables 2.10 and 2.11). Complicating this comparison even further is the fact that this low early season animal biomass may reflect the life cycles of the various fish species. In some species collected, mean individual size was lowest in the early growing season and steadily rose throughout the summer and into fall, while in other species, the proportion of juveniles increased in August collections.

These results do not provide a clear answer to the question of whether or not aquatic macrofauna abundance varies with plant community composition and abundance. While ANOVA suggests that both measures of plant and animal biomass do significantly differ between the creeks, they do not appear well correlated over time, as the graph of

Figure 2.19. Mean total animal wet biomass and mean low marsh plant dry biomass (*Nuphar lutea*) in **Marshyhope Creek**. Gray bars present mean biomass for *Nuphar lutea* in low marsh while black circles depict mean total animal biomass in throw trap samples. In both cases, the error bars are ± one standard error of the mean.
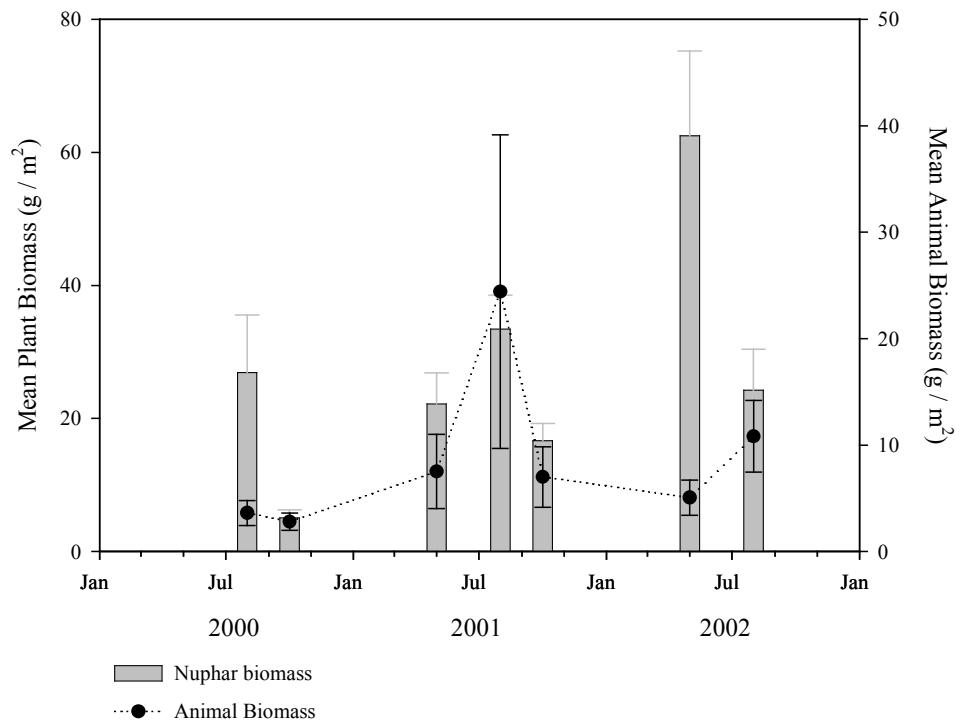
Figure 2.20. Mean total animal wet biomass and mean low marsh plant dry biomass (*Nuphar lutea*) in **Broad Creek**. Gray bars present mean biomass for *Nuphar lutea* in low marsh while black circles depict mean total animal biomass in throw trap samples. In both cases, the error bars are ± one standard error of the mean.
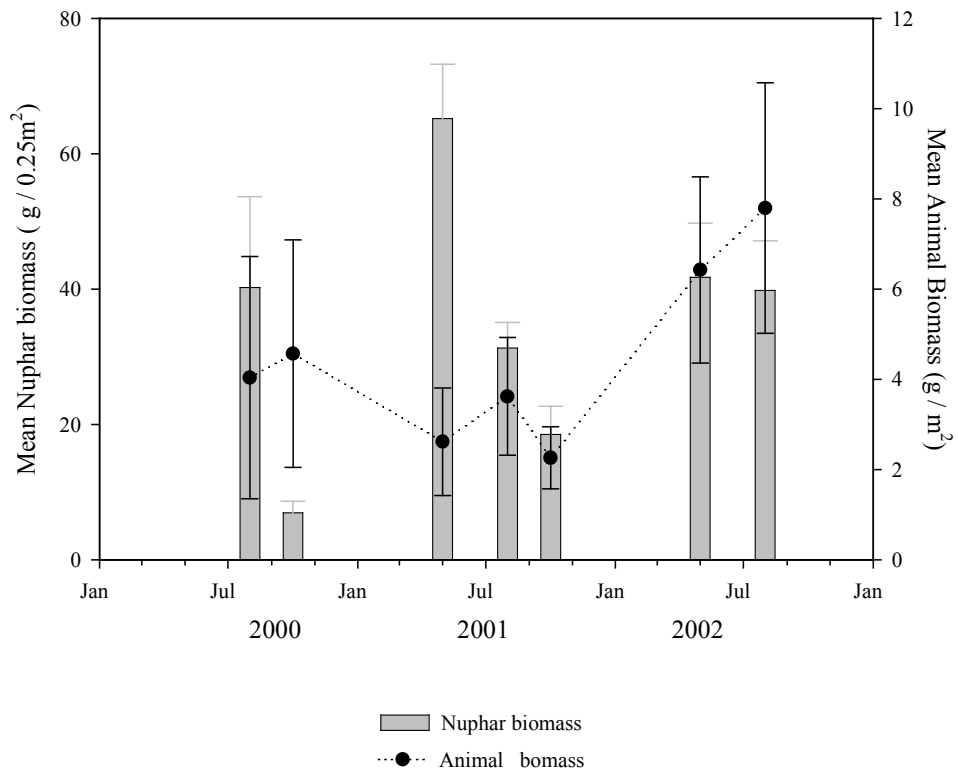
simultaneous abundance suggested (Figure 2.19 and 2.20). The emerging pattern suggests

that the creeks possess differences in the abundance of animals, but whether this is

directly related to plant community structure is unclear. The effects of the changes in

plant community structure may affect the various species of the aquatic macrofauna

differently (Chick and McIvor 1994). Depending on the size, trophic position and habits

of the organism, the animals will likely respond differently to structural changes in the

habitat (Chick and McIvor 1997). The temporary nature of the marsh habitat also

complicates the response – the marsh surface is intermittently available to the aquatic

macrofauna and other near shore habitat changes may be occurring simultaneously with

those occurring in the emergent marsh vegetation. Several studies identify that aquatic

vegetation offers improved habitat for small fish and invertebrates in tidal freshwater

systems (Serafy et al. 1994; Rozas and Odum 1987a). Others have observed the trend in

estuarine and marine systems (Thayer and Chester 1989; Sheridan 1997; Hughes et al.

2002). These studies suggest that the structure provided by the vegetation results in

increased abundance and species richness for small aquatic animals. Several studies

identified the relationship between increased plant stem density and increased survival

rates for small fish (Savino and Stein 1989; Gotceitas and Colgan 1989) and also for

invertebrates (Savino et al. 1992). Yet in my study, as structure increased (assuming

increased biomass is correlated with increased stem density), the biomass and numerical

density of small fish and invertebrates declined. It is possible that other factors are more

important than stem density that result in higher aquatic macrofauna abundance. Changes

in the relative abundance of plant species in the marsh may be more beneficial than

merely increasing structural complexity (Chick and McIvor 1997).

The response of the faunal community to changes in vegetative cover may be more nuanced, and both the community variables of community level properties and the characteristics of individual species were ill-suited to handle the complexity inherent in the nekton community dynamics. The next chapter addresses whether there are unique multi-species faunal responses resulting from landscape level environmental factors across the marshes in a multivariate context. Furthermore, the consequences of shifting plant community composition and the changes in faunal abundance also impact the function of the entire ecosystem. Chapter Four will examine how these differences may be affecting system trophic dynamics, and how the direct and indirect relationships among the flora and fauna contribute to overall ecosystem development.

CHAPTER 3

SPECIES ASSEMBLAGES OF TIDAL FRESHWATER MARSH ECOSYSTEMS: COMMUNITY PATTERNS ALONG A RIVER TRANSECT

INTRODUCTION

The previous chapter suggested that some interesting differences existed between the two creek systems of the Nanticoke River. These contrasts were, however, neither entirely clear nor expansive enough to support strongly the hypothesis that the differences in animal community composition and structure of the two creeks were related to differences in the marsh vegetation. Landscape-level patterns could also be confusing the interpretation of creek comparison. Two factors, seasonal patterns and the salinity rise, likely influenced both the plant and animal communities in a manner that was not dependent upon creek identity. The comparisons in Chapter 2 likely would not be able to capture these larger-scale trends in both plant and animal community assemblages. Furthermore, the earlier chapter's focus on either community level properties or individual species could be missing relationships that actually exist among the aquatic macrofauna. It is also possible that, given the similarity of the respective species pools of the two creeks, there are significant overlaps between them along measured environmental gradients that better explain how the plants and nekton are distributed. Animal abundance also tends to be very patchy, resulting in difficult and unwieldy data sets (McCune and Grace 2002). Infrequently collected species make it difficult to perform parametric analyses, yet these species could still be important components of the

system and should not be discarded because they create problem-laden data sets. Multivariate analyses can provide a means to take large and uncooperative data and find patterns that more traditional techniques may be unable to detect, and are able to retain the information that is otherwise lost via coarser-scale analyses or deletion of rarer species (McCune and Grace 2002; McGarigal et al. 2000; Hair et al. 1992).

In Chapter 2, I explained that the marsh sites were selected to contrast the two creeks. But they also represent a longitudinal transect along the tidal freshwater zone of the Nanticoke River. Using the channel marker in the Marshyhope Creek Nanticoke River confluence as an arbitrary starting point, the sites span a river distance gradient of 15 kilometers from the downstream-most to the upstream-most marsh sites (Table 3.1). Thus, the linear sequence of sites increases in distance from the mouth of the river in the following order: Marshyhope Site 1 (M1), M3, Broad Creek Site 1 (B1), M2, B2 and B3.

Table 3.1. River distance gradient for marsh sites. These measures represent the distance upstream each marsh site is from an arbitrary point in the main branch of the Nanticoke River (Latitude 38.52631N Longitude 75.75439W). Distances are in kilometers.

Site	M1	M3	B1	M2	B2	B3
Distance	1.22	4.85	10.92	13.11	13.64	14.09

The linear upstream difference across these sites averages about 2.5 km between sites, and likely will present a better picture of the marsh ecosystem responses to external forces, particularly salinity.

Marsh plant community composition could also exhibit different characteristics along this gradient. The plant communities of both the Nanticoke and Patuxent Rivers demonstrate significant, albeit small, changes in plant species richness across a low salinity gradient (Peter Sharpe, University of Maryland, personal communication). Analyses of faunal distributions with respect to marsh plant communities typically span a a well-defined salinity gradient. In upper and lower Delaware Bay, for example, plant community composition of marshes differs, where upper bay low salinity sites contain *Phragmites australis* while plant communities in regions in the lower bay with higher salinity have high abundance of *Spartina alterniflora* and *S. patens.* Fish community composition differed between these two bay regions, but the trend was largely due to salinity regime rather than vegetative characteristics of the marsh plant communities (Able et al. 2001). In a study examining the patterns of fish community composition and structure along a polyhaline to tidal freshwater gradient in Virginia's tidal tributaries, researchers observed four overlapping assemblages of littoral fishes. In particular, they identified two groups associated with tidal freshwater. The first group, those fish found near the tidal freshwater interface, were dominated by animals that use tidal fresh habitats in early life stages, particularly *Morone saxitalis, M. americana*, and *Trinectes maculatus*. The fish associated with permanent tidal freshwater were dominated by adult cyprinnid fishes. Salinity accounted for much of the differences in the assemblages, but structural attributes of the various sites also helped distinguish species associations (Wagner and Austin 1999). These species assemblages, however, were collected using beach seines, and likely under-represent the fundulid species that tend to dominate the

fish communities associated with vegetated habitats (Rozas and Odum 1987; Odum et al.

1984). Analysis of over 300 species and life stages of fishes occurring in both the

Chesapeake and Delaware Bays suggested that there were four overlapping species

assemblages based on salinity, with the freshwater species found in salinities ranging

from 0 to 4 ppt, while the adjacent assemblage spanned waters of 2 to 14 ppt (Bulger et

al. 1993). The salinity barrier between freshwater and estuarine animal communities

likely resides somewhere between 0 and 2 ppt (Deaton and Greenberg 1986), so what

may appear as a rather innocuous change in the ionic concentration of the river water

may actually denote a boundary for freshwater and estuarine community types. Given

that the fish assemblage shifts typically occur at these low salinity levels, the marsh sites,

over time, ought to reflect significant differences between the downstream and upstream

sites. It is also possible that if the drought persisted long enough that the plant community

would also show signs of species replacements, as plants more attuned to handling

salinity stress would receive a competitive advantage (Howard and Mendelssohn 1999;

Flynn et al. 1995).

Accordingly, the focus of this chapter shifts from the explicit comparison of the

two creeks presented in the previous chapter to a broader examination of how the

individual marshes are related to each other across both creeks. This chapter hypothesizes

that environmental variables along the longitudinal gradient will affect how both the plant

and animal communities will be assembled at each site, the effect of which may

transcend any trends that distinguish the two creeks. Also carrying over from the previous

chapter, I can also re-examine the hypothesis that animal abundance in the marshes

across the watershed will be related to differences in plant community composition and structure. This chapter addresses the following specific objectives:

1. Identify differences in the composition and species assemblages of the plant community across the marshes, and determine if there is a trend related to plant species richness and community biomass across the longitudinal gradient.

2. Identify differences in the composition and species assemblages of two separate measures of animal abundance across the marshes, and identify what measured environmental factors are related to the species assemblages.

3. Assess the relationship between plants and animals in the marshes and how composition and structure of the plant and animal communities are related to environmental factors.

RESEARCH METHODS

I collected plant, macroinvertebrate and small fish samples from the six study sites from May 2000 through August 2002 (briefly described in Chapter Two). However, only data acquired during the surveys from May 2001 through August 2002 were considered. This time period was when all sampling methods overlapped and provided the most complete data set describing the conditions surrounding the co-occurrence of the

various plant and animal species. The remainder of this section presents details about the data analysis procedures and rationales. Extensive details for all the sampling protocols appear in Appendix I.

Multivariate Analysis

This chapter focuses on the differences in the distribution and abundance of species at a landscape level spanning the tidal freshwater region of the Nanticoke River using ordination techniques to identify the patterns. Therefore, I used the marsh sites on each date as the focal level for this evaluation. I constructed matrices of mean abundance for the dominant aquatic macrofauna and macrophytes species on every date, discounting any species that appeared in less than five percent of the total number of samples in the individual collection methods (McGarigal et al. 2000). I constructed three matrices, two for the aquatic macrofauna based on different measures of mean animal abundance, and one for the macrophytes based on mean plant biomass. For both of the data sets based on animal abundance, each sample unit was a row vector of individual species abundances incorporating as distinct variables both the throw trap and flume trap estimates. Each of these values was transformed ($\ln (x+1)$) to minimize the differences in the magnitudes of the catches between the trapping methods as the dissimilarity matrix for the ordination was calculated (McCune and Grace 2002). Since the plants were collected in a uniform manner, the data within the vegetation matrix was left untransformed.

Both aquatic macrofauna and macrophyte abundance in the marshes was affected by various environmental factors. For the animals, this also includes the patterns of

emergent macrophyte distribution and abundance. Therefore, a second matrix was constructed that identified the respective relevant environmental parameters associated with each marsh. For the aquatic macrofauna, this included salinity, dissolved oxygen, conductivity, water temperature and mean water depth and also characteristics of the marsh plant communities (species richness, community biomass and abundant individual species in both the low and high marsh). For the plants, measures of community biomass, species richness and salinity were considered as variables of interest. These matrices were used to explain how the ordination axes, sites and species distributions were related to environmental parameters.

The three primary matrices were evaluated using Non-metric Multi-dimensional Scaling (NMS), an ordination method that is well suited for the evaluation of either non-normal or arbitrarily scaled data, a common condition for ecological data. NMS iteratively positions sample units across k-dimensions attempting to minimize the stress of the k-dimensional configuration (McCune and Grace 2002). Since the properties of each axis are dependent upon the total number of meaningful axes identified, it is of critical importance to identify a proper level of dimensionality for the final solution. The software PC-ORD allows the user to perform multiple runs based on real data in order to find potential global minima at each level of dimensionality, and then it uses a Monte Carlo test to identify the optimal number of dimensions by comparing the stress of the real data at each dimensional configuration with that of the random data. The dimensionality least likely to be reproduced randomly is the best solution (McCune and Grace 2002).

The distances between sample units in the dissimilarity matrices were calculated using Sørensen's Similarity (Bray-Curtis). Each real data set was run 40 times to identify optimum configurations across six dimensions, and then the data sets were randomly shuffled 50 times in order to determine which level of dimension represented the best configuration. This was accomplished by comparing the real stress levels with the random stress levels. Dimensions were included if they reduced the stress value by five or more from the previous configuration. The final stress of this k-dimensional ordination also had to be lower than that calculated for 95 percent of the randomized runs, otherwise the k-1 configuration was selected (McCune and Grace 2002). This best configuration was then used as the starting point for the final run of the real data for all three data sets, limiting the number of iterations to 100 and identifying an instability criterion of 0.00001. Each ordination is presented in two ways, depicting both the site-date sample units and each species in the k-dimensional space. Joint plots of significant environmental variables are also included on each ordination. Only those environmental variables with r^2 values greater than 0.15 accompany the ordinations as joint plots. I used PC-ORD software for the NMS analysis (McCune and Medford 1999).

RESULTS

Plant Community

The NMS plots of aboveground vegetation resulted in well-defined groups of sites largely based on the time the samples were collected over two dimensions. Final stress for this ordination was 13.182, which is well within the generally accepted range of

acceptable stress (Clarke 1993). Three principal groups emerged in the analysis that demonstrated high fidelity to seasonal patterns in the plant community (Figure 3.1). The site-date sample units from late-spring all appeared in the upper-right quadrant (group 1), while the late summer and early fall sites tended to fall in the lower left quadrant (groups 2 and 3). Of the six variables considered in the secondary matrix, only three possessed r^2 values sufficiently high enough to be included in the graphical display of the ordination (Table 3.2). The three variables associated with the axes were plant biomass in both the low and high marsh and plant species richness in the high marsh. Low marsh plant biomass and high marsh plant species richness were most closely associated with axis 1 (r^2 were 0.251 and 0.228, respectively), while high marsh plant biomass had relatively equivalent positive relationships with both axes (0.198 and 0.231, for axes 1 and 2, respectively). The spring samples tended to have the highest mean plant biomass as this was when *Acorus calamus*, or sweetflag, is at its highest, as was the biomass of the low marsh dominant plant species *Nuphar lutea*, or spatterdock. High marsh species richness tended to be fairly similar between the summer and spring collection dates, but fall samples had appreciably lower plant species richness than the other two dates.

Plant species sort out in the ordination space largely along axis 1 and do associate with their respective seasonal abundance (Figure 3.2). For example, *Acorus calamus*, the dominant spring plant, appears in the upper left quadrant where the spring sample units all reside. Dead plant material became more abundant as the growing season advanced, and it appropriately appears on the left side of axis 1, amidst the fall and summer groups. The summer sample units reside closest to the center of the ordination where summer

Figure 3.1. NMS ordination of macrophytes identifying site-date sample units for the creeks. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r^2 values greater than 0.15. HVBIO = high marsh plant biomass, LVBIO = low marsh plant biomass, HVRICH = high marsh plant species richness. Ovals identify groups of site-date sample units associated with season. Oval 1 = late spring, Oval 2 = mid-summer, oval 3 = early fall.
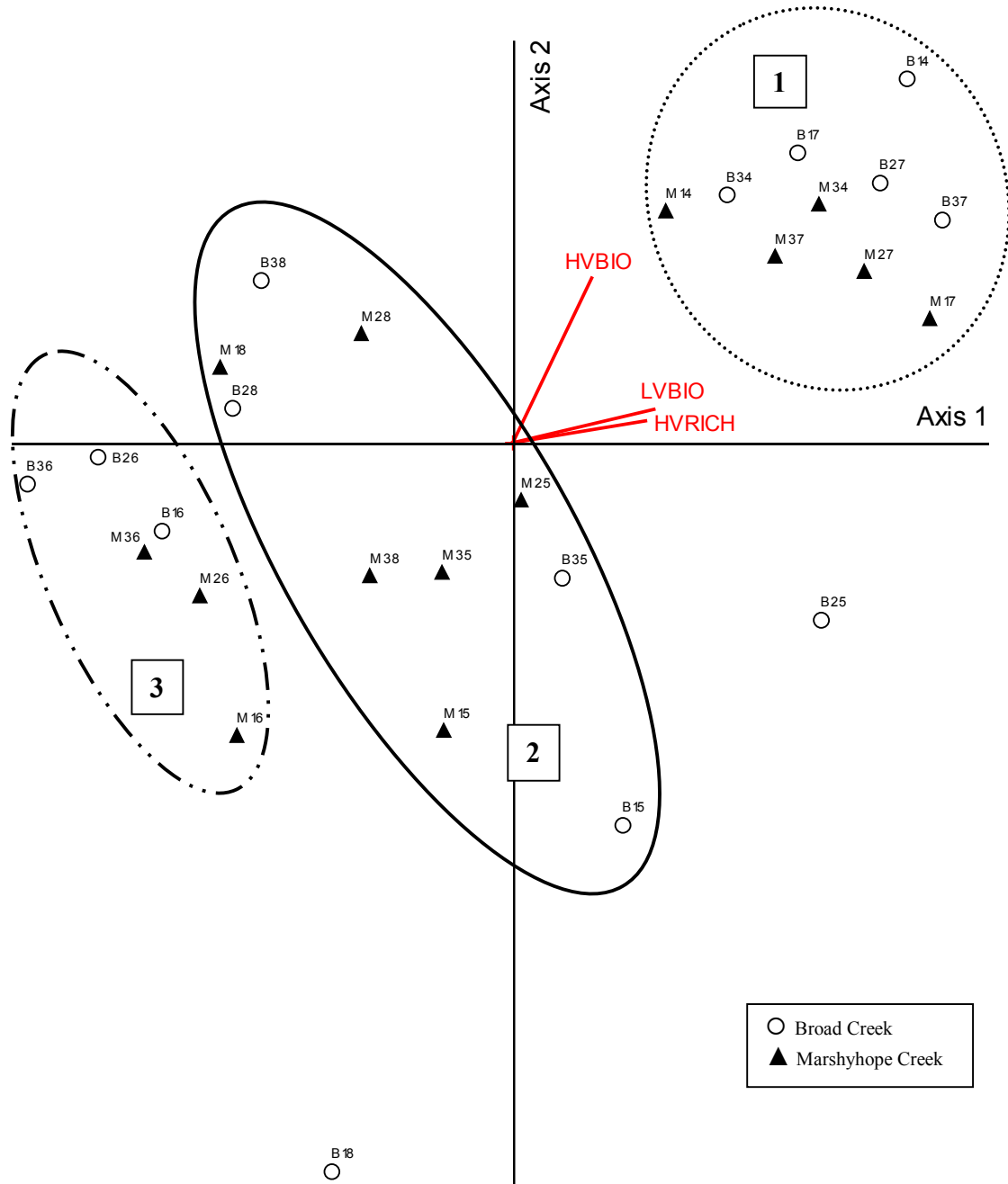
Table 3.2. Pearson correlation coefficients for ordination joint-plots of environmental variables related to <u>marsh vegetation</u>. Both r and r^2 values are presented for variables that are possible covariates with the ordination sample units. Only the variables with r^2 values on either axis over 0.15 are included in the ordination figures. These variables are identified in bold type.

	Axis 1		Axis 2	
	r	r^2	r	r^2
Water Conductivity	-0.087	0.008	0.065	0.004
Salinity	-0.056	0.003	0.097	0.009
Low Marsh Plant Species Richness	0.214	0.046	0.002	<0.001
Low Marsh Plant Biomass	**0.501**	**0.251**	**0.090**	**0.008**
High Marsh Plant Species Richness	**0.477**	**0.228**	**0.046**	**0.002**
High Marsh Plant Biomass	**0.445**	**0.198**	**0.480**	**0.231**

Figure 3.2. NMS ordination of macrophytes identifying species variables. NMS indicated that two dimensions sufficiently depicted the relationships among the sample units. Final stress was 21.13 in two dimensions. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r^2 values greater than 0.15. HVBIO = high marsh plant biomass, LVBIO = low marsh plant biomass, HVRICH = high marsh plant species richness. Species codes are listed in Table 4.1.
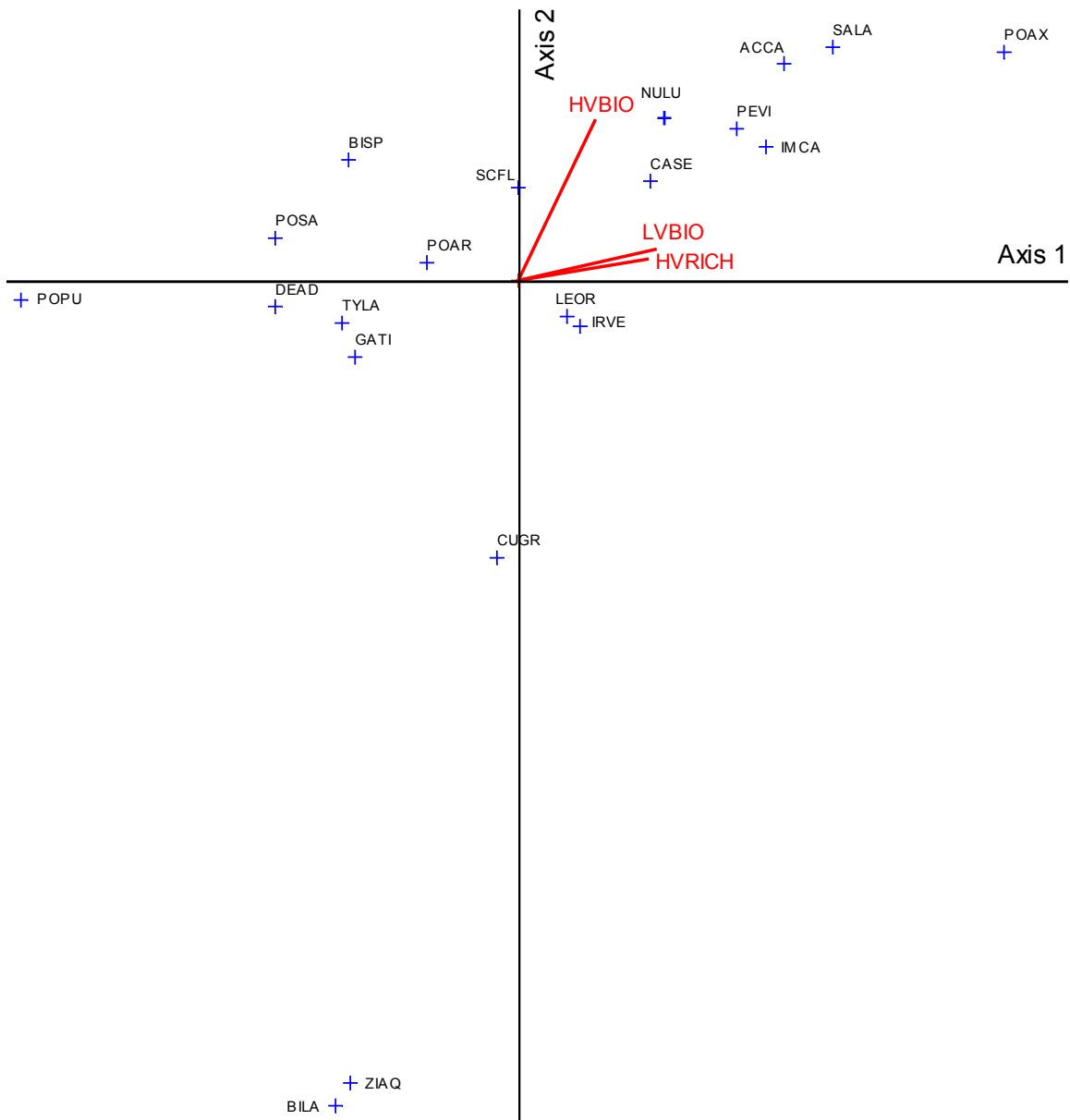
dominant annual species such as *Polygonum arifolium*, or halberd-leafed tearthumb (POAR), *Leersia oryzoides*, or rice cut-grass (LEOR) and *Bidens* sp. (BISP) appear.

There were two outlier sample units that did not fall into positions close to any of the three groups: Broad Creek Site 1 August 2002 (B18) and Broad Creek Site 2 August 2001 (B25). B18 deviates from the other summer groups along axis 2. The likely reason for the positioning of this sample unit is its extremely high abundance of *Zizania aquatica*, or wild rice, and *Bidens laevis*, or burr marigold. For example, only six other sample units had wild rice, where mean biomass ranged from 0.05 to 1.9 g dry mass 0.25 m^2. B18 averaged 45.4 g dry mass 0.25 m^2, a substantially higher amount of wild rice than any other site. Ordination of the species data highlights the relationship between this site and these two plant species (Figure 3.2). Both *Bidens* (BILA) and *Zizania* (ZIAQ) appear in the lower left quadrant and show the highest level of association with axis 2, very similar to the position seen with sample unit B18 (Figure 3.1). The other outlier, B25, deviates from summer sample units along axis 1. It had very high biomass of *Iris versicolor* (IRVE) and *Leersia oryzoides* (LEOR) but also relatively high biomass of *Acorus calamus* (ACCA), unlike the other sample units collected in the late-summer.

Some segregation based on creek appeared within these seasonal groups seemed to occur, especially in spring and fall groupings. In both cases, Broad Creek sites tended to ordinate at a higher position along axis 2 than those from Marshyhope Creek (Figure 3.1). There is no pattern related to creek identity among the summer sample groups,

although it appears that the Marshyhope Creek sample units tended to reside closer to the center of the ordination.

Animal Biomass

The NMS of the sample units based on animal biomass produced both the highest stress and the fewest well-defined groups. PC-ORD determined that two dimensions best represented the sample units, but stress was high at 21.104. This is a relatively high level of stress, which can complicate interpretation of the ordination (Clarke 1993), but given the low number of dimensions relative to the total number of sample units, it is possible that the high stress is an artifact of a high sample unit to dimensionality ratio (McCune and Grace 2002). Unlike the previous ordination, there are no distinct groups of sample units emerging (Figure 3.3). The spread of sample units appears fairly uniform across both dimensions, although most Broad Creek sample units are on the left side of axis 1 while Marshyhope Creek sample units tend to appear on the right side. Five environmental variables met the cut-off criteria and are included as joint-plots in the diagram. Three of these variables, salinity (SAL), conductivity (COND) and *Peltandra virginica* (PEVI) are associated with the lower right quadrant, while *Galium tinctorium* (GATI) and dissolved oxygen (DO2) are related to the upper left quadrant (Figure 3.3). Salinity and conductivity are largely associated with axis 1 (r^2 values are 0.226 and 0.228, respectively), as is the plant species, *Galium* (r^2 of 0.228). *Peltandra virginica* and dissolved oxygen are most closely associated axis 2 (r^2 values of 0.150 and 0.182, respectively) (Table 3.3).

Figure 3.3. NMS ordination of animal biomass identifying site-date sample units for the creeks. NMS indicated that two dimensions sufficiently depicted the relationships among the sample units. Final stress was 21.13 in two dimensions. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r^2 values greater than 0.15 and are exaggerated by 200 percent. GATI = *Gallium tinctorium*, PEVI = *Peltandra virginica*, DO2 = dissolved oxygen, SAL = salinity, COND = conductivity.

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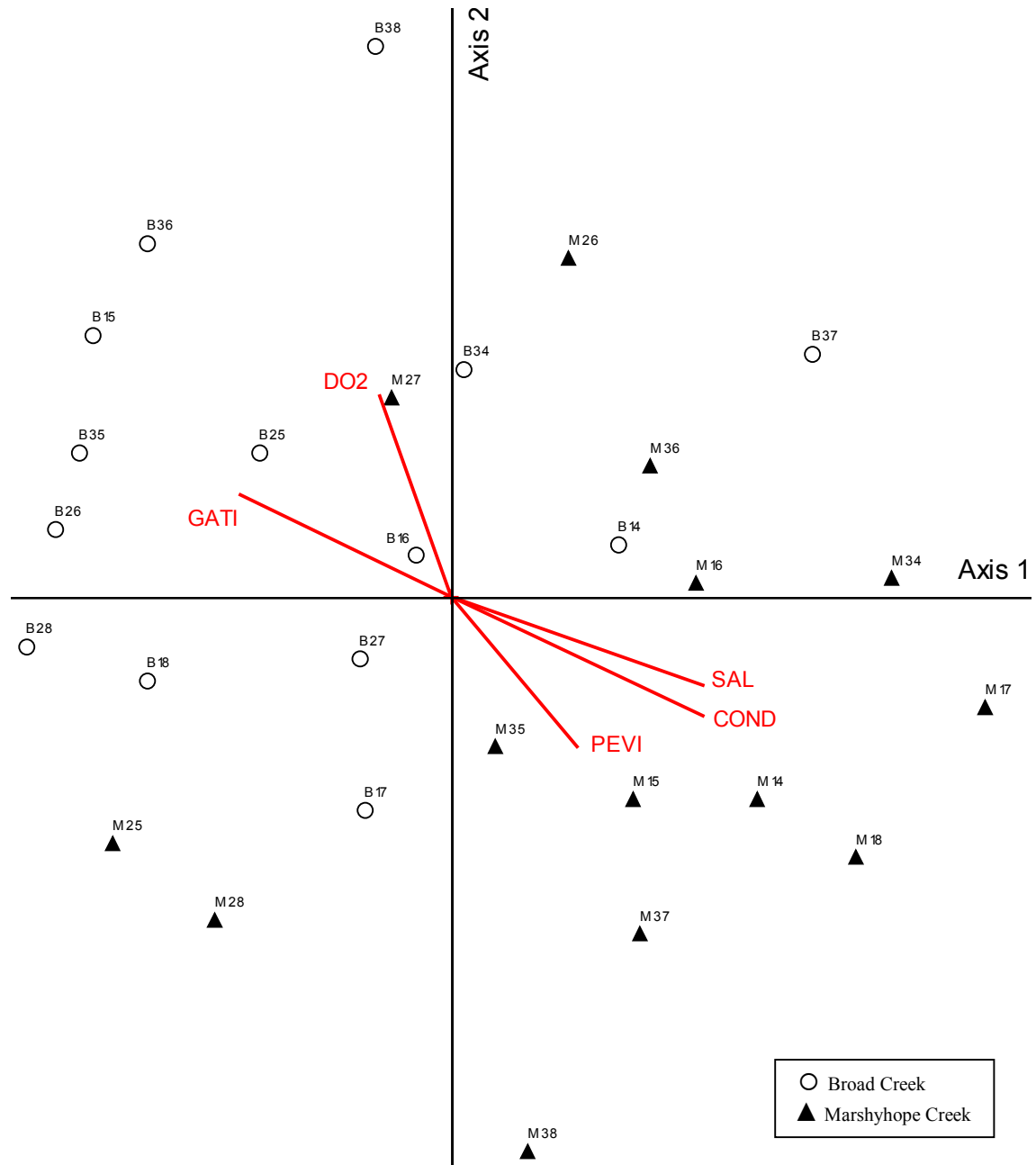
Table 3.3. Pearson correlation coefficients for ordination joint-plots of environmental variables related to <u>animal biomass</u>. Both r and r^2 values are presented for variables that are possible covariates with the ordination sample units. Only the variables with r^2 values on either axis over 0.15 are included in the ordination figures. These variables are identified in bold type.

	Axis 1		Axis 2	
	r	r^2	r	r^2
Animal Species Richness	-0.169	0.028	-0.199	0.040
Water Depth	0.058	0.003	0.135	0.018
Dissolved Oxygen	**-0.255**	**0.065**	**0.426**	**0.182**
Water Conductivity	**0.477**	**0.228**	**-0.328**	**0.107**
Salinity	**0.476**	**0.226**	**-0.281**	**0.079**
Water Temperature	-0.125	0.016	-0.264	0.070
Stem Density	0.172	0.03	0.211	0.044
Low Marsh Plant Species Richness	0.313	0.098	-0.171	0.029
Low Marsh Plant Biomass	0.252	0.064	-0.001	<0.001
High Marsh Plant Species Richness	0.119	0.014	-0.13	0.017
High Marsh Plant Biomass	0.135	0.018	-0.036	0.001
Acorus calamus	0.368	0.135	-0.055	0.003
Bidens laevis	-0.361	0.130	0.050	0.002
Calystegia sepium	-0.186	0.034	0.013	<0.001
Cuscuta gronovii	-0.232	0.054	-0.064	0.004
Galium tinctorium	**-0.438**	**0.192**	**0.303**	**0.092**
Impatiens capensis	0.206	0.042	0.153	0.024
Leersia oryzoides	-0.345	0.119	-0.100	0.01
Peltandra virginica	**0.315**	**0.099**	**-0.388**	**0.150**
Polygonum arifolium	-0.003	<0.001	0.012	<0.001
Polygonum sagittatum	-0.374	0.140	-0.012	<0.001
Schoenoplectus fluviatilis	0.263	0.069	0.015	<0.001
Typha latifolia	0.049	0.002	-0.219	0.048
Zizania aquatica	-0.152	0.023	-0.042	0.002
Sagittaria latifolia	0.148	0.022	0.275	0.076

The main pattern emerging in this ordination is largely based on creek identity. Only three Marshyhope sample units are on the left side of Axis 1, all from Marshyhope Site 2 in August 2001, May 2002 and August 2002 (M25, M27 and M28, respectively). Only three sample units from Broad Creek appear on the right side of axis 1 (Broad Creek Site 3, May 2001 and May 2002 (B34 and B37) and Broad Creek Site 1, May 2001 (B14)). These sites appear largely distributed relative to salinity in the two creeks, as the SAL and COND joint-plots suggest. Animal species typically found in oligohaline habitats all appear in the quadrant most closely associated with increasing salinity (Figure 3.4). The species within the oval, the grass shrimp *Palaemonetes pugio* (PAPU), the blue crab *Calinectes sapidus* (CASA) and the naked goby *Gobiosoma bosc* (GOBO) either appeared in very low abundance or were never captured before October 2001, the onset of the regional drought and rising salinity in the Nanticoke River.

Animal Density

The NMS of the animal numerical density resulted in a mixed pattern of some groupings largely based on marsh site, but also retaining the pattern seen in the animal biomass where there is some segregation based on creek identity. Final stress levels were acceptably low for a two dimensional solution at 16.372. This ordination had the most environmental variables included as joint-plots in the graphical depiction of the ordination (Figure 3.5). *Impatiens capensis* (IMCA), High marsh plant species richness (HVRICH), salinity (SAL) and conductivity (COND) were most highly associated with axis 2 (r^2 values of 0.392, 0.184, 0.155 and 0.203, respectively) (Table 3.4). The other three environmental variables, *Acorus calamus* (ACCA), *Peltandra virginica* (PEVI) and

Figure 3.4. NMS ordination of animal biomass species variables.. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r² values greater than 0.15 and are exaggerated by 200 percent. GATI = *Gallium tinctorium*, PEVI = *Peltandra virginica,* DO2 = dissolved oxygen, SAL = salinity, COND = conductivity. Species codes are listed in Table 4.1. A "T" after the code indicates species information comes from throw trap data, while those with only the four letter code are based on flume trap data. The species in the dotted oval are those that accompanied the salinity increase.
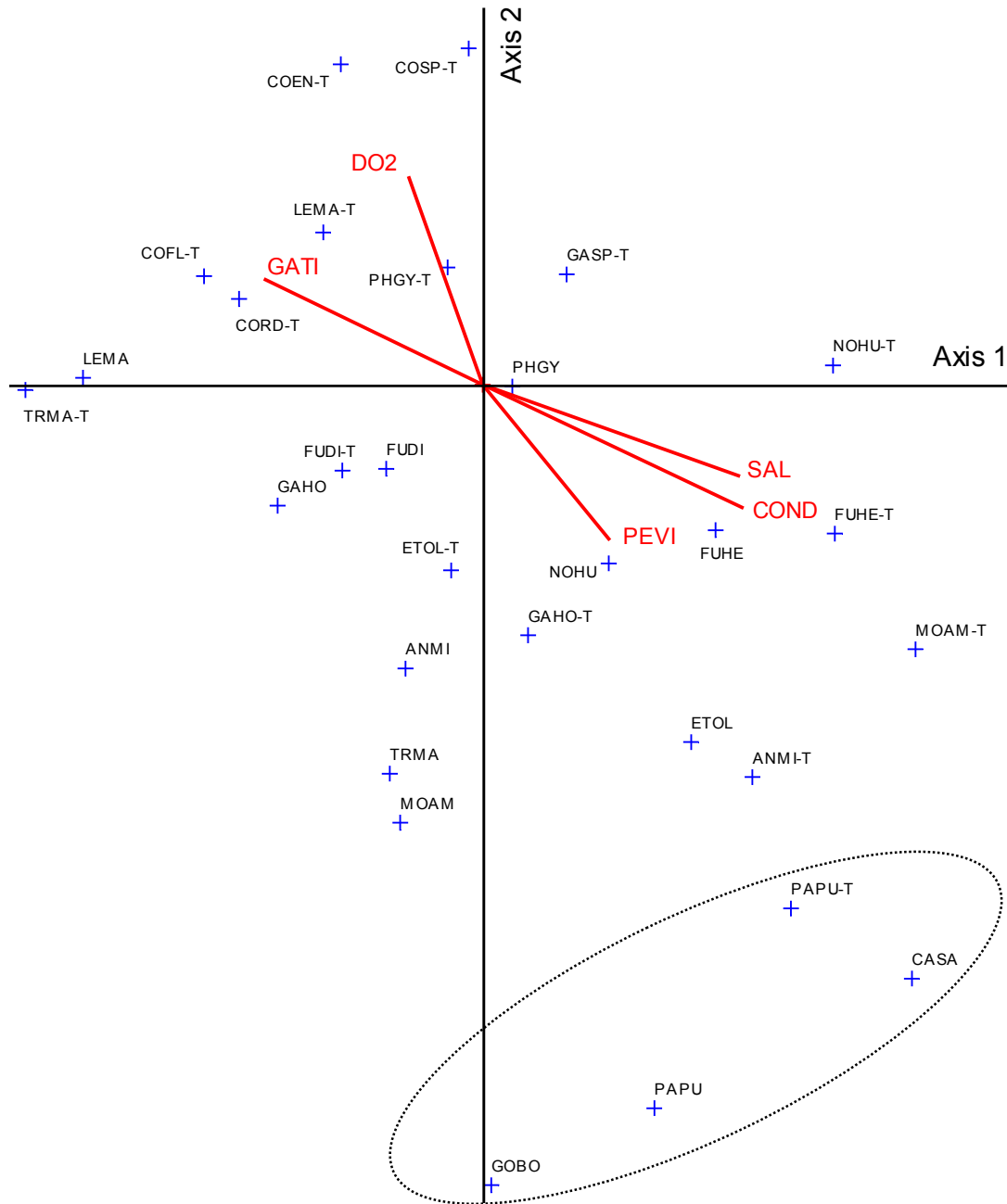
Figure 3.5. NMS ordination of animal density identifying site-date sample units for the creeks. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r^2 values greater than 0.15 and are exaggerated by 175 percent. ACCA= *Acorus calamus*, PEVI = *Peltandra virginica*, HVRICH = plant species richness in high marsh, LVRICH = low marsh plant species richness, SAL = salinity, COND = conductivity. The solid ovals identify sample units from Marshyhope Creek site 1, while the dotted oval highlights several spring units.
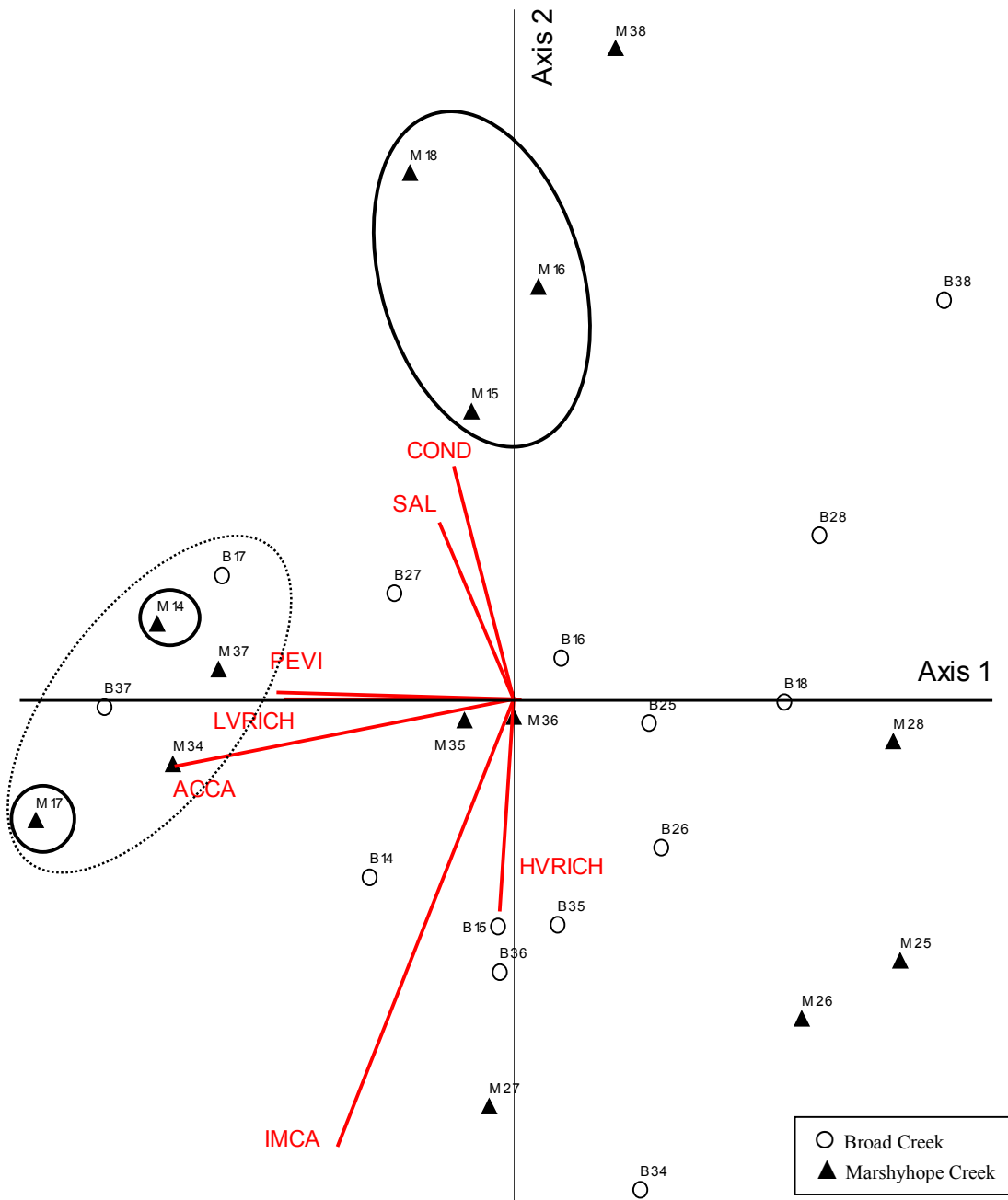
Table 3.4. Pearson correlation coefficients for ordination joint-plots of environmental variables related to <u>animal density</u>. Both r and r^2 values are presented for variables that are possible covariates with the ordination sample units. Only the variables with r^2 values on either axis over 0.15 are included in the ordination figures. These variables are identified in bold type.

	Axis 1		Axis 2	
	r	r^2	r	r^2
Animal Species Richness	-0.058	0.003	-0.230	0.053
Water Depth	-0.269	0.073	-0.032	0.001
Dissolved Oxygen	0.065	0.004	-0.351	0.123
Water Conductivity	**-0.231**	**0.054**	**0.45**	**0.203**
Salinity	**-0.256**	**0.065**	**0.394**	**0.155**
Water Temperature	-0.111	0.012	0.132	0.018
Stem Density	-0.248	0.062	-0.339	0.115
Low Marsh Plant Species Richness	**-0.447**	**0.199**	**-0.036**	**0.001**
Low Marsh Plant Biomass	-0.281	0.079	-0.247	0.061
High Marsh Plant Species Richness	**-0.110**	**0.012**	**-0.429**	**0.184**
High Marsh Plant Biomass	-0.221	0.049	-0.107	0.011
Acorus calamus	**-0.544**	**0.296**	**-0.244**	**0.06**
Bidens laevis	0.229	0.052	-0.135	0.018
Calystegia sepium	0.029	0.001	0.038	0.001
Cuscuta gronovii	0.153	0.023	-0.052	0.003
Galium tinctorium	0.299	0.089	-0.309	0.095
Impatiens capensis	**-0.391**	**0.153**	**-0.626**	**0.392**
Leersia oryzoides	0.311	0.097	-0.189	0.036
Peltandra virginica	**-0.453**	**0.205**	**0.086**	**0.007**
Polygonum arifolium	0.056	0.003	0.305	0.093
Polygonum sagittatum	0.363	0.132	-0.123	0.015
Schoenoplectus fluviatilis	-0.067	0.004	0.092	0.008
Typha latifolia	0.192	0.037	-0.006	<0.001
Zizania aquatica	0.076	0.006	-0.087	0.008
Sagittaria latifolia	-0.088	0.008	-0.370	0.137

low marsh plant species richness (LVRICH), are most closely correlated with axis 1 (r^2

values of 0.296, 0.205 and 0.199, respectively). Some groups appear to emerge, but there

is no uniform pattern to the distribution of the sample units. There is a tendency for

sample units from the same marsh sites to be located close to each other in the ordination

space, but it is not uniformly evident. For example, a majority of the units from

Marshyhope Creek Site 1 tend to reside on the upper portion of axis 2, but two sample

units, M14 and M17, are removed from the others, extended out along the left side of axis

1 (Figure 3.5, solid ovals). There is also a seasonal pattern emerging among some of the

sample units. Most sample units collected during spring are located on the left side of

axis 2, (Figure 3.5, dotted oval). The spring group is related to *Acorus calamus*, a

perennial plant species that is highly abundant early in the growing season.

Ordination of the animal species suggests a great deal of segregation based on

affinity to salinity. Species associated with the increase in salinity over the latter half of

the study appeared at the extreme upper end of axis 2, which is most closely associated

with the salinity and conductivity measures (Figure 3.6 ovals). Similar to the pattern seen

in the biomass-based sample units, this grouping contained the oligohaline species

Palaemonetes pugio (PAPU), *Calinectes sapidus* (CASA) and *Gobiosoma bosc* (GOBO).

It also contained *Anchoa mitchilli*, the bay anchovy (ANMI), which appeared before the

salinity increase, but its abundance increased substantially as salinity rose. Conversely,

freshwater invertebrate species ordinate on the opposite end of this axis (Figure 3.6 solid

oval). Species such as Corixid waterboatmen (COSP-T), Odonate larvae (CORD-T and

Figure 3.6. NMS ordination of animal density species variables. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r^2 values greater than 0.15 and are exaggerated by 175 percent. ACCA= *Acorus calamus*, PEVI = *Peltandra virginica*, HVRICH = plant species richness in high marsh, LVRICH = low marsh plant species richness, SAL = salinity, COND = conductivity. Species codes are listed in Table 2.x. A "T" after the code indicates species information comes from throw trap data, while those with only the four letter code are based on flume trap data. The dotted oval identifies species units associated with increasing salinity, while the solid oval identifies freshwater invertebrate species.
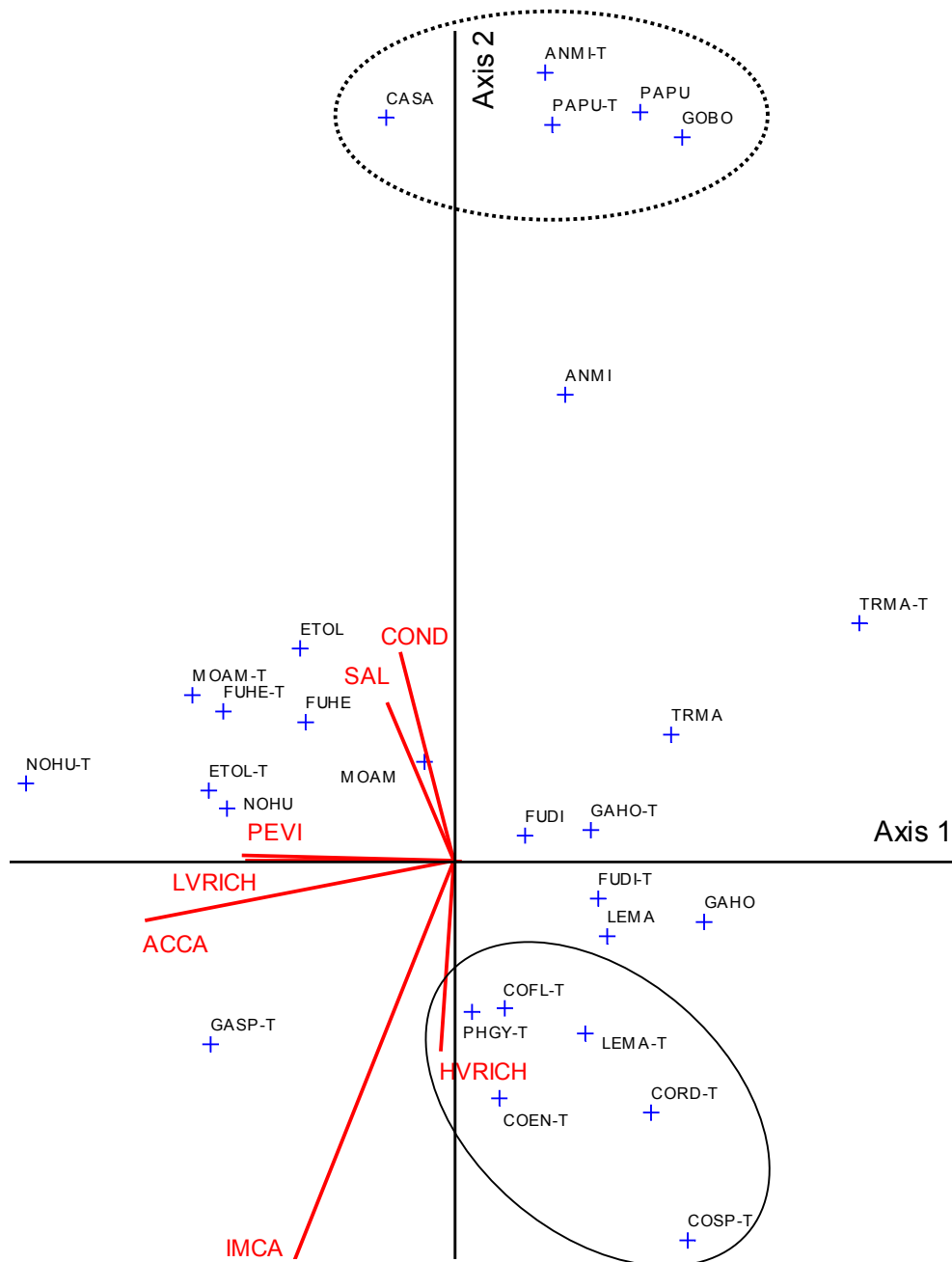
COEN-T) and the bluegill *Lepomis macrochirus* (LEMA-T) were only collected in low salinity conditions.

DISCUSSION

The ordination analysis of the plant and animal communities suggested that multiple environmental factors appeared to be related to the community structure and composition of both the plants and animals. Especially among the nekton, community composition seemed to vary across the longitudinal river distance gradient. But seasonal patterns in plant community composition and structure overwhelmingly determined how the sample units in the vegetation-based ordination were distributed. The ordination of animal biomass did not reveal any well-defined groups and did have relatively high stress, but it did suggest that there was a certain level of segregation of sample units based on creek identity of the sample units. Animal density indicated that both seasonal patterns and affinity to marsh site both influenced the ordination of sample units. The ordinations of animal community characteristics indicated that many species tended to ordinate along axes associated with salinity and conductivity, which are also a surrogate measure for distance upstream of each marsh. Among the animal community, however, there was not much evidence that patterns of plant species richness and community biomass (a measure of physical structure) were related to the distribution and abundance of the animals.

Seasonal patterns in the vegetation of tidal freshwater marshes has been well documented in tidal freshwater marshes (Odum et al. 1984; Doumlele 1981). Early season community composition is dominated by perennial plant species that have a high proportion of total biomass located below ground (Whigham and Simpson 1978). Later in the growing season, annual plants emerge in very high abundance as the perennials begin to senesce. And become the dominant plants on the marsh surface (Whigham and Simpson 1992). In the marsh sites on Broad and Marshyhope Creeks, aboveground biomass was at its highest levels in late spring, largely due to the widespread dominance of the perennial plant species, *Acorus calamus*. As the growing season progresses, this plant begins to decline in dominance, and by late summer the aboveground standing crop biomass tends to be less than half of what it was just two months before. The ordination suggests that axis 2 was more closely related to total aboveground biomass, and the sample units do decline in their magnitude along this axis based on the season they were collected.

Another interesting trend is the pattern seen in high marsh plant species richness. Richness tended to be at its highest in the spring season, and it declined across the remainder of the growing season. While the plant community is dominated by a few perennials at this time, seedling emergence of annuals is also at its highest levels at this time of year (Leck and Simpson 1995). As the season progresses, other factors, such as the extent and duration of flooding events, will help shape which annuals can persist until the perennials begin to senesce (Baldwin et al. 2001). The two outlier sample units, B18

and B25, reflect the mid-season variability that is the result of what annual plants emerge and persist until the late summer. The plant species that largely differentiated these two sample units from others collected in the summer were *Zizania aquatica* and *Bidens laevis* in B18, and *Leersia oryzoides* in B25 (Figure 3.2). These are all annual plants, and their local abundance varies greatly from year to year (Whigham and Simpson 1992; Leck and Simpson 1994). For example, in one study site in a companion plant community study along the Nanticoke River itself, *Polygonum arifolium* plants dominated the marsh surface in summer 2000, growing up to 2 m in height. At the same site the following year, the same plant was much less abundant, and typically was under 1 m in height (personal observation). Two plant species had relatively high correlations with the ordination axes related to animal biomass. These plants correspond with the salinity gradient, where the relatively salt tolerant broad-leafed plant, *Peltandra virginica*, was related to sites where salinity was highest. The other abundant fleshy stemmed marsh plant, *Nuphar lutea*, does not tolerate salinity well, and is one of the first plants to suffer effects from the altered water chemistry (McKee and Mendelssohn 1989), perhaps allowing *P. virginica* to thrive and extend into the low marsh zone. *Galium tinctorium*, on the other hand, was related to marshes on the opposite side of the ordination space as it occurs only in freshwater habitats (Tiner 1993). The seasonal patterns of vegetation abundance are so strong that they likely overwhelmed these subtle shifts as salt stress began to impact the marsh vegetation, but the onset of these changes are visible only when the plant community is considered after the sites were ordinated based on animal abundance, which is much more sensitive to the salinity gradient.

It is interesting that in both the spring group and fall group, there appears to be some segregation of the sites based on creek membership. The Broad Creek sample units tended to ordinate at higher positions along axis 2 than those from Marshyhope Creek. The joint-plot of high marsh plant biomass is highly correlated with this axis, and in the previous chapter, ANOVA indicated that Broad Creek tended to have more plant biomass than Marshyhope Creek. These factors suggest that while the species composition of the marshes in both creeks is fairly similar at these two times of the year, there is more aboveground plant material per unit area in the Broad Creek marshes. The lack of pattern in the summer months suggests that plant community composition in mid-summer is less dependent on creek identity than on annual plant recruitment. This is likely related to short-term differences in seed-bank expression and seedling emergence (Baldwin et al. 2001), as localized environmental factors can afford some species competitive advantages over others (van der Valk 1981).

Animal Community

The ordination of the animal species assemblages based on biomass distribution did not result in any well defined groups separated from each other in the two-dimensional ordination space, but it did segregate the sample units according to creek identity to a large extent (Figure 3.3). The gradient on which this distribution occurs seems related to salinity to a certain extent, but the dispersion of plots is widespread across both axes, and the r^2 values for most environmental variables were relatively low (Table 3.2). As previously mentioned, the two plant species that had high r^2 values reflect their salinity tolerance. *Peltandra virginica* tends to become the dominant low marsh

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plant in oligohaline environments, replacing *Nuphar lutea* (Odum 1988). While none of the marshes shifted to plant community types with oligohaline characteristics, the *P. virginica* potentially marks the onset of structural changes that the prolonged stress induced. The Marshyhope Creek Site 2 (M2) sample units corroborate this trend. In the ordination space, all the sample units from the other two sites, M1 and M3, appear on the right side of axis 2 (Figure 3.3). Only the fall season data point from M2 is located on that side of the axis. The other three sample units are mixed in among those from Broad Creek. In terms of the larger scale community assemblage structure (sensu Wagner and Austin 1999), animal species associated with permanent tidal freshwater (*Gambusia holbrooki* and *Fundulus diaphanus*) were being replaced by species that tended to be found at the freshwater – oligohaline interface (*Morone americana* and *Anchoa mitchilli*) (Figure 3.4).

Only one site, Marshyhope Creek Site 1 (M1), seemed to ordinate into a relatively tight group in the animal biomass (Figure 3.7). The marsh sample units are in the lower right portion of the ordination space and form a fairly tight cluster without any internal overlap with other marsh sites. This site was the most downstream location, and had the most frequent and prolonged occurrences of oligohaline associated animal species. This is the general region of ordination space where these oligohaline species reside, although they tend to be found in an even lower position along axis 2 than the Marshyhope Site 1 sample units. The implications of salt water intrusions are not very well understood for freshwater fish, and the responses probably occur on multiple levels (Peterson and Meador 1994). Most of the species, even those that declined once the salinity reached its

Figure 3.7. NMS ordination of animal biomass identifying site-date sample units for the creeks. NMS indicated that two dimensions sufficiently depicted the relationships among the sample units. Final stress was 21.13 in two dimensions. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r^2 values greater than 0.15 and are exaggerated by 200 percent. GATI = *Gallium tinctorium*, PEVI = *Peltandra virginica*, DO2 = dissolved oxygen, SAL = salinity, COND = conductivity. The black line connects all sample units from Marshyhope Site 1 in chronological sequence.
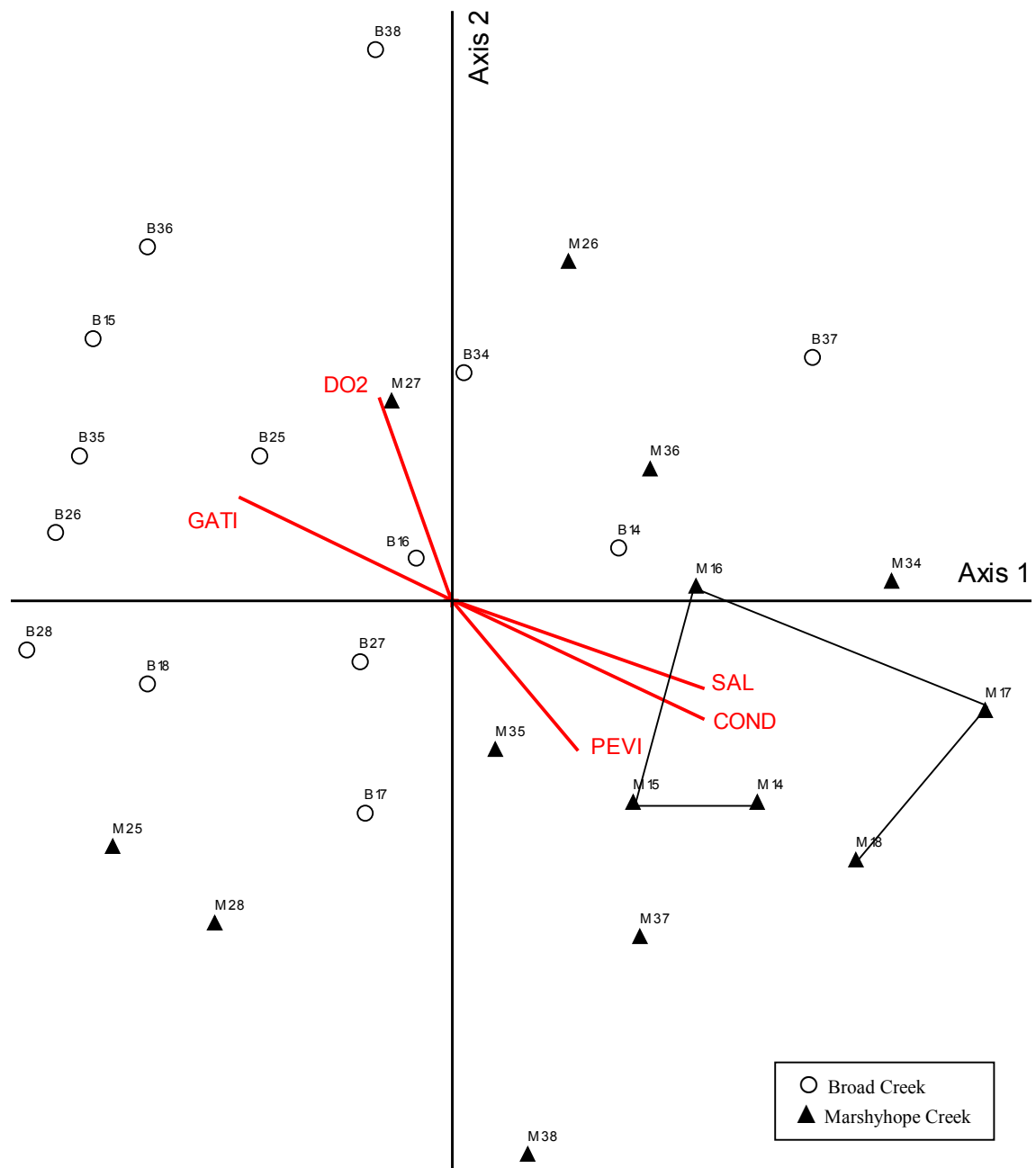
highest levels, exhibit fairly high levels of tolerance (Murdy et al. 1997). It is possible

that the frequently changing osmotic conditions on each tidal cycle prevent fish in these

environments from being able to acclimate to the salinity regime (Peterson et al. 1987).

Thus, the ordination results of animal abundance are likely a consequence of species

replacements as the range of species pools associated with downstream osmotic

conditions eventually extended into what was originally considered a permanent tidal

freshwater region where the marshes were located (Wagner and Austin 1999).

The patterns emerging in the ordination of the animal density estimates portrayed

a more complicated dynamic than did the biomass ordination. While there was a certain

level of sample unit segregation based on marsh site and date in this ordination, the Broad

Creek sample units tended to ordinate closer to the center than did the units from

Marshyhope Creek. There appeared to be less segregation of sites along axis 2 with

which salinity and conductivity were most closely associated (Figure 3.5). Only four

Marshyhope sample units sorted out along this axis in the direction associated with

increasing salinity, although three of the four units come from Marshyhope Creek Site 1,

the marsh most affected by the rising salinity. Broad Creek sample units appear to be

sandwiched between those from Marshyhope Creek. The explanation for this pattern

seems to be related largely to relative up-stream distance. Marshyhope Site 1 (M1) was

the most downstream marsh, and sample units from this location ordinated to the upper

left. Just upstream (3.63 km) was Marshyhope Site 3 (M3), which appears in close

proximity to the M1sample units. Next in river distance upstream come Broad Creek

Sites 1 and 2, followed by Marshyhope Site 2 and Broad Creek Site 3, at almost the same

distance upstream from the Marshyhope-Nanticoke confluence. The relationship to distance upstream seems to follow a descending diagonal direction (Figure 3.8). This distance also corresponds to an extent with the salinity gradient, which is the likely factor determining which animal species are present (Peterson and Ross 1991; Able et al. 2001; Tsou and Matheson 2002).

<u>Plant Community Characteristics and Nekton Abundance</u>

Interestingly, no measure of plant community abundance was strongly correlated with any axes in both ordinations of animal abundance. In both cases, the surrogate measure for increasing plant structure, mean aboveground plant biomass, had r^2 values less than 0.1 with the axes. This would indicate that the variation in the animal species assemblages had little to do with the differences in total community biomass. The NMS for both the animal density and biomass matrices suggest that animal community composition and structure are more likely influenced by the longitudinal pattern of salinity levels than to variation in the biomass of plant communities, as was the case in other habitats in which researchers compared animal density to plant community composition (Able et al. 2001). Measures of plant species richness, however, correlated with both axes in the ordination based on animal density. Several fish species, including *Fundulus heteroclitus, Morone americana,* and *Etheostoma olmstedi*, are associated with increasing low marsh plant species richness, while freshwater invertebrates tended to occur in sample units where high marsh plant species richness was higher (Figure 3.6). This could be a residual seasonal effect, where the presence of the invertebrate species

Figure 3.8. NMS ordination of animal density identifying site-date sample units for the creeks. Sample unit codes identify creek, site and date. B = Broad Creek, M = Marshyhope Creek. Site numbers range from 1 to 3 on each creek. Date 4 = May 2001, Date 5 = Aug 2001, Date 6 = Oct 2001, Date 7 = May 2002, Date 8 = Aug 2002. Joint plots included all have r^2 values greater than 0.15 and are exaggerated by 175 percent. ACCA= *Acorus calamus*, PEVI = *Peltandra virginica*, HVRICH = plant species richness in high marsh, LVRICH = low marsh plant species richness, SAL = salinity, COND = conductivity. Dotted line represents distance upstream of each site, increasing from left to right. Ovals identify sample units from spring 2001.
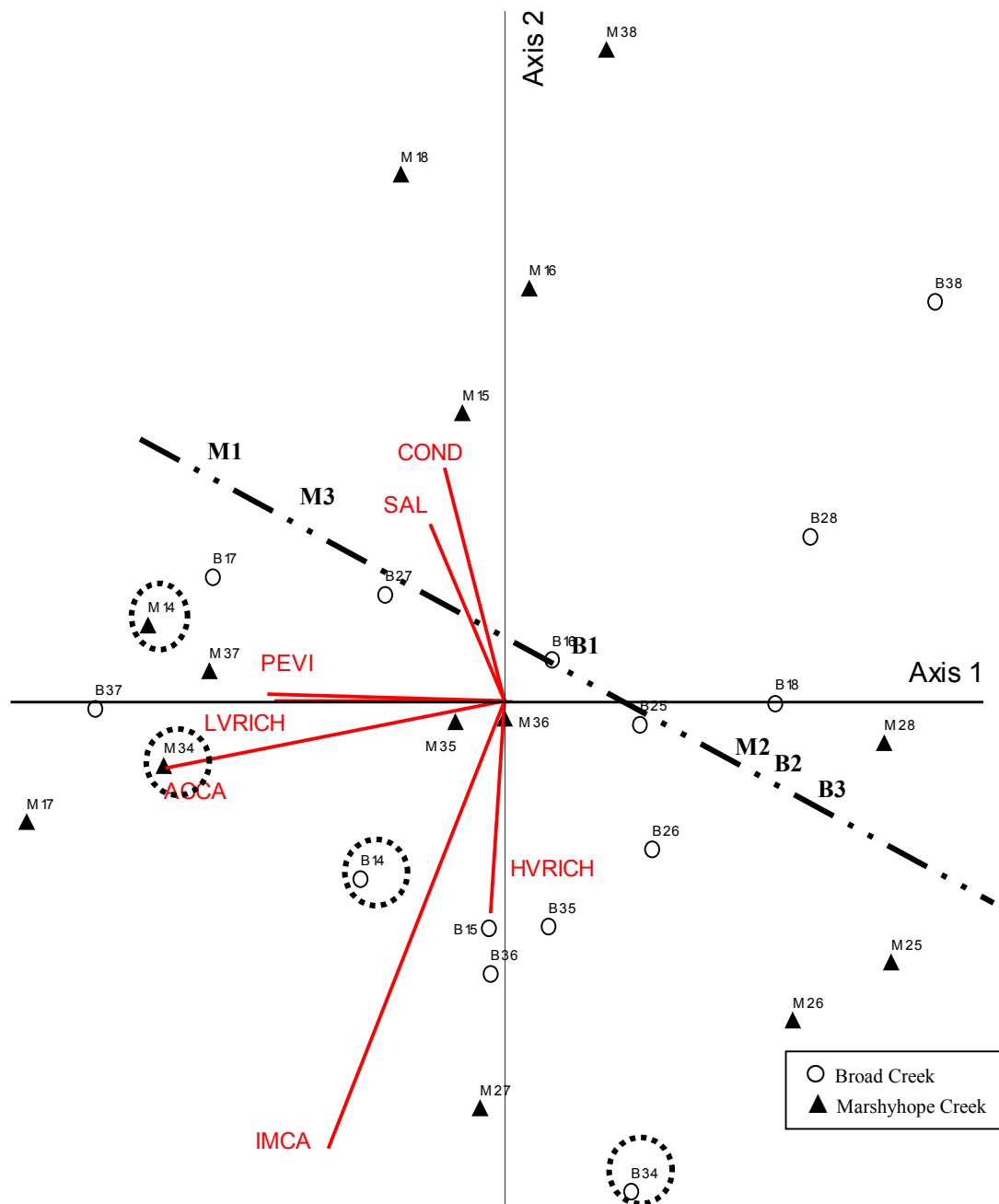
tended to be higher in the spring, the same time that marsh plant species richness was often at its highest levels.

Individual plant species did not offer much of an explanation for the patterns in animal abundance. In the animal biomass ordination, the two plant species offer a depiction of the opposite ends of the salinity spectrum, where *Galium tinctorium* is associated with freshwater animal species, while the abundance of the more salt tolerant *Peltandra virginica* correlates with the presence of oligohaline species (Figure 3.4). Two of the plant species in the animal density ordination, *Acorus calamus* and *Peltandra virginica*, are strongly correlated with the axis associated with a group of sample units collected in the spring sample periods (Figure 3.5). But rather than identifying a significant relationship between these two plant species and animal abundance, the pattern identifies sample units collected in the spring, as the ordination of the plant community also indicated (Figure 3.1). The third plant species, however, is not so easily explained. *Impatiens capensis* had the highest correlation with any axis in any of the three ordinations (Table 3.3), but there are very few sample units that reside deeply within the lower left quadrant. The only sample dates that do not appear to ordinate in this direction along axis 2 are sample units from August 2002. Both *I. capensis* and high marsh plant species richness correlate in the same direction opposite that of salinity, so these plant community variables maybe reflecting an effect of the salinity increase on plant community composition. August 2002 was the point when salinity was at its highest level, and was likely beginning to affect plant species that had been able to withstand the slowly growing salt stress. Prolonged exposure to salt stress will ultimately lead to tidal

freshwater marshes assuming a more oligohaline character (McKee and Mendelssohn 1989), which may have begun to occur in the final months of the drought.

Patterns in emergent marsh vegetation do affect nekton abundance and composition. Differences in plant stem density can affect predator foraging success rates, and in habitats with higher plant stem densities, prey species are more abundant as capture rates decline for predatory fish (Savino and Stein 1982; Harrison et al. 2005; Savino and Stein 1982). There may be, however, a threshold related to stem density that affects the ability of predators to prey upon smaller animals in marshes (Gotceitas and Colgan 1989). The differences in plant biomass across the sites may not translate into more stems, as higher biomass may just be a consequence of greater somatic growth of plant tissue. Some fish species may have preferences for specific vegetative cover in habitats with heterogeneous plant community composition (Chick and McIvor 1997), but in these ordinations, axis correlation with individual plant species tends to be a function of either seasonal trends or likely impacts of salt stress on the plant community. There is also evidence that nekton assemblages in tidal freshwater communities can vary according to season (Peterson and Ross 1991; Tsou and Matheson 2002). For example, some species I collected, particularly *Trinectes maculatus*, the hogchoker, and *Palaemonetes pugio*, the grass shrimp, tended to be collected only from late summer into the fall. While Wagner and Austin (1999) suggested that there should be higher degree of stability to the species pool of nekton assemblages in permanent tidal freshwater regions, life history behaviors may be magnified by rising salinity (Brown-Peterson and Peterson 1990). For example, both hogchoker and grass shrimp abundance increased in 2001 and

2002, corresponding with the rising salinity, amplifying the seasonal pattern. Hogchoker abundance in the Chesapeake Bay tributaries has associated with the transitional zone between permanent tidal fresh and oligohaline waters (Wagner and Austin 1999). As this transition zone moved upstream, so did the animal species that thrive within it, hence their increase in abundance.

Position along the river-distance gradient affected the nekton assemblages. For example, the four sample units collected in May 2001 suggest that the assemblages differed along the distance gradient before the drought and the subsequent salinity increase (Figure 3.8). Two species in particular distinguish these sample units along the gradient, *Fundulus heteroclitus* (mummichog) and *Corixia* spp. In both collection methods, the mummichog declined in abundance as river distance increases, while Corixidae density increased in the upstream marshes (Table 3.5). Conductivity, the more sensitive measure of the ionic concentrations in the river water, suggested a slightly increasing gradient, ranging from 117 µS cm^{-1} at the most upstream site (B34) to 137 µS cm^{-1} at the downstream marshes (M1). Interestingly, *Notropis hudsonius*, a species that declined in abundance as salinity increased over the latter half of the study, was more abundant in the downstream sites before the drought. This could indicate that this fish prefers habitat with slightly elevated ionic concentrations, but when osmotic stress increases with higher salinity, the fish retreats to move favorable conditions upstream (Peterson and Meador 1994).

Table 3.5. Density estimates of nekton collected in spring 2001.Only four sites were comprehensively sampled in May 2001. The values are transformed mean abundance estimates (ln (x+1)). Units are numbers trap^{-1} in the flume and numbers m^{-2} for the throw trap. Flume data identified by "F" and throw data with a "T."

Species		M14	M34	B14	B34
Anchoa mitchilli	F	0	0	0	0
Calinectes sapidus	F	0	0	0	0
Etheostoma olmstedi	F	0	0	0	0
Fundulus diaphanus	F	0.567	0.204	0.772	0.138
Fundulus heteroclitus	F	0.704	0.447	0.320	0.273
Gambusia holbrooki	F	0	0	0	0
Gobiosoma bosc	F	0	0	0	0
Lepomis macrochirus	F	0	0	0	0
Morone americana	F	0	0	0	0
Notropis hudsonius	F	0	0.204	0	0
Palaemonetes pugio	F	0	0	0	0
Physia gyrina	F	0	0	0	0
Trinectes maculatus	F	0	0	0	0
Anchoa mitchilli	T	0	0	0	0
Coenagrionidae	T	0	0	0.067	0
Corbicula fluminea	T	0	0	0.067	0
Cordulidae	T	0	0	0.067	0
Corixia spp.	T	0	0.067	0.544	1.547
Etheostoma olmstedi	T	0.176	0.067	0	0
Fundulus diaphanus	T	0.176	0.336	0	0.301
Fundulus heteroclitus	T	0.439	0.336	0.067	0
Gambusia holbrooki	T	0	0.222	0	0
Gammarus sp.	T	0.860	0.727	0.740	0.176
Lepomis macrochirus	T	0	0	0	0
Morone americana	T	0.301	0	0	0
Notropis hudsonius	T	0.628	0.222	0.176	0
Palaemonetes pugio	T	0	0	0	0
Physia gyrina	T	0	0	0	0
Trinectes maculatus	T	0	0	0	0

The tidal freshwater marshes appear to be a fairly uniform environment with respect to the overall species pool. Marshes along the entire gradient tend to have the same plant and animal species. But the abundance of the individual species seems to vary in a uniform manner across the distance gradient, particularly for the nekton, which can respond rapidly to changes in local habitat conditions. As the drought-induced salinity increase began to impact both the plant and animal communities, the faunal species assemblages shifted as nekton species associated with the freshwater – oligohaline interface appeared in higher abundance. The physical structure the plant community provided was not affected by the salinity in a noticeable manner until the drought had persisted for over 10 months, and even then, the changes were fairly small, particularly in the high marsh. There does not appear to be a large-scale pattern relating fish abundance to plant community composition and biomass. Rather, it seems that what is shaping the structure of the nekton community at each marsh site was proximity to downstream influences.

The results of these ordinations also lead back to the basic question in the previous chapter: Are the two creeks different? Like the previous chapter, the results of these analyses tempt me believe that there is some sort of fundamental difference between them. It intuitively makes sense that the long-term difference in nutrient loads has resulted in changes in plant community composition and structure, which may be related to some sort of difference in the abundance of the aquatic macrofauna. Yet given the similarity of the marshes in the two creeks, the response of the marsh ecosystems may

be occurring on a level beyond the scope of these analyses based only on the stocks of organisms. The next chapter addresses these perceived differences between the creeks by focusing on the entire set of trophic relationships among all the organisms that are part of the tidal freshwater marsh ecosystem.

CHAPTER 4

THE RESPONSES OF TIDAL FRESHWATER MARSHES TO EUTROPHICATION AND NATURAL ENVIRONMENTAL STRESS: AN ECOLOGICAL NETWORK ANALYSIS

INTRODUCTION

Nutrient enrichment has been adversely affecting coastal ecosystems of the mid-Atlantic region for well over a century (Chesapeake Bay Program 2004c; Cloern 2001; Vitousek et al. 1997; Nixon 1995). Commonly, ecological research investigating the effects of eutrophication has concentrated on open-water estuarine systems (Kiddon et al. 2003; McClelland and Valiela 1998b; Valiela et al. 1991), with less emphasis on the results of nutrient enrichment on the associated wetland systems. More recently, some studies have examined the effects of excess nutrients in salt marsh habitats and how the consequences can ripple through the entirety of these ecosystems. In tidal salt marshes in New England, for example, increased human activity near coastal wetlands has resulted in greater nitrogen availability in nearby marshes (Valiela and Bowen 2002), and has been linked to the replacement of *Spartina* marshes with *Phragmites* (Silliman and Bertness 2004). In salt marshes in New Jersey, the effects of nitrogen additions cascaded through multiple trophic levels, increasing plant biomass, altering insect population densities and lingered for two to three years after the treatment application (Gratton and Denno 2003). But it has been more than 25 years since anyone has explicitly examined the effects of nutrient enrichment in tidal freshwater marshes (Whigham et al. 1980).

These marshes are exposed to other environmental factors that can have substantial impact on system function and integrity. The location of tidal freshwater marshes in the landscape guarantees that external events, such as short-term weather fluctuations and long-term climatic changes, can and will influence salinity levels in tidal river systems. A look at salinity in the Nanticoke River at Sharptown, Maryland, which is right in the middle of the tidal freshwater zone, indicates that at multiple times over the past 15 years, salinity has risen to oligohaline levels on multiple occasions (Figure 4.1). The effects of salinity pulses has been well documented, particularly in coastal Louisiana, where salt pulses linked to sea level rise and coastal subsidence have been linked to tidal marsh degradation (Willis and Hester 2004; McKee and Mendelssohn 1989). Wetland loss is occurring in the Chesapeake watershed (Horton 2003), and has been historically documented in the Nanticoke River watershed (Tiner 2005). The river has suffered significant wetland loss largely due to sea level increases that have significantly affected salt marshes, but tidal freshwater marshes have so far remained relatively unaffected (Kearney et al. 1988).

The previous two chapters of this dissertation identified several distinct differences between the tidal freshwater marshes of the two tidal tributaries of the Nanticoke River, Marshyhope Creek and Broad Creek, that may be linked to coastal eutrophication. Certain differences, such as increased macrophyte biomass, reduced plant

Figure 4.1. Salinity fluctuations in the Nanticoke River, 1990 through 2004. The
Maryland Department of Natural Resources routinely evaluates water quality at
permanent stations around the Chesapeake Bay watershed. This data summary presents
field measured salinity (parts per thousand) from a depth of 0.5 m in Sharptown,
Maryland (station ET6.1), approximately 1.5 miles downstream from the Maryland-
Delaware border. The reference line indicates a salinity of 0.5 ‰, which represents the
maximum salinity considered to be freshwater.
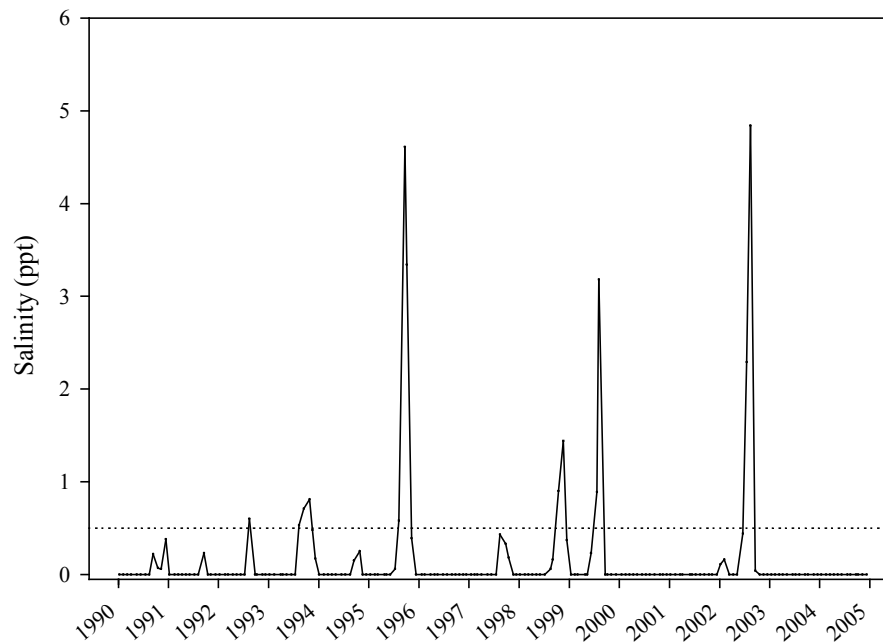
species richness and enriched nitrogen isotope signatures in Broad Creek, are outcomes associated with increased nutrient loading. Other differences, such as those seen among the various fish and invertebrate species using the marshes, led to less certain conclusions about the ecological processes in these marshes and may reflect ecosystem responses to salinity increases. These analyses in the previous chapters, however, have focused on the standing stocks of organisms in the wetlands, with ecosystem process relegated to inferential afterthought. The integration of a process-oriented analysis could identify the differences in the ecosystem function that examination of the stocks of living components of the Nanticoke tidal freshwater marshes could not reveal.

Ecological network analysis is an analytical tool that evaluates the activity and development of ecosystems on multiple levels through the trophic exchanges among their constituent elements (Ulanowicz 2004). Principally, it relies on matrix properties and linear algebra to identify the extent and impact of the indirect pathways of flow in the system (Szyrmer and Ulanowicz 1987). Network analysis also incorporates information theory to construct a description of the extent of growth and development inherent in the entire ensemble of parts revealed in the matrix of interactions (Hirata and Ulanowicz 1984). The actual measure of the scope and organization of the ecosystem is called ascendency, which, in the absence of other factors, is purported to increase as the ecosystem develops (Ulanowicz 1997). This is the fundamental theoretical concept of network analysis; the other properties of network analysis essentially function as corollaries to this tendency to increase system organization over time.

In the presence of an external stress, however, ecosystem development tends to arrest or even reverse. Stressed ecosystems may suffer degradation of numerous properties including a decline in ability to cycle nutrients, a loss of redundancy in ecosystem processes and shortened food chain lengths (Odum 1985). Ulanowicz (1996) documented that these effects of stress could be observed in trophic networks, using tidal aquatic habitat adjacent to marshes in Florida as an example. Habitats stressed by thermal effluent from a power plant saw their trophic efficiencies decline, recycle pathways degrade and system size and organization negatively impacted when compared to more pristine habitats (Ulanowicz 1996).

Network analysis has also been applied to investigations looking at the effects of nutrient enrichment in coastal systems. Ulanowicz (1986, 1997) defined eutrophication in network terms as an increase in ascendency that is created by an increase in total system activity with concurrent loss of system organization. With a quantifiable definition of eutrophication, it is possible to assess its effects in real ecosystems. For example, comparative network analysis of carbon flow in three coastal ecosystems of the East Coast of the United States (Narragansett, Delaware and Chesapeake Bays) sought to determine which system had been most affected by anthropogenic stress. The results suggested that the Chesapeake Bay was the most stressed system of the three with the least ability to mitigate perturbations stemming from a loss of system-wide resilience (Monaco and Ulanowicz 1997). In the Mondego estuary of Portugal, trophic networks of non- and strongly eutrophic regions of the bay indicated that the strongly eutrophic regions had less complicated cycling pathways, reduced system activity and a concurrent

decline in system level organization (Patrício et al. 2004). Total system behavior, however, may actually mask the effects of eutrophication expressed in network analysis. The benthic sub-system could be exhibiting the effects of eutrophication if examined alone, but at the ecosystem level, compensating factors, such as a shift of dependence from one resource base to another, could lead to system-wide measures that contradict the expected results (Almunia et al. 1999).

The tidal freshwater marshes of the two tributaries of the Nanticoke River do not present a clear-cut study of pristine versus impacted system as the previous examples. The central lower Eastern Shore has some of the highest nitrogen loading rates in the entire Chesapeake watershed (Brakebill and Preston 2003; Preston and Brakebill 1999). While Broad Creek has historically had higher nutrient loading rates than Marshyhope Creek, both creeks receive above average nitrogen inputs, producing an aquatic environment that never experiences nitrogen limitation, unlike other nearby rivers (Maryland DNR 2004). The species pools of both creeks were almost identical from 2000 through 2002, with most differences expressed in variations in the abundance of shared species rather than possessing fundamentally different species composition. Furthermore, along with any effects imparted by nutrient enrichment, a significant rise in salinity affected the marshes of the two creeks over the latter half of the study. Changes in salinity regimes began to exert influence in Marshyhope Creek by October 2001. Compositional differences among the animal species due to the increase in salinity were apparent in its marshes by May 2002, and also in Broad Creek by August 2002.

This chapter seeks to determine whether the differences observed in the components of the tidal marsh reveal ecosystem-level properties that are indicative of environmental stress. Specifically, I will address whether the differences in nutrient loads and salinity regime alter ecosystem function and organization in a trophic network sense, demonstrating changes in pathways of carbon flow, degradation of system level organization and altered trophic relationships.

RESEARCH METHODS

This section will only describe the methodologies and assumptions underlying the development and analysis of the trophic networks. Specific information about sample sites and sampling protocols are briefly described in Chapter Two, while a thorough explanation of all collection methods is presented in Appendix I.

Characterization of the Marshes

The tidal freshwater marshes of the Nanticoke River consist of areas of high marsh abutting low marshes that gradually slope down to the subtidal zone of the river. Most of these marshes form narrow belts that separate the open water from inland tidal swamps. At many river bends, however, expansive tidal marshes have developed where both low and high marsh can cover large areas. These marshes often can be described as depositional, where the low marsh gradually rises in elevation up to the high marsh (McIvor and Odum 1988). On the other hand, most of the belt marshes are erosional and typically have a well-defined "step" between the marsh types, where the high marsh is

perched 20 – 40 cm above the low marsh. The marshes in these networks refer specifically to the depositional marshes of the Nanticoke River.

In these depositional marshes, much of the high marsh surface floods regularly on each high tide. Preliminary throw trapping during spring and early summer 2000 in high marshes suggested that at high tide, faunal distributions were fairly similar between the two adjacent marsh types near the interface. Fish abundance in particular appears to be more a function of water depth than preference for floral characteristics of the marsh types. Given the similarity between high marsh and low marsh distributions of fish and macroinvertebrates, microhabitat preferences were considered to be neutral for all but a few species.

Compartment Descriptions

Network construction begins with the identification of components that have important ecosystem roles (Ulanowicz 2004). The ecosystem is then defined as a collection of compartments that are linked together via trophic pathways, with the linkages answering the initial network analysis questions, "who eats whom, and by how much?" Specificity of compartment membership often ranges from narrowly defined subgroups within a population to broadly inclusive groups of similarly functioning species, with dimension recast in terms of biomass per unit area. One then determines how much biomass there is in each compartment, providing dimension to the "who" in the networks. In order to figure out the rates explicitly asked for in the latter half of the

question, energy budgets for each compartment are needed that determine the demands of each compartment. In simplest terms the energy budgets are expressed as:

$$C = P + R + E$$

where C is consumption, P is production, R is respiration and E is egestion. Ideally, one could directly measure all biomasses and process rates of all compartments (Ulanowicz 1996), but the feasibility of this decreases very quickly as the number of compartments rises. More commonly, the researcher relies on published ratios and equations estimating the relationships between processes and biomass for the target taxon (Christian and Luczkovich 1999; Hendriks 1999; Wilson and Parkes 1998; Longhurst 1983). As network analysis has become more frequently used for ecosystem analysis, the scope and sophistication of networks has increased dramatically and the characterizations of many compartments are utterly reliant on the work of others (e.g., Ulanowicz et al. 2000).

Data on abundance of plants, macroinvertebrates and fishes from six depositional marshes located on two tidal tributaries on the Nanticoke River were compiled to generate ten distinct trophic networks, five each for Broad Creek and Marshyhope Creek. These networks are further identified by specific dates based on the field collection dates: May 2001, August 2001, October 2001, May 2002 and August 2002. There were 46 distinct compartments identified, but no creek ever had more than 43 at one time (Table 4.1). The average biomass of each compartment is reported as g carbon m^{-2}. Flows are reported as g carbon m^{-2} y^{-1}. For the purpose of clarity, when compartments are referred

Table 4.1. List of compartment identification numbers and codes. There were 46 total compartments defined over the span of the study, but they all never occurred in the same network, with the number of compartments present in the networks ranging from 39 to 43. For the purpose of clarity, compartment identification numbers were standardized for all networks, and abbreviations were frequently used instead of longer compartment names in tables and figures.

#	Code	Name	#	Code	Name
1	BALG	Benthic Algae	24	COSP	Corixidae
2	PICO	Picophytoplankton	25	GASP	Gammarus sp.
3	PHYTO	Phytoplankton	26	ODLRV	Odonate larvae
4	LROOT	Low Marsh Root	27	OINVT	Other Insects
5	HROOT	High Marsh Roots	28	PAPU	Palaemonetes pugio
6	NULU	Nuphar lutea	29	CASA	Calinectes sapidus
7	ZIAQ	Zizania aquatica	30	ANRO	Anguilla rostrata
8	ACCA	Acorus calamus	31	ANMI	Anchoa mitchilli
9	POAR	Polygonum arifolium	32	NOHU	Notropis hudsonius
10	LEOR	Leerzia oryzoides	33	FUDIS	Fundulus diaphanus < 35
11	PEVI	Peltandra virginica	34	FUDIL	Fundulus diaphanus >35
12	IMCA	Impatiens capensis	35	FUHE	Fundulus heteroclitus
13	BISP	Bidens spp.	36	GAHO	Gambusia holbrooki
14	SCFL	Schoenoplectus fluviatilis	37	GOBO	Gobiosoma bosc
15	OMAC	Other Macrophytes	38	MOAM	Morone americana
16	FBACT	Free Bacteria	39	ETOL	Etheostoma olmstedi
17	PBACT	POC Bacteria	40	LEMA	Lepomis macrochirus
18	SBACT	Sediment Bacteria	41	TRMA	Trinectes maculatus
19	MICROZ	Microzooplankton	42	MDET	Macrophyte Detritus
20	MESOZ	Mesozooplaknton	43	SPOC	Suspended POC
21	MEIO	Meiofauna	44	DOC	DOC
22	MBENTH	Macrobenthos	45	HMPOC	High Marsh Soil POC
23	COFL	Corbicula fluminea	46	LMPOC	Low Marsh Soil POC

to in this text, the first letter will be capitalized (e.g., Meiofauna). Figure 4.2 presents a hypothetical flow network of all the compartments and all possible direct links that were ecologically possible. This idealized topology presents a general view of the complicated flow pathways in the ecosystem. Specific depictions of each of the ten networks identifying biomass and flow rates are included in Appendix IV, as are the details describing each compartment.

Network Properties

Trophic networks can be represented as matrices of interactions between the identified compartments. The ten networks I developed initially were structured in the "least-inference" format, where interactions between compartments are denoted merely by their presence or absence. Each network also contained two row vectors at the bottom specifying the inputs to and the biomass of each compartment. Two column vectors at the right end of the matrix presented specific compartmental values for exports and respirations. Thus each row represents the likely flows from a given compartment, while each column presents the compartmental input plus a description of biomass.

Trophic relationships among the compartments were specified using MATLOD, a least inference scheme that loads the network matrix by adding a small amount to the set of all designated flows. After all the flows receive this increment of input, the algorithm examines the availability of each prey and the demand of each predator, looking to see if either is exhausted, proceeding until all flows fall to zero (Ulanowicz 2004).

Figure 4.2. Idealized flow network of all trophic interactions in the tidal freshwater marshes of the Nanticoke. The network represents all possible compartments and linkages, but this configuration never occurred. Specified networks of the creeks on each date are presented in Appendix IV. For convenience, the 10 functionally similar macrophyte species are grouped into one network node, "Macrophytes." Inputs enter each node on the left side, outputs exit from the right side.
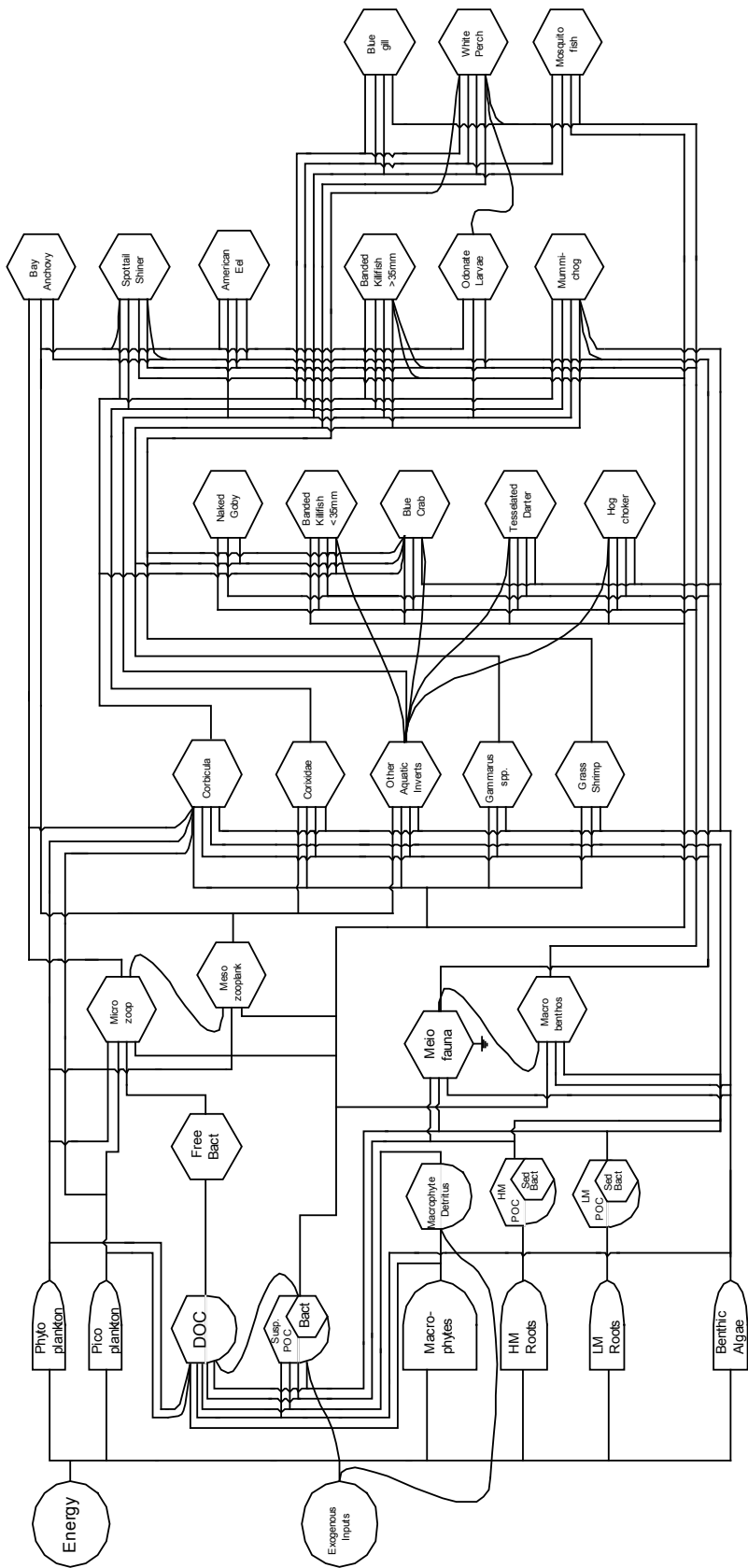
The intercompartmental flows created by MATLOD were inspected to ensure that they were consistent with any additional information I had about trophic relationships (e.g., using published dietary preferences of species or stomach content analysis of species captured). Large carbon imbalances were addressed manually by adding inputs to the detrital components of the networks. Tidal freshwater marshes are net importers of material during the growing season (Pasternack and Brush 2001), and input of particulate organic carbon was the most likely path through which marsh carbon demand was supplemented (Anderson et al. 1998).

Aboveground macrophyte production was exported from all May and August networks as stored biomass and used as a carbon input to Macrophyte Detritus to the network next in the temporal sequence for each creek. The vegetation community accumulates aboveground biomass in spring and early summer, and by mid-summer, senescence begins for many species and then accelerates through the remainder of the growing season (Neubauer et al. 2000). Thus, the May networks have the greatest rate of biomass storage, most of which is exported to the August networks. August networks are intermediates, where there is still a high rate of production (mostly in annual species (Whigham and Simpson 1992)) that carries over as exports to October, but also processes the macrophyte detritus the system receives. The October networks received the macrophyte detrital input from August, plus I assumed that these networks utilized all late season macrophyte production. A portion of the October exports represent the contributions to the litter layer embedded in the soil particulate carbon pool (Findlay et al. 1990).

The hand-balanced networks were then fine-balanced using a processing algorithm called FORBAL to put the networks into steady state (i.e., inputs = outputs for all compartments). There are multiple balancing routines that can be used to accomplish this (Allesina and Bondavalli 2003). FORBAL was selected because most compartmental process rates were based on biomass measured directly in the field, and FORBAL preserves the biomass : input relationships better than alternative methods. At this point the networks are ready for analysis.

Network Analysis

Each network was analyzed using an application called NETWRK 4.2b (Ulanowicz 2002). This program consists of four separate analyses: ecological input/output analysis, Lindeman trophic analysis, calculation of global attributes describing system organization and development and cycle analysis.

Input/output analysis (I/O) relies on the properties of matrices to investigate the indirect relationships among the entities of the network. Initially developed as a tool in economic research, it was introduced to ecology in the 1970s (Hannon 1973), and was later refined by Szyrmer and Ulanowicz (1987). In network analysis, I/O determines how any activity originating in compartment i ultimately affects compartment j. These relationships are described in two output matrices, one comprised of total contribution coefficients (TCC) and the other of total dependency coefficients (TDC) (Szyrmer and Ulanowicz 1987). TCC identifies exactly what fraction of the total amount of carbon

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leaving compartment *i* eventually enters compartment *j*, through all possible pathways. TDC is the fraction of total ingestion by *j* that passed through *i* directly or indirectly on its way to *j* (Ulanowicz 2002).

The Lindeman trophic analysis translates the web of interactions into a simple linear chain of flow based on the classic trophic concepts of ecology (Lindeman 1942). This analysis partitions each compartment to a series of integer trophic levels, representing the fraction of activity that each compartment engages in at each distinct trophic level (Ulanowicz 1995). The output identifies the average trophic position of each species and the components of various flows associated with each integer trophic level.

The third component of NETWRK 4.2b describes the global attributes of the organization and development of the network (Ulanowicz 1997; Hirata and Ulanowicz 1984; Ulanowicz 1980). These properties are defined as ascendency (A), development capacity (C) and overhead (Φ). These measures are derived from informational indices that assess the orderliness and coherence of the flows, called average mutual information (AMI), and the residual disorder that remains, or the conditional entropy (H_c) (Ulanowicz 2004). More simply, AMI measures the constraint that the development of flow pathways imposes on the system, while H_c describes corresponding freedom remaining in the system imparted by pathway redundancies, and capacity is the sum of these two values. The network indices are provided dimension by multiplying their informational values by the total system throughput (TST) of the network, or the total activity of the system calculated by summing all flows into, out of and between every compartment (Ulanowicz

2004). Ascendency represents a measure of a network's size and organization and describes how well the system processes the medium of exchange (Ulanowicz 1997). Development capacity represents the upper bound on ascendency, describing the maximum scope for potential development of the ecosystem (Ulanowicz 1997). Overhead is the difference between development capacity and ascendency, quantifying the complement of ascendency, or the inefficiency and uncertainty inherent in the system. In a closed system, all overhead would be accounted for by pathway redundancy, but in open networks, like ecosystems, overhead also originates in the uncertainty provided by inputs, exports and respiration (Ulanowicz and Norden 1990).

The last analysis NETWRK 4.2b provides is a decomposition of all the possible cyclical pathways that exist in the network. The output details the number of cycles within the system, their length, the amount that circulates around each pathway and the percentage of total ecosystem activity devoted to cycling (Finn Cycling Index) (Ulanowicz 1983).

RESULTS

Input/Output Analysis

The total contribution coefficient matrices do not suggest a great deal of difference between the two creeks (Tables 4.2 – 4.11). Seasonal differences in TCC's are not as widespread among the living components as they are in the detrital compartments. The detrital fates of carbon vary significantly between the seasons, but it also reflects the

Table 4.2. Total contribution coefficient matrix (percentages) for Broad Creek, May 2001. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	32	33	34	35	36	38	39	42	43	44	45	46
1	BALG	7	0	3	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	33	2	2
2	PICO	4	0	1	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	21	1	1
3	PHYTO	5	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	0	0
4	LROOT	0	0	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	20	55
5	HROOT	1	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	55	18
6	NULU	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
7	ZIAQ	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	7	3	1
8	ACCA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
9	POAR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
10	LEOR	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	7	3	1
11	PEVI	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	0	0
12	IMCA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	1	0
13	BISP	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	7	3	1
14	SCFL	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	1	0
15	OMAC	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	7	3	1
16	FBACT	0	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
17	PBACT	0	0	7	24	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	10	2	6	5
18	SBACT	1	0	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	37	36
19	MICROZ	0	0	5	0	2	0	0	1	0	0	0	2	1	11	2	0	2	0	0	0	0	7	2	4	3
20	MESOZ	1	0	12	0	0	0	1	0	11	1	11	2	1	0	2	2	2	1	3	1	0	16	4	9	8
21	MEIO	0	0	34	0	0	0	0	0	2	0	0	1	1	0	2	0	1	1	0	0	0	1	2	25	24
22	MBENTH	0	0	9	0	0	0	0	0	0	0	3	2	2	1	2	2	10	1	2	2	0	4	1	7	6
23	COFL	1	0	10	0	0	0	0	0	0	0	0	0	0	0	8	11	12	0	0	0	0	13	3	8	7
24	COSP	1	0	9	0	0	0	0	0	0	0	0	0	0	5	0	10	13	1	0	0	0	12	3	7	6
25	GASP	1	0	8	0	0	0	0	0	0	0	0	0	0	12	0	17	20	0	9	0	0	11	3	7	5
26	ODLRV	1	0	19	0	0	0	0	0	0	0	0	0	0	12	0	0	0	6	25	0	0	25	6	15	12
27	OINVT	1	0	10	0	0	0	0	0	0	0	10	0	4	0	1	8	16	6	7	5	0	14	3	8	7
30	ANRO	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	2	4	4
32	NOHU	1	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	26	6	15	13
33	FUDIS	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1
34	FUDIL	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1
35	FUHE	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	2	1
36	GAHO	2	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	36	8	22	18
38	MOAM	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	2	2
39	ETOL	2	0	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51	12	31	25
42	MDET	10	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	52	51	19
43	SPOC	5	1	77	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	60	49
44	DOC	20	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	HMPOC	2	0	92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	34	33
46	LMPOC	1	0	99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	36	36

Table 4.3. Total contribution coefficient matrix (percentages) for Broad Creek, August 2001. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	33	34	35	36	39	40	42	43	44	45	46
1	BALG	10	1	11	2	0	7	1	0	3	1	0	0	0	1	1	1	0	0	0	0	40	33	11	6
2	PICO	5	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	17	2	1
3	PHYTO	5	0	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	17	2	1
4	LROOT	1	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	16	55
5	HROOT	1	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	55	16
6	NULU	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	4	1
7	ZIAQ	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	4	1
8	ACCA	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	4	1
9	POAR	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	6	4	1
10	LEOR	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	6	4	1
11	PEVI	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	4	1
12	IMCA	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	4	1
13	BISP	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	6	4	1
14	SCFL	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	4	1
15	OMAC	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	6	4	1
16	FBACT	1	0	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	1	0
17	PBACT	6	1	8	34	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	21	8	4
18	SBACT	1	0	44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	35	34
19	MICROZ	4	1	5	1	2	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	22	15	6	3
20	MESOZ	4	1	5	1	2	0	4	3	16	2	0	4	1	1	3	2	2	1	3	0	21	14	5	3
21	MEIO	2	0	18	0	0	0	4	0	11	0	0	0	1	4	2	2	1	1	1	0	8	6	14	13
22	MBENTH	3	1	10	1	0	0	0	0	0	0	0	0	1	11	8	9	3	2	1	0	16	11	9	7
23	COFL	5	1	7	2	0	0	0	0	0	0	0	0	0	4	11	7	11	0	11	0	27	18	7	3
24	COSP	7	1	9	2	0	0	0	0	0	0	0	0	0	12	12	12	11	0	12	0	35	23	9	4
25	GASP	7	1	9	2	0	0	0	0	0	0	0	0	0	0	20	17	0	0	0	0	38	25	10	5
26	ODLRV	8	1	10	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	31	0	43	28	11	5
27	OINVT	6	1	8	2	0	0	0	0	0	0	2	0	0	4	9	7	9	7	12	0	31	21	8	4
30	ANRO	10	2	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	35	14	7
33	FUDIS	4	1	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	13	5	2
34	FUDIL	8	1	11	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	43	29	11	5
35	FUHE	10	2	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	35	14	7
36	GAHO	10	2	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	35	14	7
39	ETOL	10	2	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	35	14	7
40	LEMA	10	2	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	35	14	7
42	MDET	7	0	67	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	24	81	23
43	SPOC	19	3	25	6	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	67	26	13
44	DOC	29	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
45	HMPOC	2	0	82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	29	28
46	LMPOC	1	0	83	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	29	29

Table 4.4. Total contribution coefficient matrix (percentages) for Broad Creek, October 2001. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	31	32	33	34	35	36	39	40	42	43	44	45	46
1	BALG	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	29	2	1
2	PICO	3	0	0	10	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	29	2	1
3	PHYTO	2	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	28	1	0
4	LROOT	2	0	16	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	28	5	55
5	HROOT	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	54	1
6	NULU	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
7	ZIAQ	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
8	ACCA	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
9	POAR	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
10	LEOR	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
11	PEVI	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	57	30	22	29	2
12	IMCA	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	57	30	22	29	2
13	BISP	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
14	SCFL	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
15	OMAC	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	30	22	29	2
16	FBACT	1	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	9	4	1
17	PBACT	1	0	1	40	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	34	14	6	27
18	SBACT	1	0	9	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	29	2
19	MICROZ	1	0	1	0	1	0	0	1	0	0	3	0	2	0	0	0	0	0	0	1	0	33	14	6	2
20	MESOZ	2	0	1	1	0	0	2	3	3	1	3	3	68	1	0	1	1	1	1	0	0	57	24	10	3
21	MEIO	1	0	5	0	0	0	0	0	1	1	0	1	0	2	3	1	1	1	1	0	0	4	11	18	16
22	MBENTH	1	0	1	0	0	2	0	0	0	0	5	4	0	2	3	6	8	8	0	4	0	22	10	7	3
23	COFL	1	0	1	0	0	0	0	0	0	0	0	0	0	3	3	16	20	0	0	2	0	35	14	6	2
24	COSP	1	0	1	0	0	0	0	0	0	0	0	0	0	6	3	15	13	12	0	4	0	34	14	6	2
25	GASP	1	0	1	0	0	0	0	0	0	0	0	0	0	6	0	19	14	0	0	0	0	37	15	6	2
26	ODLRV	2	0	1	1	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	15	0	42	17	7	2
27	OINVT	1	0	1	0	0	0	0	0	0	0	7	0	0	0	7	7	7	21	5	6	0	36	15	6	2
31	ANMI	3	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	74	31	13	4
32	NOHU	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	22	9	3
33	FUDIS	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	22	9	3
34	FUDIL	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	22	9	3
35	FUHE	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	22	9	3
36	GAHO	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	22	9	3
39	ETOL	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	21	8	3
40	LEMA	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	22	9	3
42	MDET	3	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52	32	50	3
43	SPOC	4	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	42	17	5
44	DOC	9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0
45	HMPOC	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	1
46	LMPOC	4	0	29	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	51	9	8

Table 4.5. Total contribution coefficient matrix (percentages) for Broad Creek, May 2002. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	31	32	33	34	35	36	38	39	40	42	43	44	45	46
1	BALG	16	0	26	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	28	1	1
2	PICO	15	0	8	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	26	0	0
3	PHYTO	15	0	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	26	0	1
4	LROOT	2	0	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	17
5	HROOT	2	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	59	33
6	NULU	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
7	ZIAQ	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
8	ACCA	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
9	POAR	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
10	LEOR	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
11	PEVI	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
12	IMCA	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
13	BISP	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
14	SCFL	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
15	OMAC	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
16	FBACT	1	0	22	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	2	2	2
17	PBACT	2	0	35	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	4	2	2
18	SBACT	2	0	50	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	34	70
19	MICROZ	3	0	42	0	1	0	0	2	0	0	1	4	1	1	0	6	1	1	1	0	0	1	0	48	5	0	0
20	MESOZ	1	0	23	0	0	0	0	9	5	1	1	4	1	11	9	2	4	5	1	1	1	1	0	26	5	0	0
21	MEIO	1	0	28	0	0	0	1	0	1	1	2	3	3	0	2	2	13	1	0	1	1	3	0	5	2	0	0
22	MBENTH	1	0	23	0	0	0	0	0	0	0	2	3	3	0	5	2	22	17	0	4	1	3	0	25	2	0	0
23	COFL	2	0	34	0	0	0	0	0	0	0	0	0	0	0	0	2	21	27	1	4	0	2	0	39	2	0	0
24	COSP	2	0	40	0	0	0	0	0	0	0	0	0	0	0	10	0	16	30	19	8	0	2	0	45	4	0	0
25	GASP	2	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	10	0	2	0	38	4	0	0
26	ODLRV	2	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	29	0	35	3	0	0
27	OINVT	2	0	32	0	0	0	0	0	0	0	4	6	4	0	0	6	12	12	7	6	0	6	0	36	3	0	0
30	ANRO	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
31	ANMI	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
32	NOHU	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
33	FUDIS	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
34	FUDIL	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
35	FUHE	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
36	GAHO	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
38	MOAM	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
39	ETOL	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
40	LEMA	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
42	MDET	20	0	49	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	35	0	0
43	SPOC	5	1	87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	10	38	51
44	DOC	57	0	13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	1	2	2
45	HMPOC	3	0	87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	2	2
46	LMPOC	3	0	97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	2	2

Table 4.6. Total contribution coefficient matrix (percentages) for Broad Creek, August 2002. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	26	27	28	30	31	32	33	34	35	36	38	39	40	41	42	43	44	45	46
1	BALG	13	1	12	3	0	13	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	33	42	11	8
2	PICO	8	0	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	26	2	1
3	PHYTO	8	0	3	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	26	3	2
4	LROOT	1	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	16	55
5	HROOT	1	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	55	17
6	NULU	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
7	ZIAQ	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
8	ACCA	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
9	POAR	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
10	LEOR	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
11	PEVI	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
12	IMCA	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
13	BISP	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
14	SCFL	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
15	OMAC	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	5	2
16	FBACT	7	1	9	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	23	8	6
17	PBACT	8	0	11	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39	27	10	7
18	SBACT	1	0	46	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	35	35
19	MICROZ	10	1	13	3	1	0	0	11	0	0	0	0	1	0	0	0	3	1	0	0	0	2	0	0	49	34	12	8
20	MESOZ	5	0	6	1	0	0	2	0	6	1	5	2	1	0	1	5	9	1	0	2	3	0	1	0	22	15	5	4
21	MEIO	2	0	26	0	0	0	0	0	0	6	1	0	1	4	0	5	0	0	0	1	0	5	1	0	6	6	20	20
22	MBENTH	4	0	9	1	0	0	0	0	0	0	6	0	0	0	1	1	18	5	4	3	0	3	2	0	17	12	8	6
23	COFL	6	1	9	2	0	0	0	0	0	0	0	0	0	0	0	0	6	1	4	0	0	0	5	0	32	22	8	5
24	COSP	6	1	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	14	0	0	7	0	28	19	7	5
26	ODLRV	8	1	11	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	23	0	23	0	0	41	28	10	7
27	OINVT	7	1	9	2	0	0	0	0	0	1	0	0	0	1	0	2	17	7	7	5	4	10	3	0	35	24	8	6
28	PAPU	10	1	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	6	0	0	0	0	47	32	11	8
30	ANRO	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	55	37	13	9
31	ANMI	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
32	NOHU	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
33	FUDIS	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
34	FUDIL	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
35	FUHE	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
36	GAHO	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
38	MOAM	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
39	ETOL	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
40	LEMA	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
41	TRMA	11	1	15	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	37	13	9
42	MDET	6	1	74	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	21	84	27
43	SPOC	21	2	27	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	69	25	17
44	DOC	30	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	7	2	2
45	HMPOC	2	0	88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7	30	31
46	LMPOC	2	0	83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	29	29

Table 4.7. Total contribution coefficient matrix (percentages) for Marshyhope Creek, May 2001. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	32	33	34	35	36	38	39	42	43	44	45	46
1	BALG	13	0	23	0	0	7	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	27	29	23	11
2	PICO	10	0	4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	22	4	2
3	PHYTO	11	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	24	3	1
4	LROOT	1	0	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	20	54
5	HROOT	1	0	49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	53	18
6	NULU	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
7	ZIAQ	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	5	2	1
8	ACCA	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
9	POAR	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	1	1
10	LEOR	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	5	2	0
11	PEVI	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	1	1
12	IMCA	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	1	0
13	BISP	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	5	2	1
14	SCFL	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	1	0
15	OMAC	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	5	1	1
16	FBACT	1	0	10	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	3	10	5
17	PBACT	3	0	25	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	6	26	11
18	SBACT	1	0	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	39	37
19	MICROZ	2	0	17	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	17	17	8
20	MESOZ	2	0	16	0	0	0	0	4	13	0	2	4	0	4	0	6	5	1	1	0	0	21	4	17	7
21	MEIO	1	0	34	0	0	0	1	0	3	1	0	1	0	1	1	1	1	0	0	0	0	3	2	25	23
22	MBENTH	1	0	17	0	0	0	0	0	0	0	2	3	3	1	2	13	15	2	2	3	0	15	3	16	9
23	COFL	2	0	21	0	0	0	0	0	0	0	0	0	0	8	5	30	17	3	3	0	0	27	5	22	10
24	COSP	2	0	19	0	0	0	0	0	0	0	0	0	0	0	0	30	25	4	2	0	0	24	5	19	9
25	GASP	2	0	20	0	0	0	0	0	0	0	0	0	0	13	0	12	15	0	3	0	0	25	5	20	9
26	ODLRV	3	0	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0	33	6	26	12
27	OINVT	2	0	20	0	0	0	0	0	0	0	4	0	3	0	6	17	21	10	4	3	0	25	5	20	9
30	ANRO	5	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	10	42	19
32	NOHU	5	0	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	10	42	19
33	FUDIS	5	0	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	10	42	19
34	FUDIL	3	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	7	28	13
35	FUHE	1	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	2	9	4
36	GAHO	5	0	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	10	42	19
38	MOAM	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	5	2
39	ETOL	5	0	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	10	42	19
42	MDET	19	0	58	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	42	61	24
43	SPOC	9	0	78	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	20	79	35
44	DOC	46	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	2
45	HMPOC	3	0	91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	35	34
46	LMPOC	2	0	98	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	38	37

Table 4.8. Total contribution coefficient matrix (percentages) for Marshyhope Creek, August 2001. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	28	30	32	33	34	35	36	38	39	40	41	42	43	44	45	46
1	BALG	7	1	9	1	0	7	1	0	16	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	17	28	9	4
2	PICO	7	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	26	2	1
3	PHYTO	7	0	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	27	2	1
4	LROOT	1	0	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	14	44
5	HROOT	1	0	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	48	13
6	NULU	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
7	ZIAQ	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
8	ACCA	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
9	POAR	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
10	LEOR	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
11	PEVI	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
12	IMCA	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
13	BISP	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
14	SCFL	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
15	OMAC	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
16	FBACT	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	2	1
17	PBACT	3	0	13	24	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	11	15	6
18	SBACT	1	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	35	34
19	MICROZ	3	1	12	2	1	0	0	4	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	26	10	13	6
20	MESOZ	2	1	9	1	1	0	4	0	15	0	4	3	1	1	3	0	1	2	1	1	4	1	0	0	20	8	10	4
21	MEIO	1	0	18	1	0	0	4	0	16	0	2	1	1	0	0	10	4	4	4	1	4	0	1	0	8	4	15	12
22	MBENTH	1	1	10	1	0	0	0	0	0	0	2	1	1	1	0	4	1	4	2	4	1	2	1	0	10	5	10	6
23	COFL	2	1	10	1	0	0	0	0	0	0	0	0	0	0	11	6	6	12	0	5	0	8	1	0	22	9	11	5
24	COSP	2	1	9	1	0	0	0	0	0	0	0	0	0	0	0	0	6	8	1	1	0	8	2	0	19	7	10	4
25	GASP	3	1	12	2	0	0	0	0	0	0	0	0	0	0	15	0	12	15	0	8	0	0	0	0	27	10	14	6
26	ODLRV	4	1	18	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	20	0	20	0	0	40	15	20	9
27	OINVT	3	1	14	1	0	0	0	0	0	0	5	0	3	3	0	5	6	7	22	7	3	6	0	0	30	12	15	7
28	PAPU	4	1	20	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	27	0	0	0	0	42	16	21	9
30	ANRO	5	2	25	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	21	27	12
32	NOHU	5	2	25	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	21	27	12
33	FUDIS	1	0	5	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	4	6	2
34	FUDIL	2	1	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	8	11	5
35	FUHE	1	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	3	4	2
36	GAHO	5	2	25	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	21	27	12
38	MOAM	5	2	23	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	19	25	11
39	ETOL	5	2	25	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	21	27	12
40	LEMA	5	2	25	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	21	27	12
41	TRMA	5	2	25	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	21	27	12
42	MDET	6	7	67	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	22	83	23
43	SPOC	10	3	47	7	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	39	51	22
44	DOC	26	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
45	HMPOC	2	0	81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	28	28
46	LMPOC	2	0	89	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	31	30

Table 4.9. Total contribution coefficient matrix (percentages) for Marshyhope Creek, October 2001. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	28	31	32	33	34	35	38	39	42	43	44	45	46
1	BALG	3	0	0	1	0	3	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	22	35	5	1
2	PICO	3	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	27	1	0
3	PHYTO	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	27	1	0
4	LROOT	2	0	17	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	5	55
5	HROOT	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	55	1
6	NULU	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
7	ZIAQ	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
8	ACCA	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
9	POAR	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
10	LEOR	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
11	PEVI	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
12	IMCA	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
13	BISP	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
14	SCFL	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
15	OMAC	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	25	19	34	1
16	FBACT	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	3	2	0
17	PBACT	1	0	1	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31	12	7	1
18	SBACT	1	0	9	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	29	27
19	MICROZ	1	0	0	0	0	0	0	0	0	0	3	1	0	34	6	0	0	2	0	0	0	25	9	6	1
20	MESOZ	1	0	0	0	0	0	2	2	8	0	3	0	0	0	6	8	1	2	2	1	0	17	6	4	0
21	MEIO	1	0	0	0	0	0	2	0	11	0	0	0	15	0	1	4	1	16	1	1	0	13	9	12	0
22	MBENTH	1	0	2	0	0	0	0	0	0	0	1	0	0	0	2	4	4	16	10	4	0	16	8	7	4
23	COFL	1	0	1	1	0	0	0	0	0	0	0	0	0	0	2	4	16	60	9	0	0	33	12	7	1
24	COSP	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	9	6	0	0	27	10	6	1
25	GASP	1	0	0	1	0	0	0	0	0	0	0	0	0	0	6	0	18	24	20	0	0	30	11	7	1
26	ODLRV	1	0	1	1	0	0	0	0	0	0	0	0	0	0	6	0	0	0	29	6	0	34	13	7	1
27	OINVT	1	0	0	0	0	0	0	0	0	0	5	0	0	0	0	4	3	46	9	6	0	27	10	6	1
28	PAPU	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	39	15	9	1
31	ANMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	1	0
32	NOHU	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	20	12	1
33	FUDIS	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	13	8	1
34	FUDIL	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	20	12	1
35	FUHE	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	12	7	1
38	MOAM	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	6	4	0
39	ETOL	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	20	12	1
42	MDET	2	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44	26	60	2
43	SPOC	4	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	38	22	2
44	DOC	9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
45	HMPOC	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	7	1
46	LMPOC	4	0	31	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	44	9	8

Table 4.10. Total contribution coefficient matrix (percentages) for Marshyhope Creek, May 2002. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	31	32	33	34	35	36	38	39	40	42	43	44	45	46
1	BALG	16	0	26	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	28	1	1
2	PICO	15	0	8	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	26	0	0
3	PHYTO	15	0	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	26	0	1
4	LROOT	2	0	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	17
5	HROOT	2	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	59	33
6	NULU	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
7	ZIAQ	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
8	ACCA	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
9	POAR	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
10	LEOR	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
11	PEVI	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
12	IMCA	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
13	BISP	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
14	SCFL	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
15	OMAC	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0
16	FBACT	1	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	2	2	2
17	PBACT	2	0	35	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	4	0	0
18	SBACT	2	0	50	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	34	70
19	MICROZ	3	0	42	0	1	0	0	2	0	0	0	4	0	1	0	0	1	1	0	0	0	1	0	48	5	0	0
20	MESOZ	1	0	23	0	0	0	0	9	5	0	1	3	1	11	9	0	4	5	1	1	0	1	0	26	2	0	0
21	MEIO	1	0	28	0	0	0	1	0	0	1	0	0	0	0	0	6	0	1	1	0	1	0	0	5	2	0	0
22	MBENTH	1	0	23	0	0	0	0	0	0	0	2	3	3	0	2	2	13	17	1	4	1	3	0	25	2	0	0
23	COFL	2	0	34	0	0	0	0	0	0	0	0	0	3	0	5	2	22	27	19	4	0	2	0	39	4	0	0
24	COSP	2	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	21	30	0	8	0	2	0	45	4	0	0
25	GASP	2	0	33	0	0	0	0	0	0	0	0	0	0	0	10	0	16	20	0	10	0	0	0	38	4	0	0
26	ODLRV	2	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	29	0	35	3	0	0
27	OINVT	2	0	32	0	0	0	0	0	0	0	4	0	4	0	0	6	12	12	7	6	6	6	0	36	3	0	0
30	ANRO	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
31	ANMI	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
32	NOHU	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
33	FUDIS	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
34	FUDIL	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
35	FUHE	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
36	GAHO	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
38	MOAM	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
39	ETOL	3	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
40	LEMA	3	0	46	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	5	0	0
42	MDET	20	0	49	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	35	38	51
43	SPOC	5	1	87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	10	2	2
44	DOC	57	0	13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	1	2	2
45	HMPOC	3	0	87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	2	2
46	LMPOC	3	0	97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	2	2

Table 4.11. Total contribution coefficient matrix (percentages) for Marshyhope Creek, August 2002. Compartments are labeled by number and abbreviated species code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	26	27	28	29	31	33	34	35	36	37	38	39	41	42	43	44	45	46
1	BALG	9	0	9	1	0	15	0	0	0	0	0	12	0	0	1	0	0	0	0	0	0	0	0	13	28	10	5
2	PICO	8	0	3	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	26	3	1
3	PHYTO	5	0	7	16	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	11	16	8	3
4	LROOT	1	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	7	24
5	HROOT	1	0	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	48	13
6	NULU	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
7	ZIAQ	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
8	ACCA	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
9	POAR	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
10	LEOR	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
11	PEVI	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
12	IMCA	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
13	BISP	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
14	SCFL	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	3	1
15	OMAC	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	5	4	3	1
16	FBACT	0	0	3	6	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	5	1	3	1
17	PBACT	1	1	18	25	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	28	5	20	8
18	SBACT	2	0	45	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	35	34
19	MICROZ	1	1	14	2	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	22	5	16	6
20	MESOZ	1	1	17	2	1	0	0	0	10	0	0	2	1	0	0	2	2	2	0	1	0	0	0	27	5	20	8
21	MEIO	1	1	23	2	0	0	1	1	0	3	3	47	0	6	0	0	2	2	0	1	1	0	0	22	5	23	13
22	MBENTH	2	1	22	2	0	0	1	0	0	2	2	2	2	2	0	2	7	7	1	2	3	0	0	29	5	24	11
23	COFL	2	1	23	3	0	0	0	0	0	2	2	3	2	0	0	25	7	0	0	2	0	0	0	36	6	26	10
24	COSP	2	1	23	3	0	0	0	0	0	0	0	3	8	0	0	33	14	18	0	1	0	0	0	37	6	27	10
26	ODLRV	2	1	23	3	0	0	0	0	0	0	0	3	19	0	0	15	14	0	0	21	0	0	0	35	6	26	10
27	OINVT	2	1	26	3	0	0	0	0	0	4	0	3	1	0	6	21	12	23	0	2	3	3	0	41	7	30	12
28	PAPU	2	1	25	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	39	6	28	11
29	CASA	2	1	31	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	49	8	35	14
31	ANMI	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	4	2
33	FUDIS	3	1	34	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	53	9	38	15
34	FUDIL	3	1	34	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	53	9	38	15
35	FUHE	3	1	34	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	53	9	38	15
36	GAHO	3	1	34	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	53	9	38	15
37	GOBO	3	1	34	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	53	9	38	15
38	MOAM	2	1	23	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	35	6	26	10
39	ETOL	3	1	34	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	53	9	38	15
41	TRMA	3	1	34	4	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	53	9	38	15
42	MDET	6	1	73	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5	18	90	25
43	SPOC	5	3	64	8	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	6	17	72	28
44	DOC	30	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
45	HMPOC	3	0	81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	28	28
46	LMPOC	3	0	88	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	31	30

relatively large amount of macrophyte production flowing into the detritus compartments, dwarfing the flows into and among the consumer organisms. Direct relationships between prey and predator likewise present large values for TCC. As a representative example, the total contribution coefficients describing transfers of carbon from *Gammarus* spp. across all pathways to *Fundulus heteroclitus* in 2001 were:

Creek	May	August	October
Broad Creek	20%	17%	14%
Marshyhope	15%	15%	9%

These coefficients are very large compared to other possible pathways leading to the mummichog, although they do include the sum total of indirect pathways, also (e.g., flows along pathways similar to GASP $\rightarrow$ POC $\rightarrow$ COSP $\rightarrow$ FUHE have much smaller magnitudes). The availability of prey items dictated diet composition of the mummichog, and given the decline in biomass of gammarid amphipods in October a decline in TCC between the two compartments is an obvious consequence. In these marshes, however, the ecologically interesting information provided by these coefficients is in the flow of carbon from source pools to the higher order consumers.

The indirect transfers of material should be more sensitive to alterations in the flow pathways, and examining these relationships may reveal differences between the creeks. The total contribution coefficients from four compartments, Benthic Algae, Phytoplankton, Suspended POC and Sediment Bacteria, were compared in several target fish species since direct pathways were either minimal or non-existent between them. The four lower trophic level compartments represent four different pools of available carbon

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in the networks: benthic primary production, pelagic primary production, particulate

carbon in the water column and particulate carbon derived from the sediments,

respectively. The absolute magnitudes of flows from these four compartments to detritus

greatly outweigh their respective contributions to these fish compartments but

nonetheless should reflect any shifts in carbon flow.

Changes in indirect flows of carbon to higher trophic levels should appear in the

most abundant fish species, if the resource base of their prey shifts (Baird and Ulanowicz

1989). Four fish compartments that appeared in every network (*Fundulus diaphanus* < 35

mm, *F. diaphanus* > 35 mm, *F. heteroclitus* and *Etheostoma olmstedi*) may be able to

track any changes over time. Contributions to *F. diaphanus* < 35 mm TL appear to follow

something of a seasonal pattern, with contributions from benthic and planktonic primary

production and suspended POC peaking in the summer networks and benthic detrital

carbon increasing in October (Figure 4.3 a – d). The contribution coefficients seen in the

F. diaphanus >35 mm TL compartment initially followed a similar pattern across 2001,

but deviated from the smaller killifish in the networks after October 2001. The

contribution from benthic algae did not increase in either creek in May 2002 or August

2002 (Figure 4.4a). Phytoplankton contributions increased in May 2001 and August 2001

(Figure 4.4b), but there is no distinct difference between the creeks for any of the four

source compartments (Figures 4.4 a – d). The contributions to *F. heteroclitus* exhibited

some seasonal patterns in Benthic Algae and POC, but by May 2002, there appeared to

be some divergence in behavior between the two creeks. By August 2002, contribution

trajectories (i.e., an increase or decrease from previous coefficient) headed in different

Figure 4.3 a – d. Total contribution coefficients of carbon sources for *Fundulus diaphanus* < 35 mm TL. Scales among the graphs are not equivalent, as these coefficients measure the likelihood that carbon originating in compartment *i* ends up in compartment *j* (i.e., *F. diaphanus*) and are highly dependent upon the size of the carbon pool in compartment *i*.
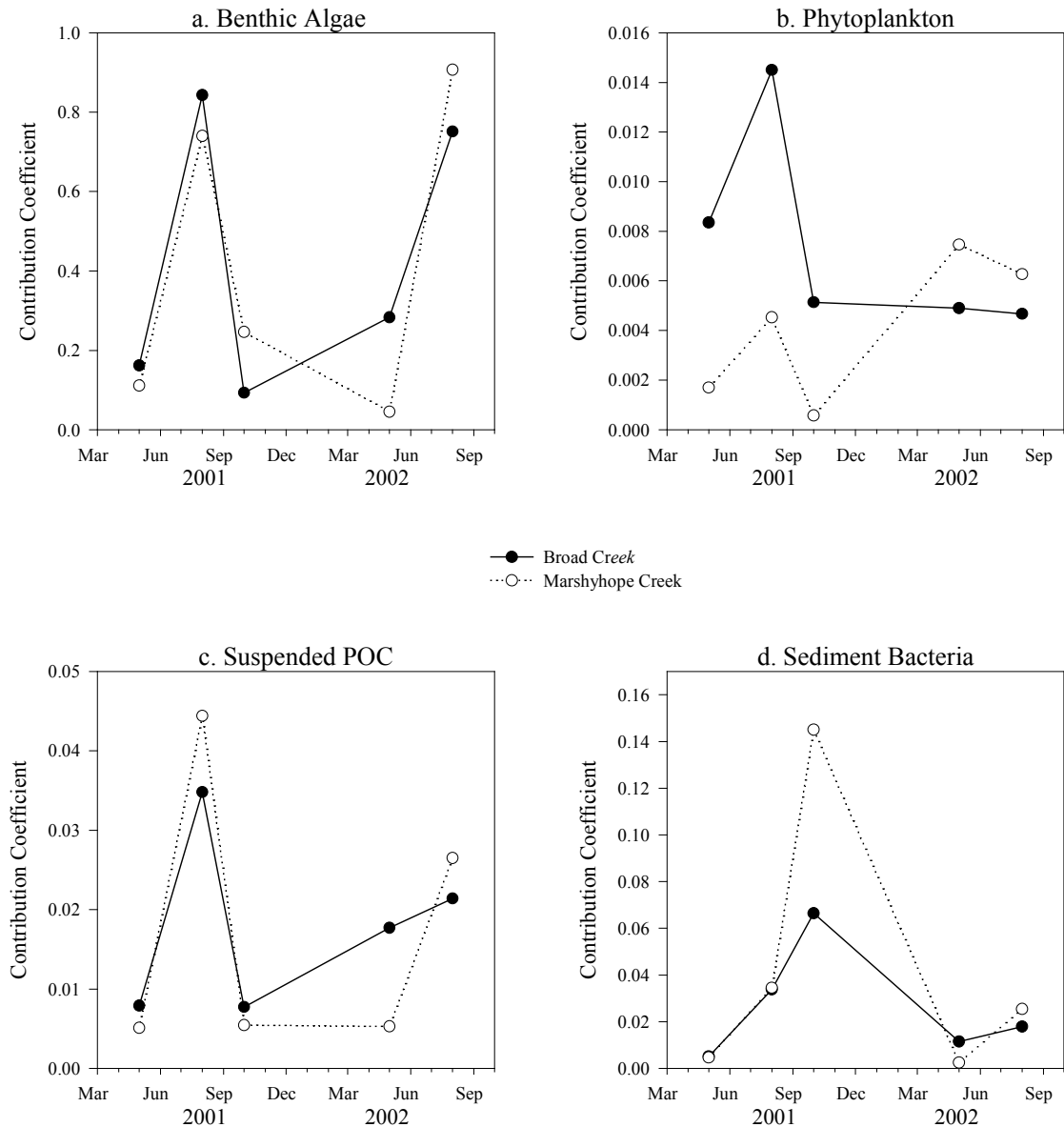
Figure 4.4 a – d. Total contribution coefficients of carbon sources for *Fundulus diaphanus* > 35 mm TL. Scales among the graphs are not equivalent, as these coefficients measure the likelihood that carbon originating in compartment *i* ends up in compartment *j* (i.e., *F. diaphanus*), and are highly dependent upon the size of the carbon pool in compartment *i*.
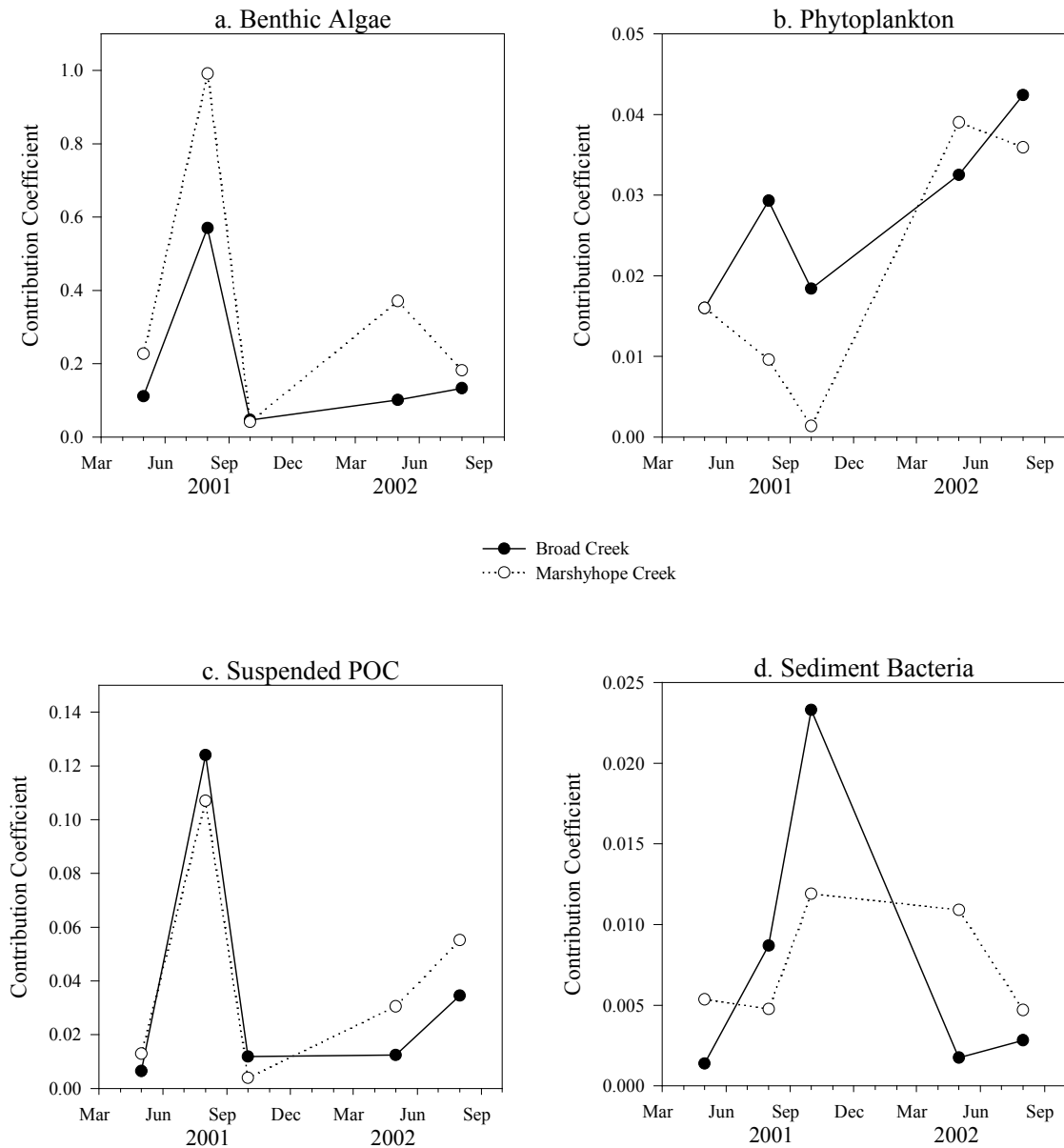
directions in all but those of Sediment Bacteria (Figures 4.5 a – d). Indirect flows from carbon sources for *Etheostoma olmstedi* were similar to that for *F. heteroclitus*. In 2001 most of the coefficients reached their maximum levels in August, but this pattern did not repeat for all sources in 2002. Phytoplankton contributions declined by August 2002 in Marshyhope Creek (Figure 4.6b), and remained flatter in Broad Creek for all sources other than Phytoplankton (Figures 4.6 a, c, d). Phytoplankton contributions to the darter species in Broad Creek August 2002 increased more than three times from the May 2002 contribution, while the contribution in Marshyhope Creek spiked in May 2002, but declined by August 2002 (Figure 4.6b).

The dependency coefficients present a different perspective, specifically, what proportion of the diet of j was at some point processed and passed on to j, either directly or indirectly, by compartment i (Szyrmer and Ulanowicz 1987). The tables of TDC's are as daunting to look at as those for TCC's (Tables 4.12 – 4.21). But a question similar to that applied to the TCC tables should work here also, specifically, are there any shifts in the sources of carbon in the diets of higher-level consumer organisms? For the same fish compartments, the top six relevant mediators of carbon were examined to identify any demonstrable differences between the creeks.

Meiofauna comprised the largest dependency coefficients for *F. diaphanus* < 35 mm TL, with usually more than 80 percent of ingested carbon passing through that compartment on its way to the killifish (Figure 4.7a). Sediment Bacteria and Benthic

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Figure 4.5 a – d. Total contribution coefficients of carbon sources for *Fundulus heteroclitus*. Scales among the graphs are not equivalent, as these coefficients measure the likelihood that carbon originating in compartment *i* ends up in compartment *j* (i.e., *F. heteroclitus*), and are highly dependent upon the size of the carbon pool in compartment *i*.
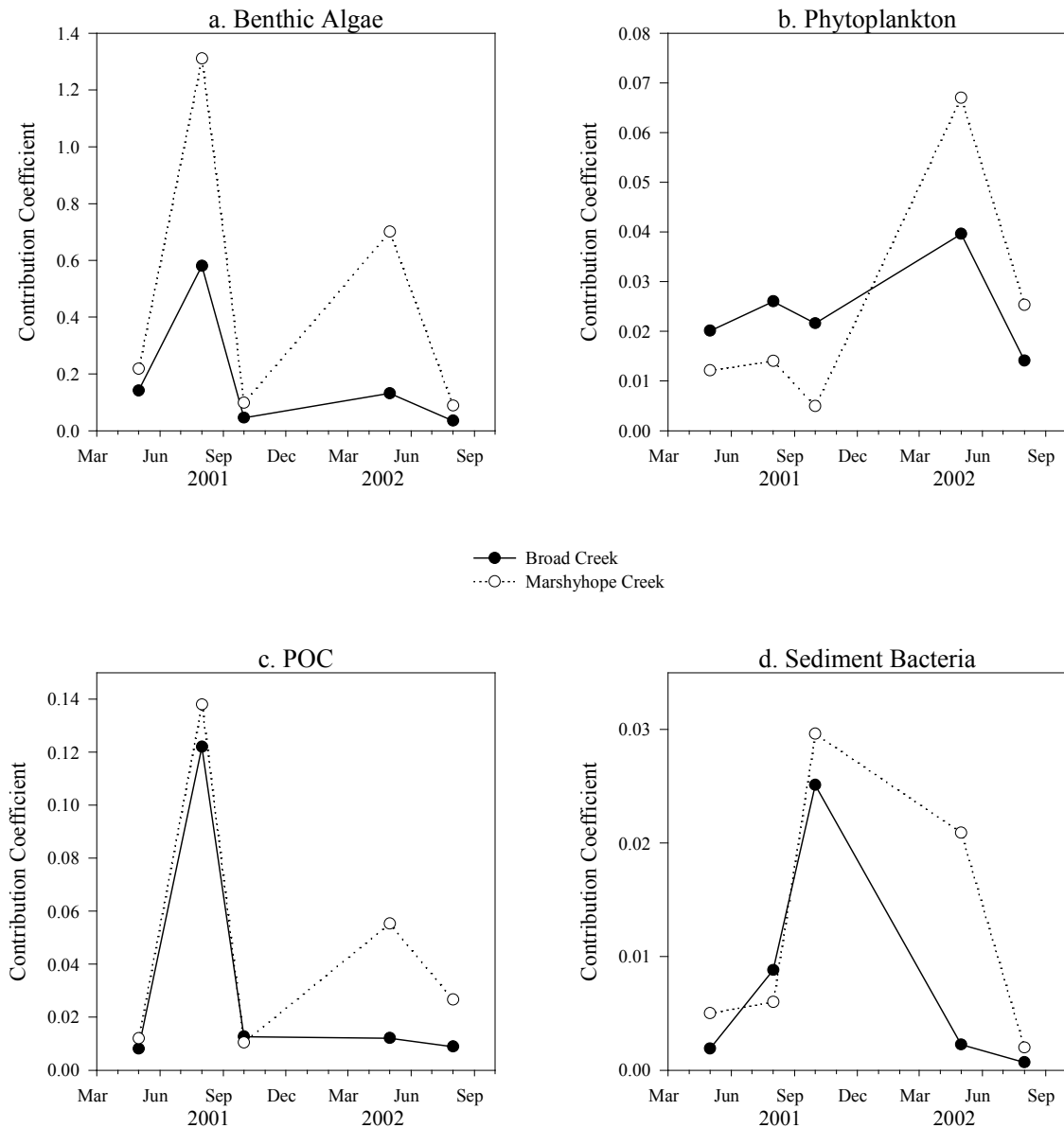
Figure 4.6 a – d. Total contribution coefficients of carbon sources for *Etheostoma olmstedi*. Scales among the graphs are not equivalent, as these coefficients measure the likelihood that carbon originating in compartment *i* ends up in compartment *j* (i.e., *E. olmstedi*), and are highly dependent upon the size of the carbon pool in compartment *i*.

Table 4.12. Total dependency coefficient matrix (percentages) for Broad Creek, May 2001. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	32	33	34	35	36	38	39	42	43	44	45	46	0	0
1	BALG	4	0	0	1	0	38	47	9	49	51	8	30	37	13	31	32	32	36	31	43	0	0	4	0	0	0	0
2	PICO	2	0	0	26	13	0	0	14	4	0	10	2	2	10	3	7	6	2	6	0	0	0	2	0	0	0	0
3	PHYTO	5	0	0	13	31	0	0	12	6	0	27	17	2	19	3	8	8	12	12	1	0	0	5	0	0	0	0
4	LROOT	2	0	11	0	0	9	4	2	4	3	1	4	8	2	8	3	3	4	3	8	0	0	2	5	21	0	0
5	HROOT	21	0	51	5	2	28	16	10	12	8	5	14	26	7	24	10	11	14	9	23	0	0	21	62	34	0	0
6	NULU	6	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	12	0	6	0	0	0	0
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
8	ACCA	6	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	12	0	6	0	0	0	0
9	POAR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	1	0	0	0	0
10	LEOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0
11	PEVI	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	1	0	0	0	0
12	IMCA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	1	0	0	0	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0
14	SCFL	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	1	0	0	0	0
15	OMAC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0
16	FBACT	0	0	0	23	11	0	0	8	3	0	9	2	0	8	2	4	4	2	5	0	0	0	0	0	0	0	0
17	PBACT	0	0	0	15	8	0	0	22	2	0	6	1	0	9	5	10	9	1	6	0	0	0	0	0	0	0	0
18	SBACT	15	0	52	3	2	50	20	17	20	15	6	22	45	12	42	17	18	21	15	41	0	0	15	41	67	0	0
19	MICROZ	0	0	0	3	49	0	0	34	15	0	40	8	1	33	7	19	17	8	21	1	1	0	0	0	0	0	0
20	MESOZ	0	0	0	0	0	0	0	0	16	0	82	12	2	54	5	5	6	11	28	1	0	0	0	0	0	0	0
21	MEIO	0	0	0	0	0	0	22	0	35	29	6	33	87	14	76	17	20	32	21	80	0	0	0	0	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	0	7	3	8	2	2	3	11	18	7	6	8	0	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	0	21	22	43	37	0	14	0	0	0	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	28	19	28	0	1	0	0	0	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	16	15	0	18	0	12	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	13	0	10	0	0	0	0	0	28	0	11	0	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	10	64	11	9	0	0	0	0	0	0	0
30	ANRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
43	SPOC	52	0	38	51	52	25	33	52	25	38	48	32	27	47	32	39	39	32	39	24	0	0	52	33	45	0	0
44	DOC	100	100	0	23	11	0	0	8	3	0	9	2	0	8	2	4	4	2	5	0	0	0	0	0	0	0	0
45	HMPOC	33	0	82	8	4	45	26	15	19	13	8	23	41	12	38	16	18	23	15	38	0	0	33	34	55	0	0
46	LMPOC	9	0	54	2	1	43	19	12	19	13	5	20	39	9	36	14	15	19	13	36	0	0	9	22	36	0	0

Table 4.13. Total dependency coefficient matrix (percentages) for Broad Creek, August 2001. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	33	34	35	36	39	40	42	43	44	45	46
1	BALG	2	11	0	3	4	26	27	4	37	43	14	21	27	25	33	33	35	26	31	0	11	2	0	0
2	PICO	7	14	0	30	16	0	3	32	6	4	10	7	1	2	7	6	6	1	9	0	14	7	0	0
3	PHYTO	5	11	0	29	49	0	2	29	7	3	28	13	1	2	8	7	7	2	10	0	11	5	0	0
4	LROOT	1	0	7	0	0	10	8	1	4	4	3	5	9	9	5	5	5	9	4	0	0	1	2	20
5	HROOT	17	1	51	5	2	35	26	9	15	15	13	19	32	33	17	17	16	31	15	1	1	17	54	44
6	NULU	4	1	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	0	1	1	1	4	1	1
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	ACCA	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0
9	POAR	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0
10	LEOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	PEVI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	IMCA	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
13	BISP	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	SCFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	OMAC	2	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0
16	FBACT	1	4	0	30	14	0	0	9	3	1	8	4	0	1	3	3	3	1	4	0	4	1	0	0
17	PBACT	0	1	0	5	2	0	1	3	1	0	1	1	0	0	1	1	1	0	1	0	1	0	0	0
18	SBACT	11	1	44	3	2	60	42	16	25	25	18	26	53	56	28	28	27	52	24	0	1	11	30	85
19	MICROZ	1	5	1	1	44	0	1	28	8	1	25	10	2	2	8	7	7	1	11	0	5	1	0	0
20	MESOZ	0	0	0	0	0	0	0	6	6	0	55	18	0	1	4	4	5	2	7	0	0	0	0	0
21	MEIO	0	1	0	0	0	0	26	2	38	41	11	18	75	90	32	33	35	76	31	0	1	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	0	28	11	32	6	21	24	14	21	4	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	0	6	9	6	0	0	13	0	0	0	0	0
24	COSP	0	1	0	0	0	0	0	0	0	0	0	0	0	6	52	55	81	0	77	0	1	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	13	0	0	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	24	0	2	1	3	3	5	11	7	0	0	0	0	0
30	ANRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	LEMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	58	63	41	31	28	28	33	24	31	31	31	35	30	29	31	31	32	30	30	0	63	58	44	36
43	SPOC	18	100	2	27	35	1	20	22	29	31	30	31	8	4	27	27	29	9	28	0	3	18	2	2
44	DOC	100	4	0	30	14	0	1	9	3	1	8	4	0	1	3	3	3	1	4	0	4	1	0	0
45	HMPOC	32	2	95	10	5	65	49	17	27	27	23	35	59	61	31	32	30	58	27	0	2	32	29	81
46	LMPOC	5	1	34	2	1	50	42	7	22	21	17	23	47	47	24	25	24	45	20	0	1	5	10	29

Table 4.14. Total dependency coefficient matrix (percentages) for Broad Creek, October 2001. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	31	32	33	34	35	36	39	40	42	43	44	45	46
1	BALG	5	2	0	1	1	30	25	4	32	44	21	27	2	23	28	21	19	27	30	22	0	2	5	0	0
2	PICO	4	2	0	34	16	0	0	22	2	0	4	1	24	6	1	9	10	1	0	5	0	2	4	0	0
3	PHYTO	8	3	0	32	46	0	1	30	3	1	16	17	38	11	3	14	16	9	3	12	0	3	8	0	0
4	LROOT	16	0	37	3	2	42	32	14	32	19	22	22	3	28	39	22	22	27	39	25	0	0	16	1	79
5	HROOT	18	0	45	4	2	17	8	8	9	8	9	14	3	11	16	9	9	11	16	10	16	0	18	76	8
6	NULU	9	15	3	5	6	2	5	4	4	5	5	3	5	3	2	4	4	4	2	4	0	15	9	4	2
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	ACCA	4	6	1	2	2	1	2	2	2	2	2	1	2	1	1	2	2	2	1	2	7	6	4	2	1
9	POAR	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
10	LEOR	1	2	0	1	1	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	2	2	1	1	0
11	PEVI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	IMCA	1	2	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	2	1	0	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	SCFL	1	2	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	1	2	2	1	1	0
15	OMAC	5	8	1	2	3	0	0	2	2	2	2	2	3	2	0	2	2	2	1	2	8	8	5	2	1
16	FBACT	1	2	0	20	10	0	0	5	1	1	3	1	14	2	0	2	3	1	0	2	0	0	1	0	0
17	PBACT	0	0	0	2	0	0	0	0	0	0	0	0	2	1	0	2	2	0	0	1	0	0	0	0	0
18	SBACT	4	0	9	1	1	32	14	4	17	14	10	12	1	21	29	15	15	14	29	14	0	0	4	2	17
19	MICROZ	1	2	0	0	0	0	0	16	4	14	11	4	70	9	1	10	11	3	1	7	0	0	1	0	0
20	MESOZ	0	0	0	46	0	0	0	22	2	0	21	4	51	8	0	2	2	3	1	5	0	0	0	0	0
21	MEIO	0	0	0	0	0	0	30	2	4	44	24	30	2	54	85	25	23	33	87	27	0	0	0	0	1
22	MBENTH	0	0	0	0	0	0	0	6	44	0	47	9	0	13	8	16	21	35	3	39	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	0	23	5	40	45	0	0	18	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	15	24	0	16	0	0	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	15	10	0	0	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	36	0	0	0	7	10	9	45	15	28	0	0	0	0	0
31	ANMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	LEMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	46	0	18	26	34	10	33	22	22	28	28	19	30	21	14	25	25	24	13	26	0	93	46	0	12
43	SPOC	33	93	7	25	36	7	33	21	22	28	28	17	30	19	11	24	24	23	9	25	0	1	33	23	11
44	DOC	100	100	0	20	10	0	1	5	1	1	3	1	14	2	0	2	3	1	0	2	0	2	1	4	0
45	HMPOC	23	2	59	5	2	23	11	10	12	10	12	18	4	15	21	12	11	14	22	13	0	1	23	1	10
46	LMPOC	20	1	46	4	2	53	40	18	40	24	28	28	4	35	49	27	27	35	49	32	0	1	20	1	8

Table 4.15. Total dependency coefficient matrix (percentages) for Broad Creek, May 2002. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

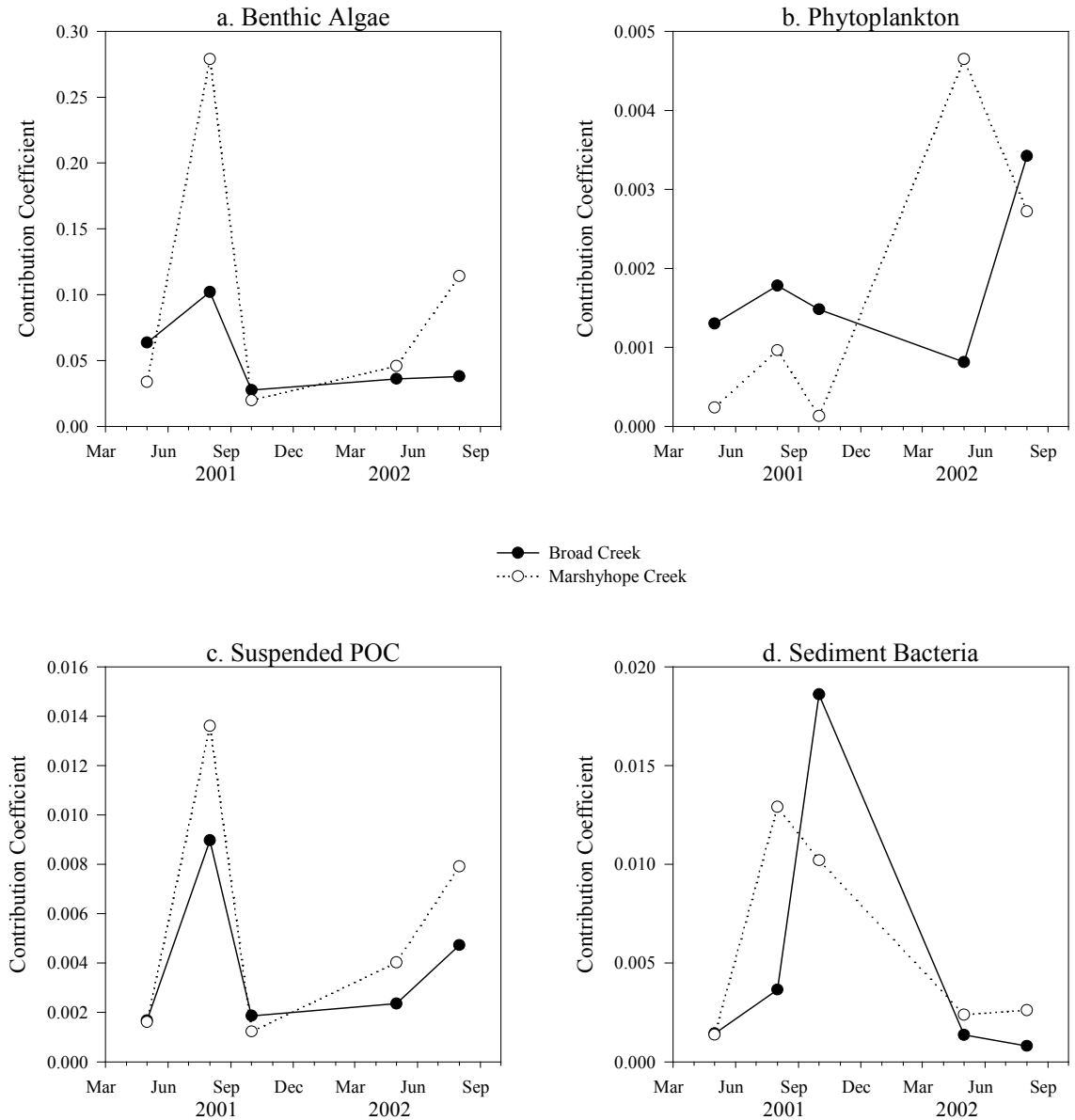| #	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	31	32	33	34	35	36	38	39	40	42	43	44	45	46
1	BALG	6	2	1	1	1	35	30	13	37	45	19	32	33	9	16	33	18	20	32	25	33	21	0	2	6	1	1
2	PICO	9	1	0	22	10	0	0	20	3	0	5	3	1	13	11	1	14	14	3	11	1	11	0	1	9	0	0
3	PHYTO	14	1	1	23	38	0	1	21	10	1	21	14	4	22	20	2	15	16	10	14	2	17	0	1	14	0	1
4	LROOT	4	0	9	1	0	9	7	1	5	4	2	2	7	2	2	8	2	2	4	3	8	2	0	0	4	3	17
5	HROOT	19	1	47	2	1	25	21	3	12	11	8	9	22	7	7	23	6	7	11	8	22	8	0	1	19	59	33
6	NULU	5	0	0	11	5	0	0	4	1	0	3	1	1	6	3	0	3	3	1	2	0	3	27	0	5	0	0
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	ACCA	8	1	0	19	9	0	0	8	2	0	4	2	1	11	6	1	5	6	2	4	0	5	47	1	8	0	0
9	POAR	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	1	0	0
10	LEOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
11	PEVI	2	0	0	6	3	0	0	2	1	0	1	1	0	3	2	0	2	2	1	1	0	1	14	0	2	0	0
12	IMCA	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
14	SCFL	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0
15	OMAC	0	0	2	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	1	2	2
16	FBACT	1	4	2	13	7	1	2	6	3	2	4	3	2	8	5	2	5	5	3	4	2	4	0	4	1	2	2
17	PBACT	0	0	0	9	4	0	0	5	1	0	2	1	0	5	3	0	4	4	1	3	0	3	0	0	0	0	0
18	SBACT	21	1	50	3	1	47	32	6	23	20	13	12	39	13	12	44	10	11	18	14	41	12	0	1	21	34	70
19	MICROZ	0	1	0	0	46	0	0	40	13	0	23	12	4	58	30	2	27	29	11	23	2	26	0	1	0	0	0
20	MESOZ	0	0	0	0	0	0	0	4	24	0	46	15	6	33	34	0	5	6	19	7	2	13	0	0	0	0	0
21	MEJO	0	0	0	0	0	0	28	1	42	41	10	10	74	24	19	91	10	11	29	17	84	10	0	0	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	0	24	4	14	0	3	1	7	9	4	10	2	16	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	4	65	69	0	49	0	50	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	8	61	10	0	6	0	0	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	8	9	0	20	0	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	13	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	37	0	12	0	0	1	4	4	28	10	11	25	0	0	0	0	0
30	ANRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	ANMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	LEMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	2	0	0	38	17	0	0	15	5	0	9	5	2	22	11	1	10	11	4	9	1	10	0	2	2	0	0
43	SPOC	33	0	44	13	33	31	44	27	30	42	37	37	34	24	34	34	36	31	38	33	35	33	0	2	33	38	51
44	DOC	100	100	2	13	7	1	2	6	3	2	4	3	2	8	5	2	5	5	3	4	2	4	0	4	1	2	2
45	HMPOC	32	1	80	4	2	43	36	6	21	18	14	15	37	13	11	40	10	11	18	14	38	13	0	1	32	2	2
46	LMPOC	24	1	56	3	2	54	39	5	27	22	15	14	44	15	13	49	11	12	22	15	46	14	0	1	24	2	2

Table 4.16. Total dependency coefficient matrix (percentages) for Broad Creek, August 2002. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	26	27	28	30	31	32	33	34	35	36	38	39	40	41	42	43	44	45	46
1	BALG	3	6	0	2	3	39	27	15	21	14	22	42	25	4	12	37	20	20	23	28	28	20	33	0	6	3	0	0
2	PICO	10	6	0	32	15	0	1	19	12	9	7	2	5	18	13	0	10	12	6	8	3	11	4	0	6	10	0	0
3	PHYTO	4	4	0	25	37	0	1	20	16	22	18	2	13	33	23	0	13	16	11	11	5	16	5	0	4	4	0	0
4	LROOT	2	1	8	1	0	7	1	3	3	2	3	3	4	1	2	7	3	3	3	3	5	3	6	0	4	2	3	22
5	HROOT	14	3	46	4	3	27	25	11	9	12	14	11	18	4	9	26	16	13	16	12	22	14	23	3	3	14	49	38
6	NULU	4	3	1	2	2	1	1	0	1	1	1	0	1	2	1	1	1	0	1	1	0	1	1	2	3	4	1	1
7	ZIAQ	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	ACCA	1	1	0	2	2	0	0	2	2	2	2	2	0	2	2	1	2	2	2	2	1	0	1	1	0	0	1	0
9	POAR	6	3	2	2	2	1	2	0	2	0	2	0	1	0	2	1	0	2	2	2	1	2	1	3	4	6	2	1
10	LEOR	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
11	PEVI	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
12	IMCA	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	1	3	0	0	2	0
13	BISP	6	4	2	2	2	1	2	0	2	2	2	0	2	0	0	0	0	0	0	0	0	0	0	0	4	6	0	0
14	SCFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	OMAC	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
16	FBACT	7	23	1	29	19	0	5	11	16	13	11	9	8	21	14	1	10	11	10	11	6	11	4	0	0	0	0	0
17	PBACT	0	1	0	3	2	0	0	2	1	1	1	0	1	2	1	0	1	1	1	1	0	1	0	0	23	7	1	1
18	SBACT	14	3	46	4	3	49	29	20	15	14	20	19	30	4	15	47	22	21	22	19	31	21	40	0	3	14	32	83
19	MICROZ	3	10	0	3	44	0	2	24	35	27	21	4	15	54	27	1	16	21	18	17	7	21	6	0	10	3	0	0
20	MESOZ	0	0	0	0	0	0	0	18	26	55	16	0	34	75	51	0	12	16	13	13	4	18	4	0	0	0	0	0
21	MEIO	0	0	0	0	0	0	27	11	16	12	23	37	53	2	16	92	18	18	22	24	42	18	73	0	0	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	36	21	0	19	1	7	7	36	21	43	12	57	25	10	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39	0	15	0	33	0	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	13	23	23	0	8	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	8	0	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	15	0	0	0	4	0	1	21	34	42	13	26	38	4	0	0	0	0	0
28	PAPU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	37	0	0	0	0	0	0	0	0
30	ANRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	ANMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	LEMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	TRMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	51	77	46	32	40	27	41	32	38	39	35	39	34	38	39	29	37	35	38	37	36	35	30	0	77	51	48	39
43	SPOC	29	100	3	33	48	2	23	28	38	37	28	38	22	44	40	6	30	29	30	34	20	29	11	0	10	29	3	4
44	DOC	100	23	1	29	19	0	5	11	16	13	11	9	8	21	14	1	10	11	10	11	0	11	4	0	23	7	1	1
45	HMPOC	29	7	94	8	6	55	51	22	18	24	28	22	37	8	19	53	32	27	33	24	46	28	46	0	7	29	30	78
46	LMPOC	10	2	35	3	2	32	19	12	12	9	14	13	19	3	9	30	15	14	15	13	21	14	26	0	2	10	11	29

Table 4.17. Total dependency coefficient matrix (percentages) for Marshyhope Creek, May 2001. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	30	32	33	34	35	36	38	39	42	43	44	45	46
1	BALG	5	2	1	1	1	40	30	7	43	46	14	28	30	32	37	36	38	37	34	38	0	2	5	1	1
2	PICO	5	0	0	29	15	0	0	21	3	0	9	3	3	4	1	5	4	3	5	0	0	0	5	0	0
3	PHYTO	11	1	0	30	40	0	0	23	6	0	24	9	8	8	2	7	6	6	9	1	0	1	11	0	0
4	LROOT	2	0	8	0	0	8	6	2	4	4	3	5	6	5	7	4	4	4	4	7	0	0	2	3	18
5	HROOT	15	0	50	3	1	27	25	8	15	12	10	15	21	18	26	15	15	16	14	26	0	0	15	55	41
6	NULU	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	2	0	0
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
8	ACCA	6	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	6	0	0
9	POAR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	1	0	0
10	LEOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0
11	PEVI	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	1	0	0
12	IMCA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0
14	SCFL	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	1	0	0
15	OMAC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0
16	FBACT	1	0	1	17	9	0	0	6	2	1	6	3	2	2	1	3	2	2	3	1	0	0	1	1	1
17	PBACT	0	2	1	6	3	1	1	5	1	0	2	1	1	1	0	1	1	1	1	0	0	2	0	1	1
18	SBACT	14	0	53	3	1	51	37	15	27	23	15	27	37	33	47	26	26	28	24	46	0	0	14	38	82
19	MICROZ	0	0	0	50	50	0	0	29	11	0	30	11	9	10	2	11	9	10	12	1	0	0	0	0	0
20	MESOZ	0	0	0	0	0	0	0	15	12	0	59	18	18	16	2	10	9	12	14	1	0	0	0	0	0
21	MEIO	0	0	0	0	0	0	29	7	50	45	15	37	61	62	90	41	41	44	37	83	0	0	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	0	22	6	23	2	4	11	14	11	11	16	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	0	8	5	13	8	0	12	0	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	59	54	62	35	0	0	0	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	11	14	0	25	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	11	0	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	0	0	11	0	5	7	9	28	12	7	0	0	0	0	0
30	ANRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
43	SPOC	52	100	42	37	43	25	40	40	29	39	42	42	33	34	28	34	34	34	36	29	0	1	52	43	42
44	DOC	100	2	1	17	9	1	1	6	2	1	6	3	2	2	1	3	2	2	3	1	0	2	1	1	1
45	HMPOC	28	1	92	5	3	50	45	15	27	23	18	27	39	33	47	27	28	28	25	47	0	1	28	35	75
46	LMPOC	11	0	45	2	1	45	36	10	24	20	14	26	34	29	42	23	24	26	22	42	0	0	11	17	37

Table 4.18. Total dependency coefficient matrix (percentages) for Marshyhope Creek, August 2001. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	28	30	32	33	34	35	36	38	39	40	41	42	43	44	45
1	BALG	2	6	0	2	2	26	29	13	69	44	15	22	46	21	19	26	63	63	44	46	26	37	26	0	6	2	0
2	PICO	10	6	0	31	17	0	2	21	1	2	10	4	2	4	12	1	2	2	2	3	0	7	1	1	6	10	0
3	PHYTO	8	6	0	31	45	0	2	26	2	2	25	16	2	11	22	1	3	3	7	5	0	12	2	0	6	8	0
4	LROOT	2	0	7	0	0	11	7	1	2	5	4	7	4	8	4	11	3	3	5	4	11	4	10	0	0	2	2
5	HROOT	16	1	49	3	2	33	20	7	7	14	11	20	12	23	12	32	8	8	14	12	32	11	29	0	1	16	52
6	NULU	3	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	0
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	ACCA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
9	POAR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
10	LEOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	PEVI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	IMCA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
14	SCFL	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	OMAC	1	0	0	0	0	0	2	0	0	0	0	0	2	3	6	0	0	0	2	2	0	3	0	0	5	1	0
16	FBACT	0	5	0	21	11	0	2	8	1	1	7	3	2	3	1	0	1	1	2	2	0	3	1	0	5	1	0
17	PBACT	1	1	0	3	2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
18	SBACT	14	1	45	3	2	66	37	14	13	28	19	37	24	43	22	63	16	15	26	23	64	21	57	0	1	14	30
19	MICROZ	1	7	0	2	50	0	2	33	3	2	27	10	2	11	25	1	3	4	5	5	0	13	2	0	7	1	0
20	MESOZ	0	0	0	0	0	0	0	14	1	0	52	15	0	21	34	0	2	2	6	4	0	18	1	0	0	0	0
21	MEIO	0	1	0	0	0	0	27	3	18	42	14	33	35	55	26	94	20	19	25	25	96	27	83	0	1	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	0	39	9	0	24	5	5	10	8	23	26	5	20	8	0	2	0	0
23	COFL	0	2	0	0	0	0	0	0	0	0	0	0	0	0	30	1	2	3	4	36	0	36	4	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	84	85	45	3	0	0	0	0	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	2	2	0	5	0	15	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5	0	12	5	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	12	0	0	14	0	0	2	0	35	24	0	0	5	0	0	0	0
28	PAPU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	ANRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	LEMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	TRMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	55	80	44	31	33	30	40	30	19	34	36	31	34	33	33	31	22	21	28	30	30	29	32	0	80	55	46
43	SPOC	8	100	2	27	36	2	29	28	17	28	31	17	30	17	27	4	18	18	19	24	3	24	8	0	3	8	2
44	DOC	100	5	0	21	11	0	2	8	1	1	7	3	2	3	6	0	1	1	2	2	0	3	1	0	5	0	0
45	HMPOC	31	2	95	7	4	64	39	14	13	27	21	39	23	44	23	62	16	16	27	24	63	22	56	0	2	31	28
46	LMPOC	11	1	35	2	1	60	38	8	12	25	19	35	21	40	19	57	15	14	25	22	58	19	52	0	1	11	11

Table 4.19. Total dependency coefficient matrix (percentages) for Marshyhope Creek, October 2001. Compartments are labeled by overall number and code (see Table 4.1 for definitions).

| #	Name	16	17	18	19	20	21	22	23	24	25	26	27	28	31	32	33	34	35	38	39	42	43	44	45	46
1	BALG	7	5	0	3	3	41	35	15	51	53	19	36	71	3	35	41	45	42	50	39	0	5	7	0	0
2	PICO	4	1	0	28	14	0	0	14	0	0	7	2	0	17	2	0	1	2	1	0	0	1	4	0	0
3	PHYTO	9	2	0	27	39	0	0	28	1	1	21	7	0	36	6	0	3	4	2	0	0	2	9	0	0
4	LROOT	13	0	35	3	1	34	34	5	20	11	17	24	15	2	28	34	22	23	22	33	0	0	13	1	82
5	HROOT	18	0	44	4	2	16	8	5	9	5	5	7	7	2	13	16	9	8	8	13	13	0	18	69	9
6	NULU	7	12	3	5	5	1	3	4	2	4	4	3	1	5	2	1	3	3	2	2	0	12	7	4	1
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
8	ACCA	3	5	1	2	2	1	1	2	1	2	2	1	0	2	1	1	1	1	1	1	6	5	3	2	0
9	POAR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	LEOR	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
11	PEVI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	IMCA	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	SCFL	1	2	0	1	1	0	0	1	0	1	1	1	0	1	0	1	0	0	0	0	2	2	1	1	1
15	OMAC	5	8	2	3	4	1	2	3	2	3	3	2	1	3	1	1	2	2	2	1	8	8	5	3	1
16	FBACT	0	1	0	21	11	0	0	6	0	0	6	2	0	12	2	0	1	1	0	0	0	1	0	0	0
17	PBACT	0	0	0	2	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
18	SBACT	3	0	9	1	0	32	17	9	18	10	8	12	14	1	25	32	17	17	17	26	0	0	3	2	20
19	MICROZ	0	1	0	0	50	0	0	28	1	0	26	7	0	59	8	0	3	4	2	0	0	1	0	0	0
20	MESOZ	0	0	0	0	0	0	0	8	1	0	51	8	0	79	15	0	1	2	2	0	0	0	0	0	0
21	MEIO	0	0	0	0	0	0	37	0	56	32	18	28	44	1	76	98	48	43	46	76	0	0	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	0	38	5	0	0	11	3	19	32	27	32	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	7	10	2	0	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	69	51	46	0	0	0	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	2	2	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	1	5	1	3	0	0	0	0	0
28	PAPU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0
31	ANMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	47	91	21	35	41	9	21	33	18	30	31	24	7	39	16	9	21	21	18	14	0	91	47	30	8
43	SPOC	32	100	5	35	43	3	20	33	16	31	32	23	5	41	12	4	19	20	16	11	0	1	32	5	6
44	DOC	100	1	0	21	11	0	0	6	0	0	6	2	0	12	2	0	1	1	0	0	0	1	0	0	0
45	HMPOC	26	0	63	5	3	23	12	7	13	7	7	10	10	3	18	23	12	12	12	19	0	0	26	1	12
46	LMPOC	15	0	42	3	2	41	41	6	25	13	20	30	18	2	34	41	26	28	27	40	0	0	15	1	8

Table 4.20. Total dependency coefficient matrix (percentages) for Marshyhope Creek, May 2002. Compartments are labeled by overall number and code (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	25	26	27	29	30	31	32	33	34	35	36	37	38	39	42	43	44	45	46
1	BALG	5	2	1	1	1	27	26	16	34	42	16	18	37	22	4	30	21	30	31	31	33	28	26	0	2	5	1	1
2	PICO	7	1	0	27	13	0	0	16	4	0	6	5	4	3	17	2	8	6	5	4	0	6	2	0	1	7	0	0
3	PHYTO	11	1	0	29	39	0	0	17	6	1	20	19	6	9	31	3	9	8	8	7	0	10	7	0	1	11	0	0
4	LROOT	3	0	8	1	0	7	6	2	4	3	3	4	2	5	1	4	4	4	4	4	5	3	5	0	0	3	3	17
5	HROOT	18	0	52	3	2	37	28	11	20	14	17	20	11	28	6	22	23	18	19	20	27	17	28	0	0	18	57	43
6	NULU	5	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	39	0	5	1	0
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
8	ACCA	5	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	35	0	5	0	0
9	POAR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
10	LEOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
11	PEVI	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	2	0	0
12	IMCA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	1	0	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	SCFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
15	OMAC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
16	FBACT	0	0	0	19	9	0	0	3	3	0	4	4	1	2	12	1	2	2	2	3	0	3	1	0	0	0	0	0
17	PBACT	0	0	0	5	2	0	0	12	1	0	1	1	3	0	3	1	6	3	2	1	0	3	3	0	0	0	0	0
18	SBACT	20	0	54	4	2	53	36	18	30	20	22	25	15	38	8	31	34	26	27	29	38	25	39	0	0	20	40	83
19	MICROZ	1	2	1	1	46	0	1	17	13	1	21	19	6	9	62	3	9	12	12	13	1	13	7	0	2	1	1	1
20	MESOZ	0	0	0	0	0	0	0	2	8	0	22	3	3	10	51	1	1	5	5	7	1	5	1	0	0	0	0	0
21	MEIO	0	0	0	0	0	0	24	15	48	39	14	16	15	54	11	50	52	38	39	44	69	32	61	0	0	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	0	19	1	16	20	0	13	3	1	3	2	6	3	7	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	11	8	18	16	0	0	24	0	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	86	0	39	0	0	0	0	0	0
25	GASP	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	39	0	59	66	0	43	16	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	13	9	0	0	4	0	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	0	61	0	8	25	0	0	3	0	0	12	0	17	35	0	0	0	0	0
29	CASA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	6	0	0	0	0	0	0	0	0	0
30	ANRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	ANMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	NOHU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	GOBO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	1	0	1	0	0	1	1	0	1	0	0	0	0	1	0	1	1	0	0	1	1	0	1	0	0	1	1	1
43	SPOC	45	100	39	38	46	29	41	38	33	42	38	35	41	34	41	40	35	36	35	34	35	36	32	0	1	45	39	38
44	DOC	100	1	0	19	9	0	0	3	3	0	4	4	1	2	12	1	2	2	2	3	0	3	1	0	1	0	0	0
45	HMPOC	32	0	92	6	3	66	49	20	36	25	31	34	19	49	11	38	41	32	33	36	47	30	50	0	0	32	37	77
46	LMPOC	17	0	45	3	2	40	32	12	25	16	20	22	12	31	6	24	25	21	22	25	29	20	32	0	0	17	18	37

Table 4.21. Total dependency coefficient matrix (percentages) for Marshyhope Creek, August 2002. Compartments are identified by number and abbreviated species codes (see Table 4.1 for definitions).

#	Name	16	17	18	19	20	21	22	23	24	26	27	28	29	31	33	34	35	36	37	38	39	41	42	43	44	45	46
1	BALG	2	5	0	1	2	39	31	9	23	11	18	28	51	4	39	26	25	24	36	27	40	42	0	5	2	0	0
2	PICO	11	9	0	34	20	0	2	29	14	14	10	4	4	22	0	7	10	10	1	5	1	1	0	9	11	0	0
3	PHYTO	2	8	0	32	47	0	2	27	19	33	24	4	5	41	1	10	14	16	4	7	2	2	0	8	2	0	0
4	LROOT	1	1	3	0	0	0	3	1	2	1	2	2	1	0	4	3	2	2	1	2	3	3	0	0	1	1	8
5	HROOT	26	3	50	6	4	29	25	11	14	11	17	14	1	6	29	21	18	17	28	14	25	25	0	3	26	51	46
6	NULU	3	1	0	1	0	0	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	1	1	3	0	0
7	ZIAQ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	ACCA	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
9	POAR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
10	LEOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	PEVI	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
12	IMCA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	BISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	SCFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	OMAC	1	0	0	0	0	0	1	7	9	10	7	4	3	15	0	4	6	7	1	4	1	1	0	7	1	0	0
16	FBACT	0	7	0	23	14	0	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0
17	PBACT	0	1	0	2	0	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	SBACT	21	4	45	5	3	57	44	19	25	17	25	26	11	7	56	35	30	29	53	26	48	47	0	4	21	29	94
19	MICROZ	0	9	0	2	56	0	2	27	38	38	27	5	5	62	1	16	25	27	1	8	2	2	0	9	0	0	0
20	MESOZ	0	0	0	0	0	0	0	17	20	62	14	0	3	72	0	8	12	13	0	5	1	1	0	0	0	0	0
21	MEIO	0	4	0	1	1	0	26	3	15	9	13	44	15	8	98	21	18	17	76	39	73	73	0	4	0	0	0
22	MBENTH	0	0	0	0	0	0	0	0	0	25	6	0	6	0	2	57	31	25	33	6	19	15	0	0	0	0	0
23	COFL	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	3	0	0	4	0	1	0	0	0	0	0
24	COSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	49	51	0	4	0	0	0	0	0	0	0
26	ODLRV	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	6	0	0	0	0	0	0	0
27	OINVT	0	0	0	0	0	0	0	0	0	16	0	0	1	0	1	14	17	26	0	3	6	6	0	0	0	0	0
28	PAPU	0	7	0	1	2	0	1	1	1	2	1	3	31	2	0	1	1	1	1	83	7	7	0	7	0	0	0
29	CASA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	ANMI	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
33	FUDIS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	FUDIL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	FUHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	GAHO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	GOBO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	MOAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	ETOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	TRMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	MDET	50	74	47	24	26	28	37	24	29	29	28	47	33	26	28	33	30	31	31	45	28	27	0	74	50	48	45
43	SPOC	3	100	3	19	28	2	20	18	20	24	16	49	38	24	3	20	19	19	8	45	7	6	0	6	3	3	4
44	DOC	100	7	0	23	14	0	1	7	9	10	7	4	3	15	0	4	6	7	1	4	1	1	0	7	0	0	0
45	HMPOC	52	6	98	12	8	57	50	21	27	22	34	27	13	12	57	41	35	34	55	28	50	49	0	6	52	28	92
46	LMPOC	13	3	32	3	2	46	41	13	23	15	22	21	9	5	46	33	28	27	44	21	40	39	0	3	13	9	30

Figure 4.7 a – e. Dependency coefficients (percentage) for *Fundulus diaphanus* < 35 mm TL. Dependency coefficients estimate the fraction of killifish consumption that was mediated by one of these six compartments.
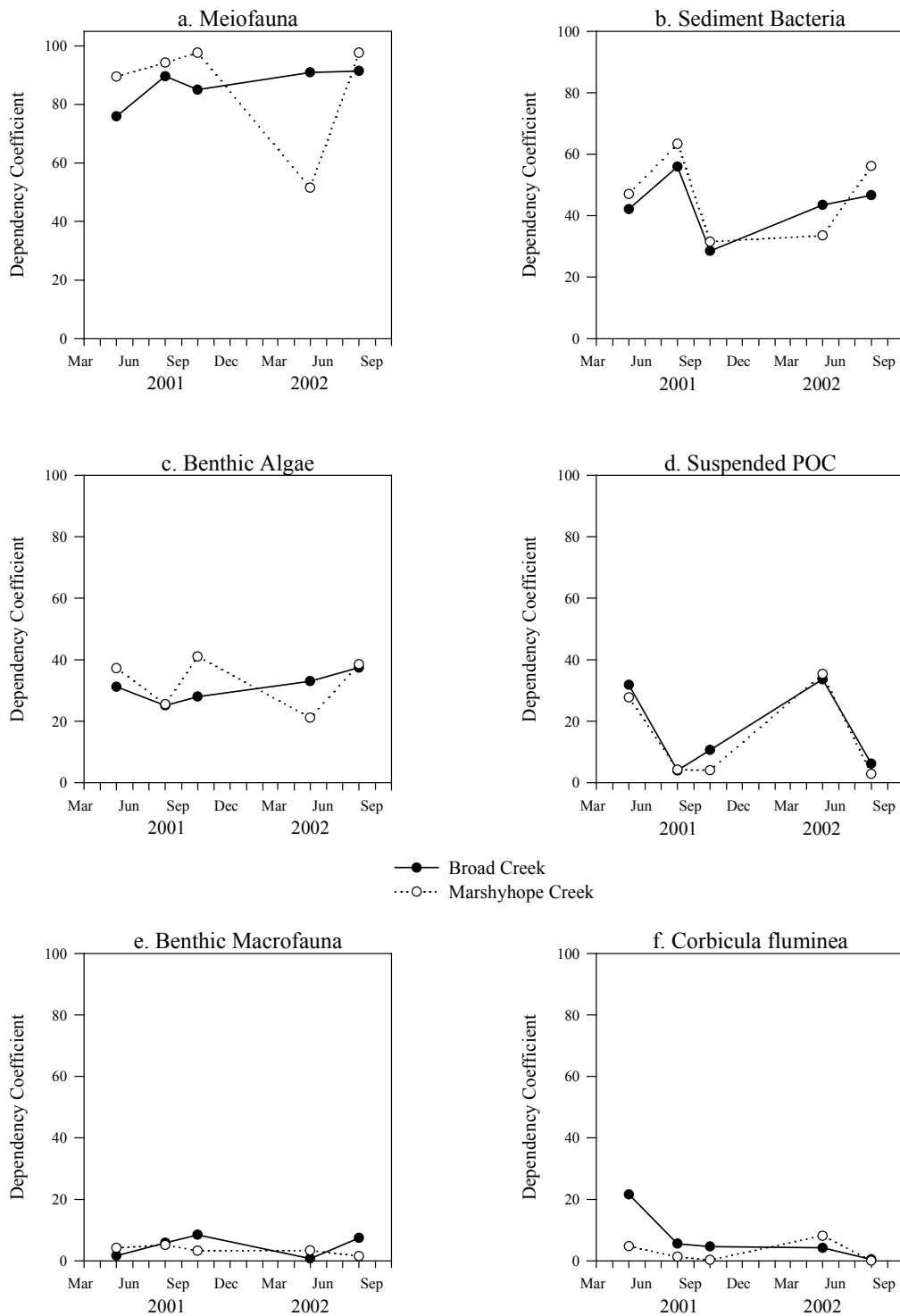
Algae indirectly mediate between 20 – 60 percent of the carbon ingested by the smaller killifish (Figures 4.7 b and c). Yet the dependency coefficients do not distinguish the creeks from each other, nor do they evidence a strong seasonal shift in dietary sources of carbon. In the larger banded killifish, *F. diaphanus* > 35 mm, TDC suggests a substantial difference in carbon pathways between the creeks. *Corbicula fluminea* and Corixidae mediated much of the carbon entering this compartment (Figures 4.8 a – d). Dependence, however, on these two compartments between the creeks is inverted. *F. diaphanus* > 35 mm TL in Broad Creek always had higher dependency on carbon that passed through the Asian clam, while Marshyhope Creek dependency coefficients were always larger for Corixidae, reflecting the higher availability of this prey item there (Figures 4.8 a and b).

Fundulus heteroclitus demonstrated similar dependencies on Corixidae and *Corbicula fluminea*. Broad Creek mummichog dependencies were always greater on *Corbicula fluminea*, while the same fish in Marshyhope Creek were more dependent on Corixidae (Figure 4.9 a and d). Trajectories of dependency are fairly uniform across creeks except for notable changes in two cases. In Corixidae dependencies in August 2002 proceed in opposite directions (declining in MC and rising in BC) (Figure 4.9d). The fraction of ingestion passing through Meiofauna is often greater in Marshyhope Creek, but drops by over 20 percentage points in both August 2001 and August 2002 from previous levels (Figure 4.9e).

The dependencies of the fourth fish compartment, *Etheostoma olmstedi*, do not differ in a uniform manner between the creeks. Across the six compartments that

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Figure 4.8 a – f. Dependency coefficients (percentage) for *Fundulus diaphanus* > 35 mm TL. Dependency coefficients estimate the fraction of killifish consumption that was mediated by one of these six compartments.
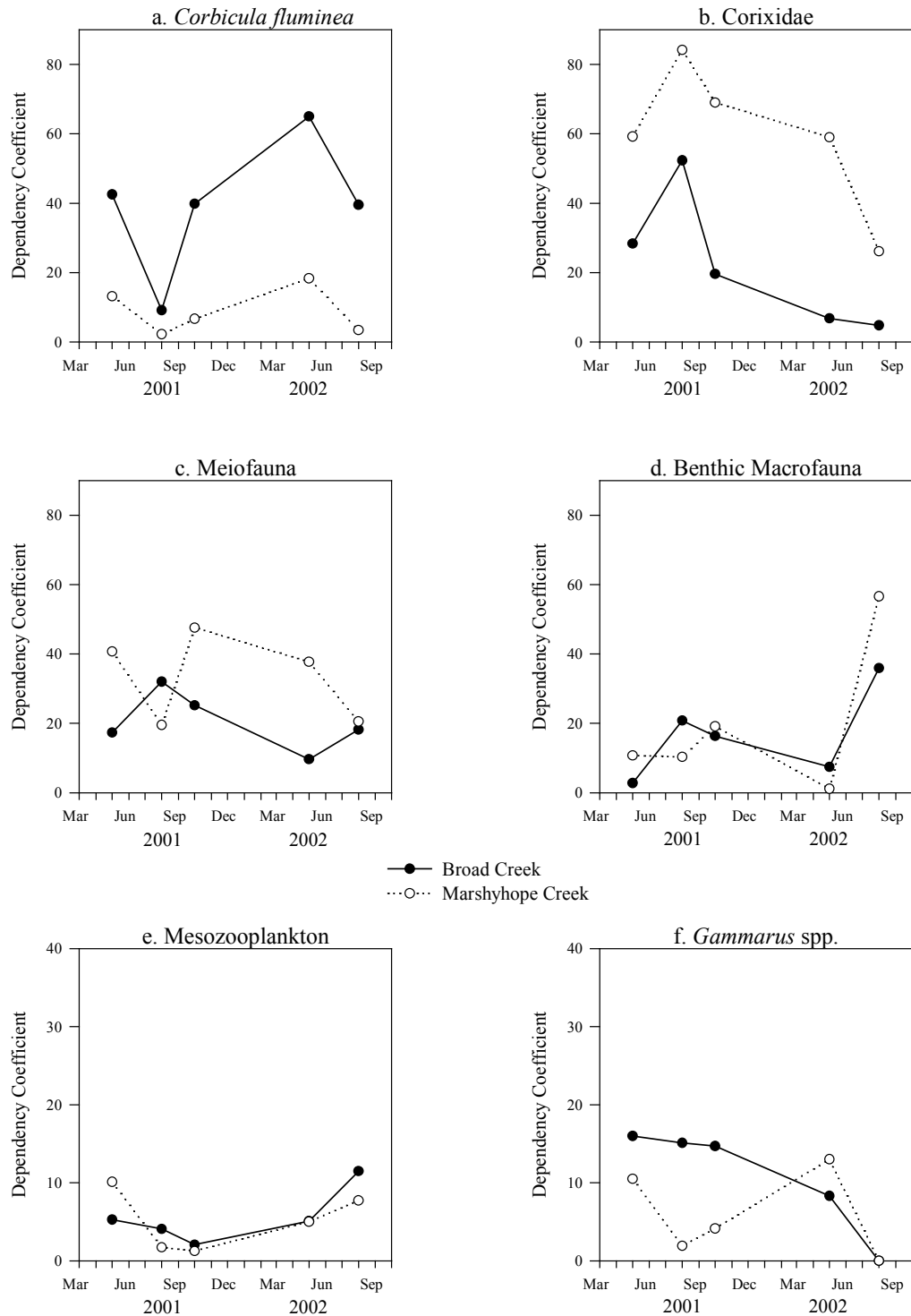
Figure 4.9 a – f. Dependency coefficients (percentage) for *Fundulus heteroclitus*. Dependency coefficients estimate the fraction of mummichog consumption that was processed by one of these six compartments.
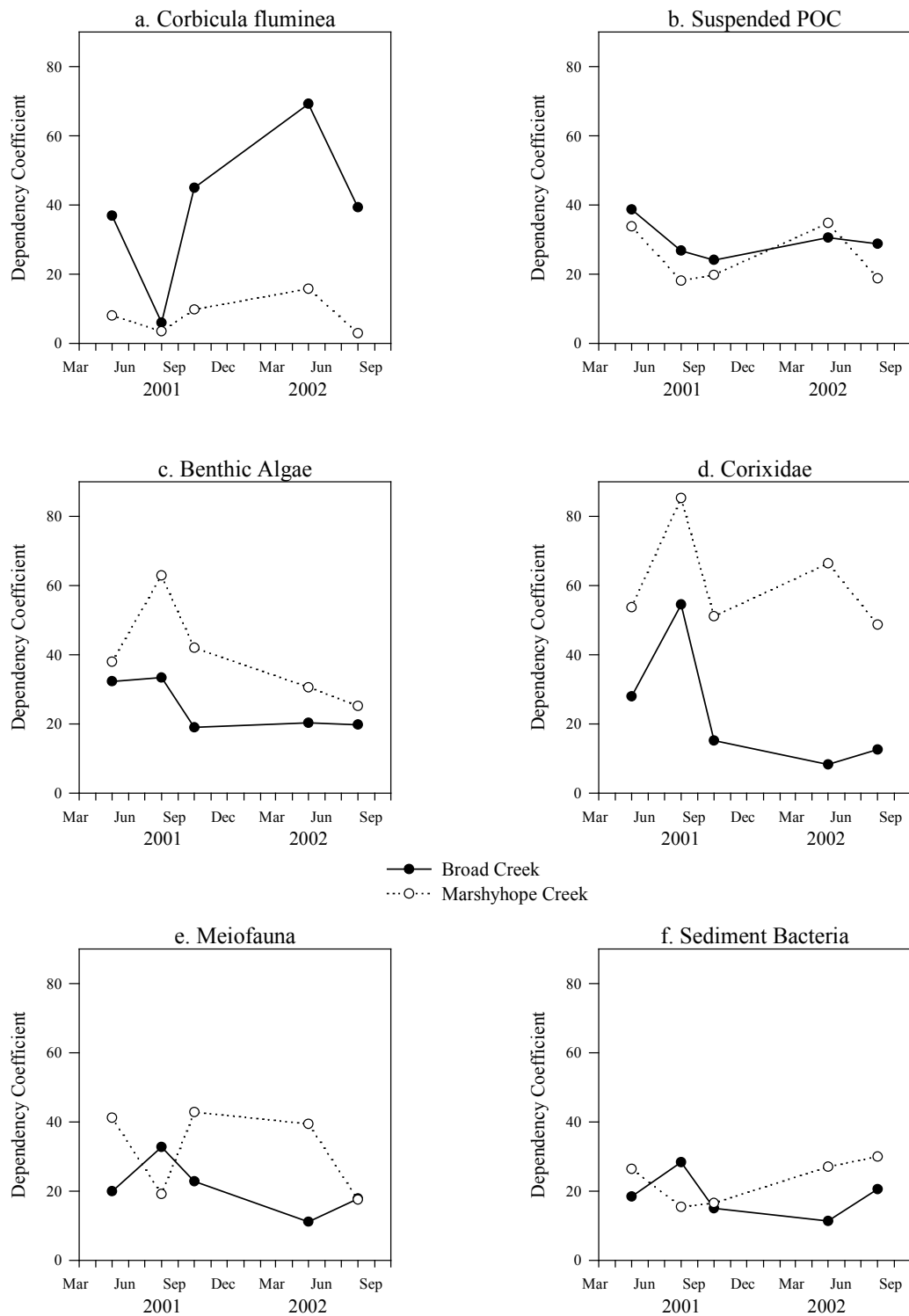
mediated much of the darter's diet, the dependencies were usually within 10 percentage

points across all dates (Figure 4.10 a – d). The notable differences were in August 2002,

where in four of the six examples trajectories diverged between the creeks (Figures 4.10

a, b, c and e). While dependency on Benthic Macrofauna increased for the fish in both

creeks in August 2002, the dependency coefficient was substantially larger for *E.*

olmstedi in Broad Creek.

<u>Lindeman Analysis</u>

   The effective trophic position of each species is another potential indicator of

stress in an ecosystem, with less material reaching the upper trophic levels in degraded

ecosystems (Ulanowicz 1996). All compartments consuming at intermediate levels

exhibit variability across seasons and creeks, but with few obvious trends (Table 4.22).

Graphical depictions of the dominant taxa suggest some differences in the trophic

positions of some organisms. Both *F. diaphanus* > 35 mm and *F. heteroclitus* tended to

have higher trophic positions in Marshyhope Creek than Broad Creek except in August

2001 and August 2002 (Figure 4.11 a and b). The sharp declines in August 2001 coincide

with the drop in Corixidae average trophic level. The two fish compartments have a high

dependency on Corixidae, and their decline in trophic position reflects this (see Figures

4.8b and 4.9d). The other four compartments show rather remarkable similarities across

the study, particularly during 2001. But in 2002, five of the six compartments

experienced shifts in trophic position (Figures 4.11 a – f).

Figure 4.10 a – f. Dependency coefficients (percentage) for *Etheostoma olmstedi*. Dependency coefficients estimate the fraction of darter consumption that was mediated by one of these six compartments.

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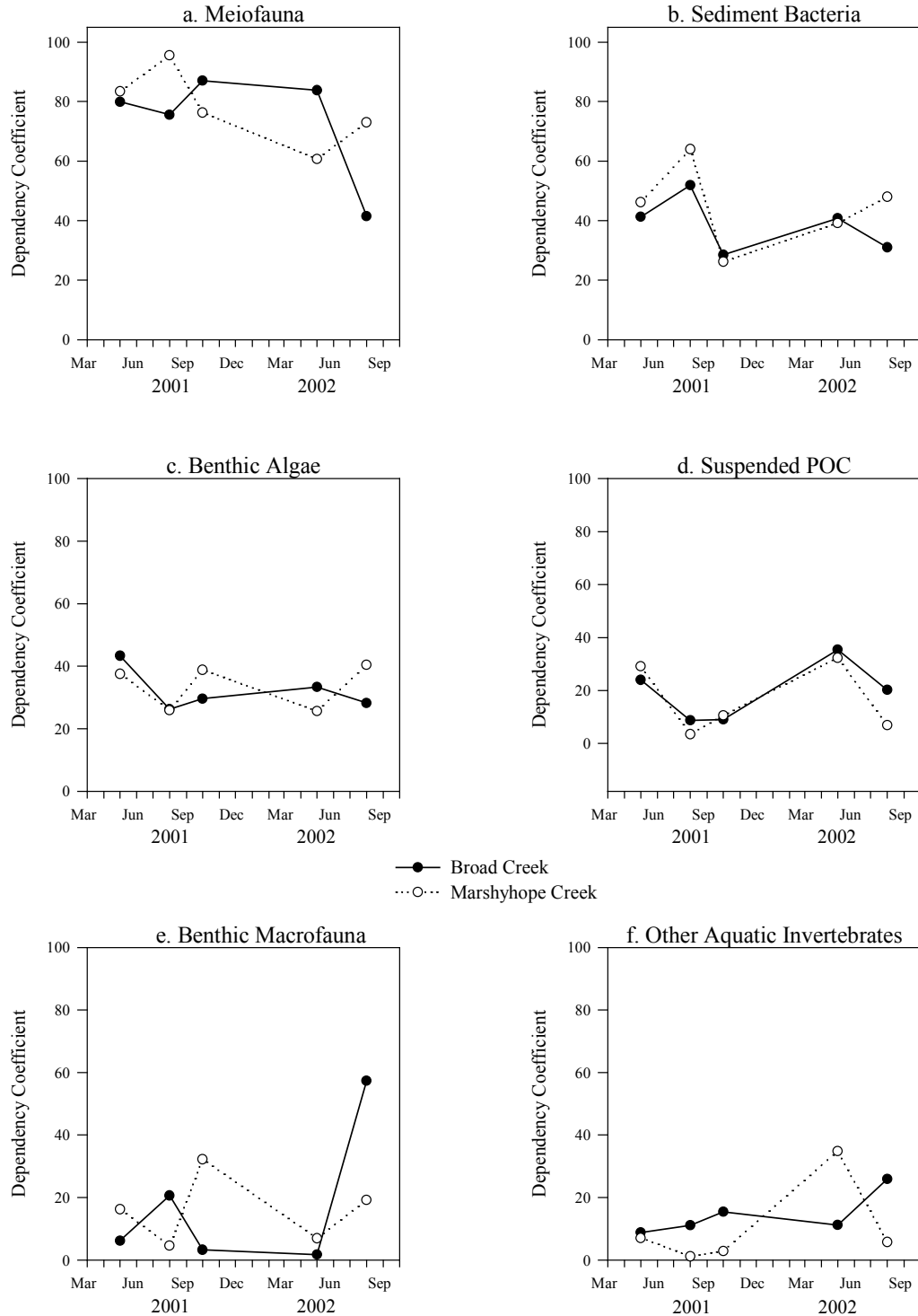
Table 4.22. Effective trophic positions of consumer organism compartments. These values represent the average trophic level at which each compartment receives carbon. Entries represented by dots indicate compartment was not present in the trophic networks during that time period.

		Broad Creek					Marshyhope Creek				
#	Name	May 01	Aug 01	Oct 01	May 02	Aug 02	May 01	Aug 01	Oct 01	May 02	Aug 02
16	Free Bacteria	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
17	POC Bacteria	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
18	Sediment Bacteria	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
19	Microzooplankton	2.39	2.34	2.20	2.21	2.25	2.23	2.22	2.23	2.23	2.23
20	Mesozooplaknton	2.68	2.58	2.54	2.56	2.50	2.62	2.60	2.60	2.56	2.67
21	Meiofauna	2.31	2.20	2.23	2.14	2.29	2.19	2.20	2.24	2.20	2.19
22	Macrobenthos	2.29	2.31	2.34	2.31	2.34	2.35	2.32	2.45	2.29	2.30
23	Corbicula fluminea	2.77	2.60	2.49	2.59	2.71	2.70	2.66	2.57	2.60	2.64
24	Corixidae	2.83	2.60	2.60	2.87	2.87	2.85	2.25	2.70	2.80	2.82
25	*Gammarus* sp.	2.38	2.49	2.49	2.46	.	2.53	2.50	2.37	2.46	.
26	Odonate larvae	3.65	3.52	3.45	3.46	3.51	3.61	3.51	3.54	3.44	3.58
27	Other Insects	2.69	2.62	2.52	2.44	2.90	2.81	2.75	2.54	2.45	2.67
28	*Palaemonetes pugio*	.	.	.	.	2.47	.	2.42	2.52	.	2.50
29	*Calinectes sapidus*	.	.	.	.	.	.	.	.	3.07	2.62
30	*Anguilla rostrata*	3.35	3.25	.	3.22	3.37	3.36	3.38	.	3.31	.
31	*Anchoa mitchilli*	.	.	3.38	3.31	3.46	.	.	3.53	3.39	3.54
32	*Notropis hudsonius*	3.61	.	3.36	3.46	3.40	3.37	3.51	3.33	3.29	.
33	*Fundulus diaphanus* < 35	3.40	3.24	3.26	3.13	3.27	3.25	3.21	3.25	3.37	3.19
34	*Fundulus diaphanus* >35	3.62	3.53	3.48	3.44	3.58	3.74	3.28	3.62	3.68	3.50
35	*Fundulus heteroclitus*	3.67	3.52	3.48	3.56	3.74	3.70	3.28	3.59	3.70	3.61
36	*Gambusia holbrooki*	3.64	3.55	3.48	3.58	3.68	3.78	3.43	.	3.75	3.65
37	*Gobiosoma bosc*	.	.	.	.	.	.	.	.	3.32	3.23
38	*Morone americana*	3.94	.	.	3.58	3.69	3.80	3.42	3.60	3.66	3.58
39	*Etheostoma olmstedi*	3.22	3.26	3.26	3.12	3.47	3.25	3.21	3.30	3.23	3.14
40	*Lepomis macrochirus*	.	3.61	3.6	3.66	3.80	.	3.59	.	.	.
41	*Trinectes maculatus*	.	.	.	.	3.37	.	3.20	.	.	3.12

Figure 4.11 a – f. Effective trophic positions of six dominant consumer organism compartments. These values represent the average trophic level at which each compartment receives carbon in both creeks across all dates.
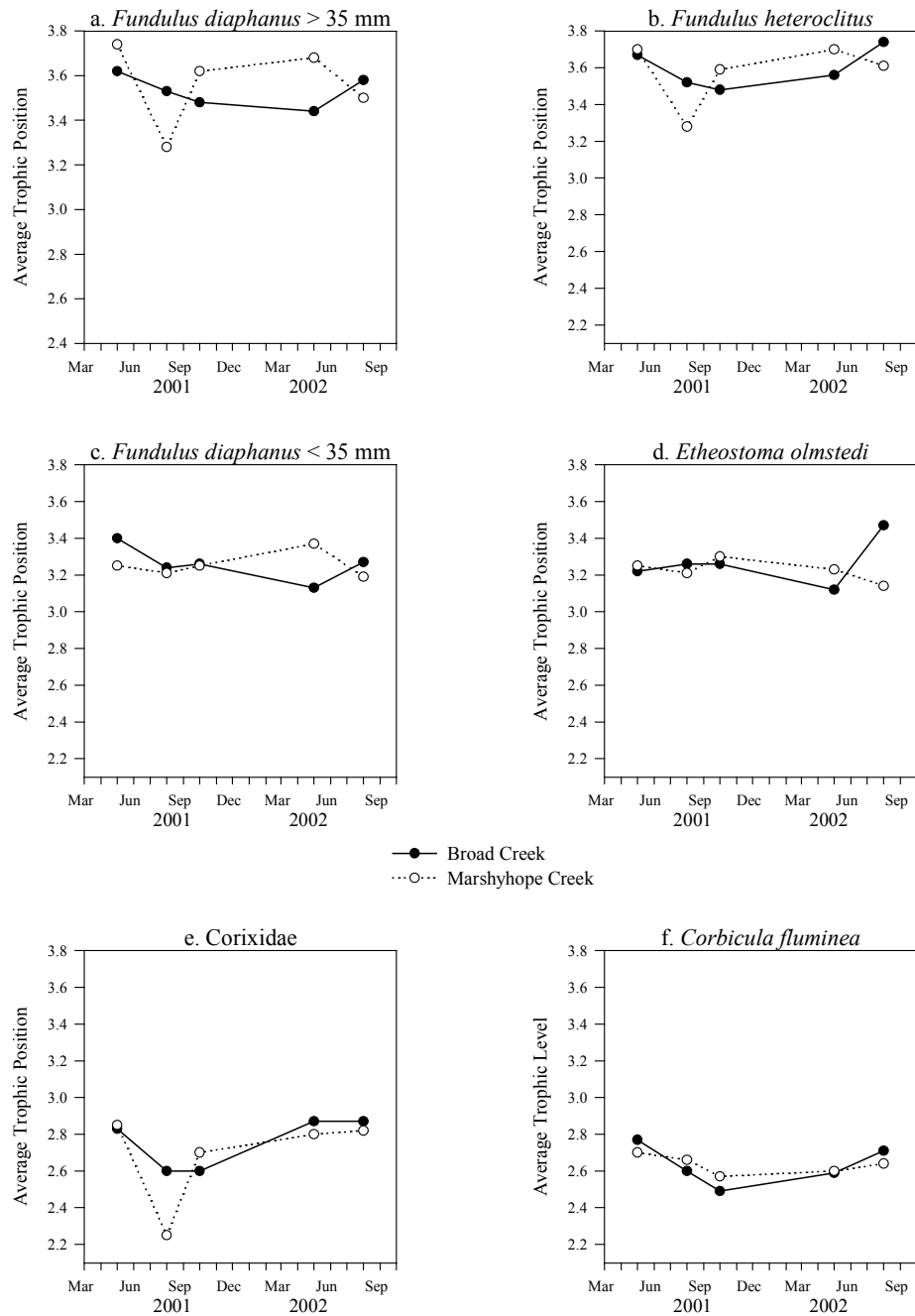
The linear food chains derived from the trophic networks suggest few uniform differences between these creeks. There were no differences in the number of trophic levels between the creeks on any date, with every network in both creeks resulting in linear chains seven trophic levels long (Figures 4.12 – 4.16).

There was no consistent pattern to carbon transfers in the networks. In May 2001 and August 2001 Marshyhope Creek, more carbon passed from trophic level I to level II than in Broad Creek (Figure 4.12 and 4.13). But total input to the second trophic level was greater in Broad Creek due to the larger available detrital pool in Broad Creek. Interestingly, the transfers to trophic levels IV and higher in Marshyhope Creek exceeded those in Broad Creek in May 2001 (Figure 4.12). By August 2001, all transfers from trophic levels II and up were greater in Broad Creek (Figure 4.13). In October 2001, carbon flow in Broad Creek from primary producers to trophic level II was greater, but the intermediate transfers from levels II to III and III to IV were greater in Marshyhope Creek supplemented by slightly more detrital input to trophic level II (Figure 4.14). Transfers at higher trophic levels then became larger in Broad Creek and continued through trophic level VII. In Marshyhope Creek in 2002, unlike the previous three networks in that creek, more carbon passed from the primary producers to the second trophic level than in Broad Creek. In May 2002, this pattern continued on all transfers to higher trophic levels except those to level VII where Broad Creek processed more carbon (Figure 4.15). And by August 2002, transfers in both creeks above trophic level IV were almost identical (Figure 4.16).

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Figure 4.12. Linear food chains of discrete trophic levels aggregated from May 2001 networks. All flows are g carbon m^{-2} y^{-1}.
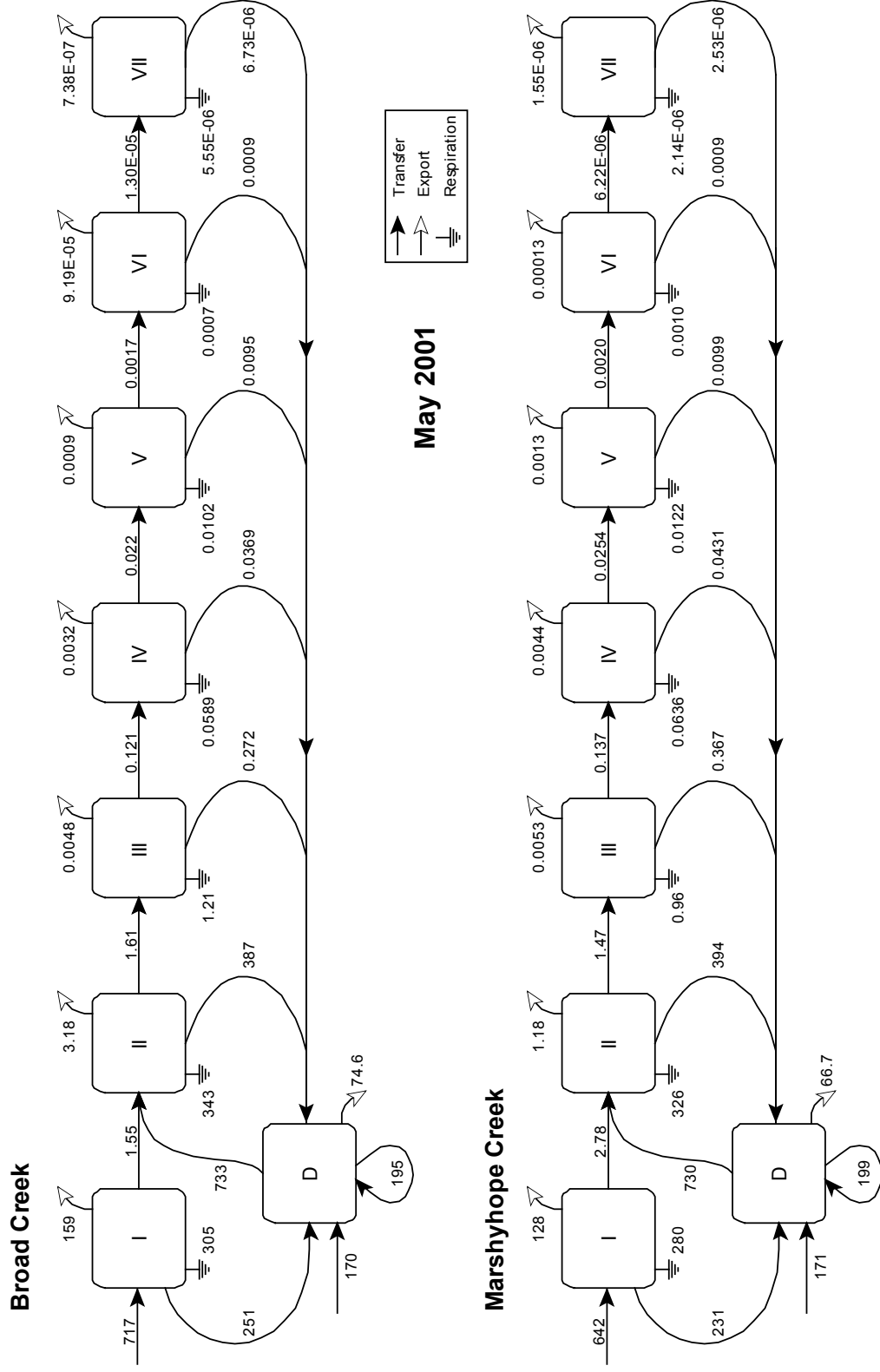
Figure 4.13. Linear food chains of discrete trophic levels aggregated from August 2001 networks. All flows are g carbon m^{-2} y^{-1}.
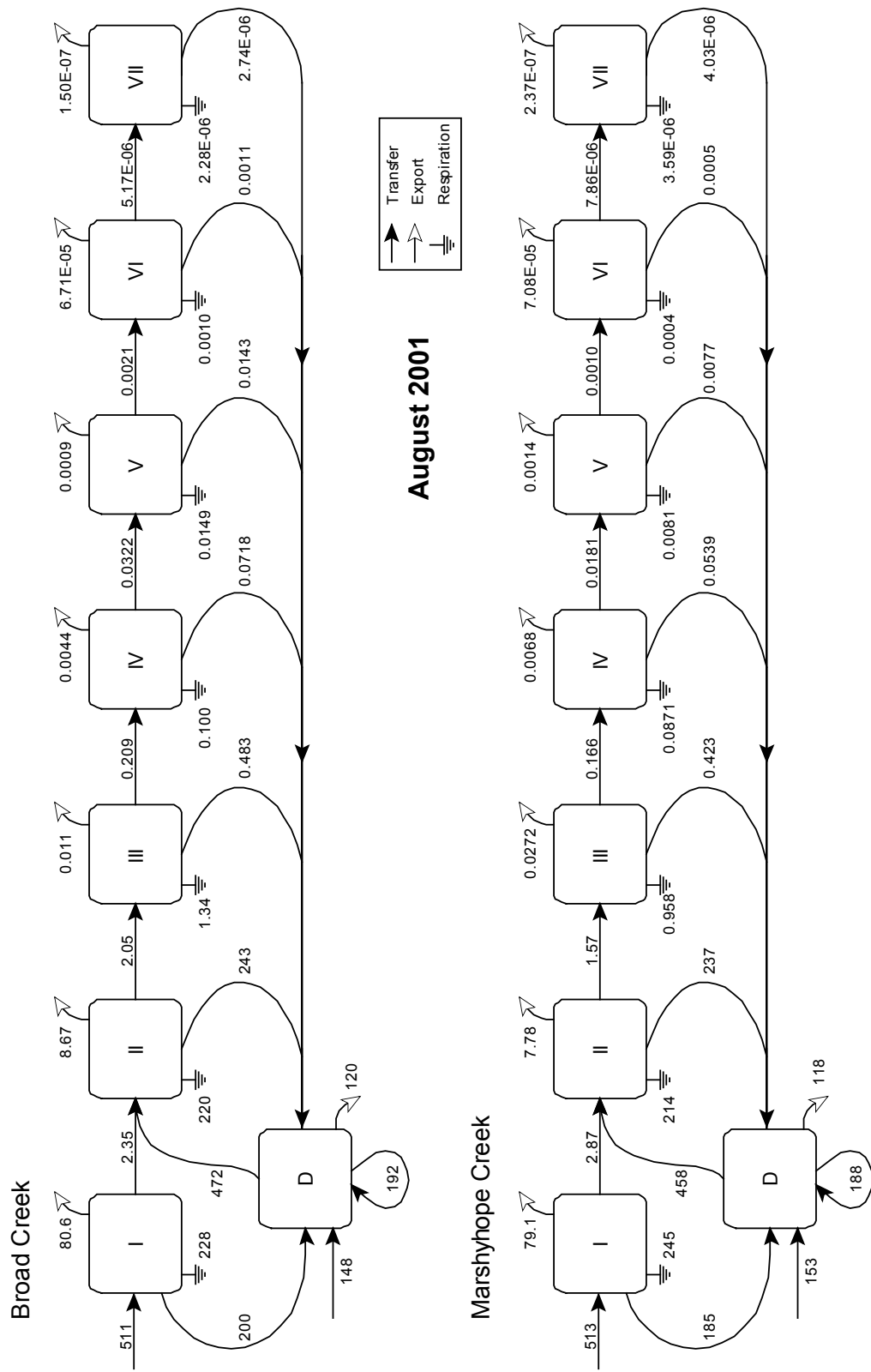
Figure 4.14. Linear food chains of discrete trophic levels aggregated from October 2001 networks. All flows are g carbon m^{-2} y^{-1}.
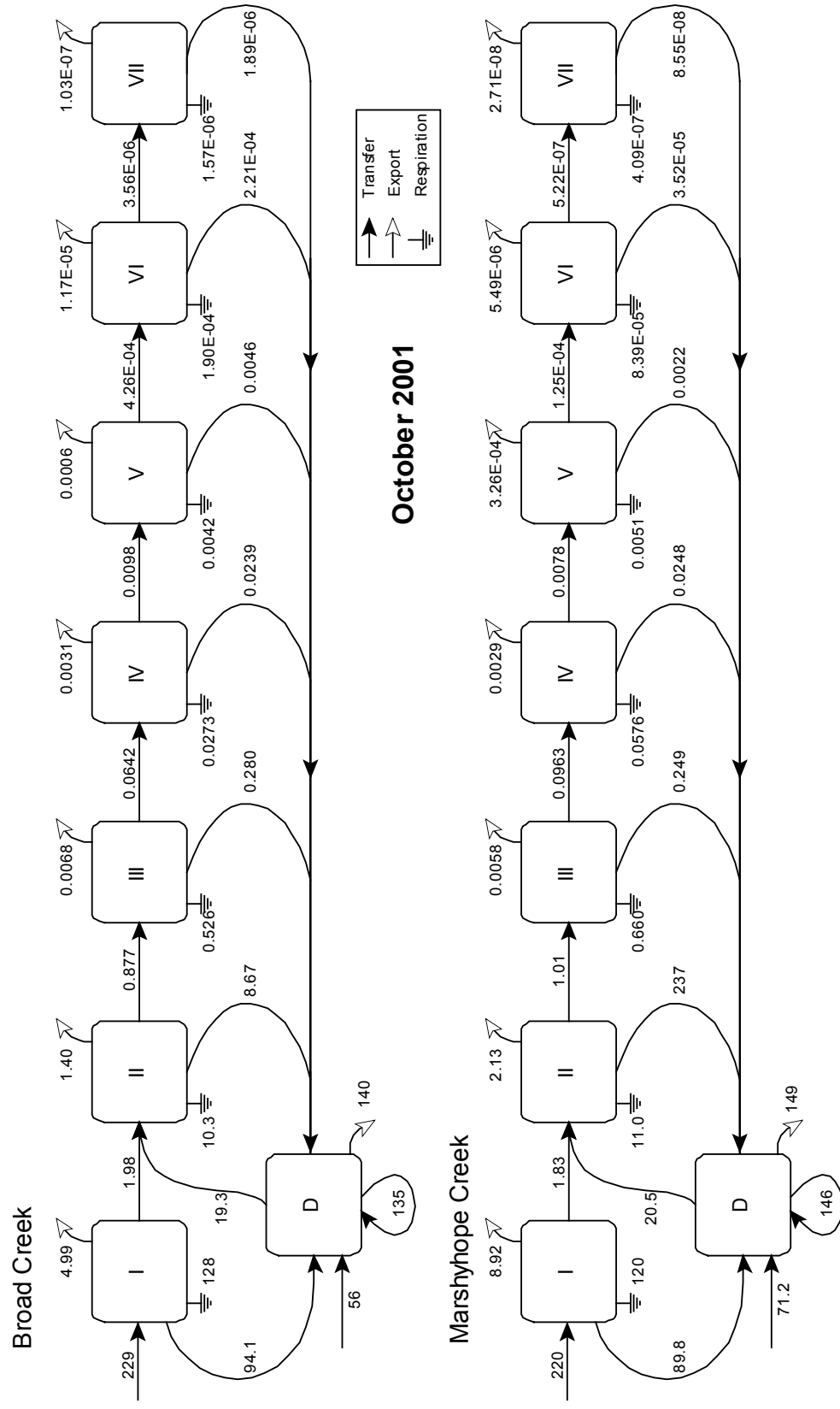
Figure 4.15. Linear food chains of discrete trophic levels aggregated from May 2002 networks. All flows are g carbon m^{-2} y^{-1}.
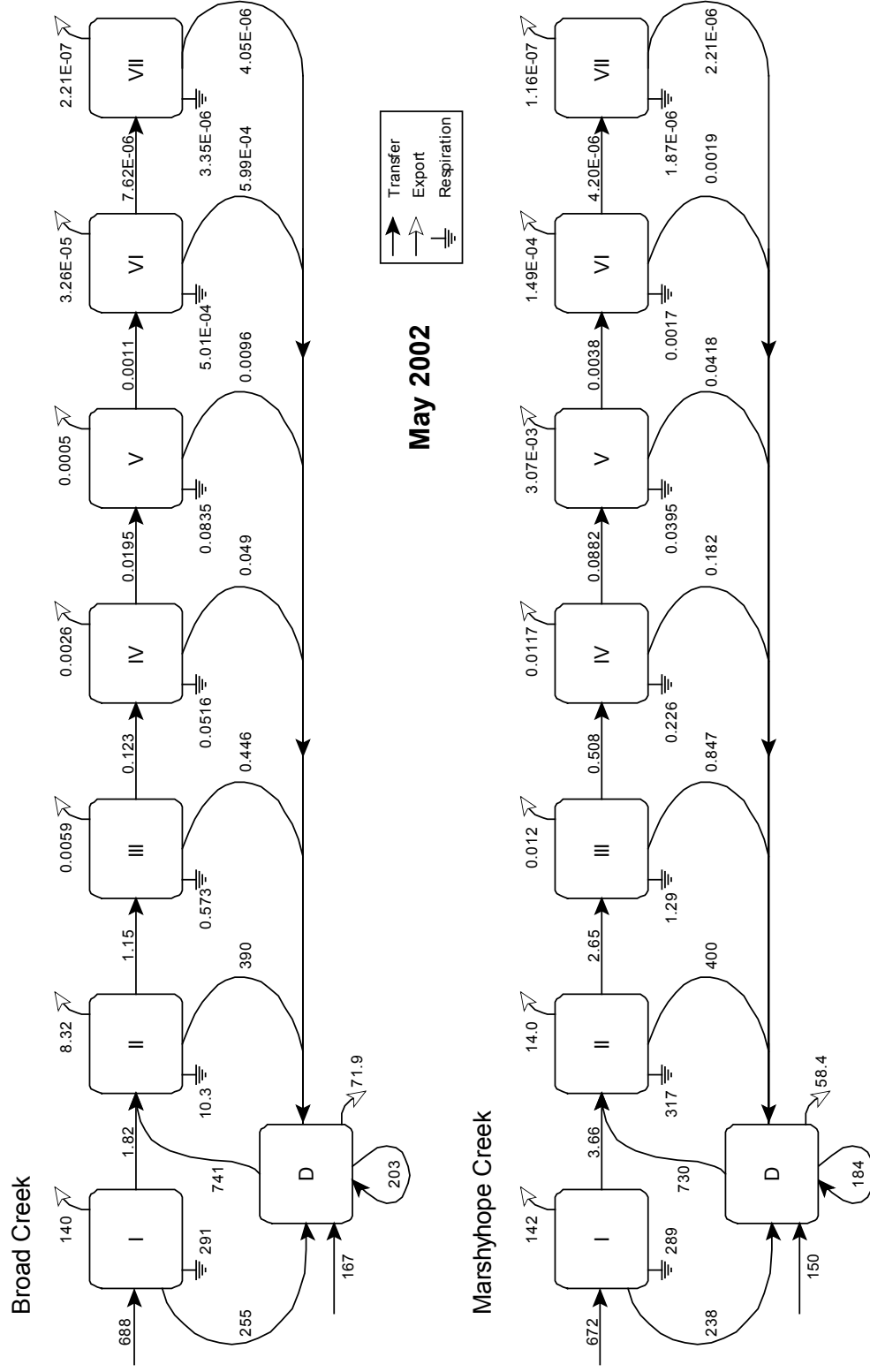
Figure 4.16. Linear food chains of discrete trophic levels aggregated from August 2002 networks. All flows are g carbon m^{-2} y^{-1}.
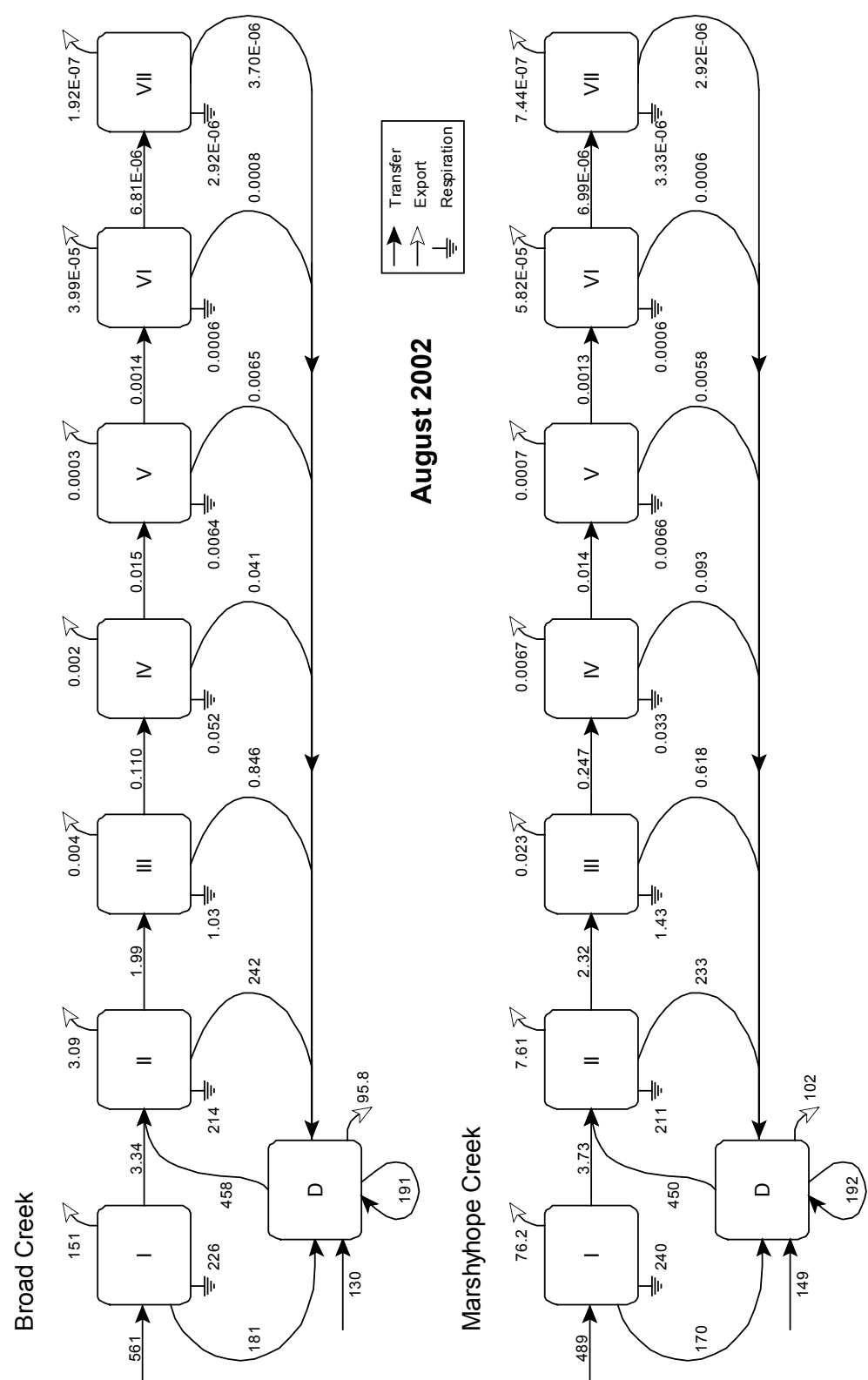
Trophic efficiencies varied to a small extent across the study. Seasonal differences were fairly uniform across both creeks and account for most variation. Yet there are some interesting differences that emerged in the higher trophic levels where it appeared that efficiencies at higher trophic levels declined over time in Marshyhope Creek (Table 4.23). Degradation of these trophic efficiencies suggests changes in ecosystem function, often resulting from stress applied to the system, in this case likely being salinity.

May 2001 and August 2001 networks exhibited similar efficiencies for all higher trophic levels (Figure 4.17 a and b). In October 2001, Marshyhope Creek deviated from the previous pattern, lacking an increase in efficiency from trophic level III to IV before declining again in the upper levels (Figure 4.17c). Aside from trophic level three, all Marshyhope efficiencies were less than the corresponding measures in Broad Creek. In May 2002, Marshyhope continued to have higher ecotrophic efficiency in trophic level II, but the higher levels were very similar between the creeks (Figure 4.17d). In August 2002, efficiencies were over five percentage points higher in Marshyhope Creek in trophic level III, but the relationship flipped for the fourth trophic level with Broad Creek efficiency more than seven percentage points greater than Marshyhope Creek (Figure 4.17e). From August 2001 onward, Broad Creek trophic efficiencies were always greater in trophic level V than in Marshyhope Creek.

Table 4.23. Ecotrophic efficiencies of linear trophic chains. Trophic efficiency is the ratio of the input to a trophic level to the amount that level passes on to the next. Since detritus and primary production are both functionally in trophic level I, they have been combined to calculate the ratios for that level.

Broad Creek

Trophic Level	May 01	Aug 01	Oct 01	May 02	Aug 02
1	57.7%	52.5%	7.2%	59.6%	49.4%
2	0.2%	0.4%	4.1%	0.2%	0.4%
3	7.5%	10.2%	7.3%	10.7%	5.5%
4	18.4%	15.4%	15.3%	15.9%	13.3%
5	7.5%	6.7%	4.3%	5.8%	9.8%
6	0.8%	0.2%	0.8%	0.7%	0.5%

Marshyhope Creek

Trophic Level	May 01	Aug 01	Oct 01	May 02	Aug 02
1	60.7%	51.0%	7.5%	60.0%	52.1%
2	0.2%	0.3%	4.5%	0.4%	0.5%
3	9.3%	10.5%	9.5%	19.1%	10.6%
4	18.6%	10.9%	8.1%	17.4%	5.8%
5	7.9%	5.6%	1.6%	4.3%	8.8%
6	0.3%	0.8%	0.4%	0.1%	0.6%

Figure 4.17 a – e. Trophic efficiencies of linear trophic chains. Trophic efficiency is the ratio of the input to a given trophic level to the amount that level passes on to the next. Since detritus and primary production are both functionally in trophic level I, they have been combined to calculate the ratios for that level.
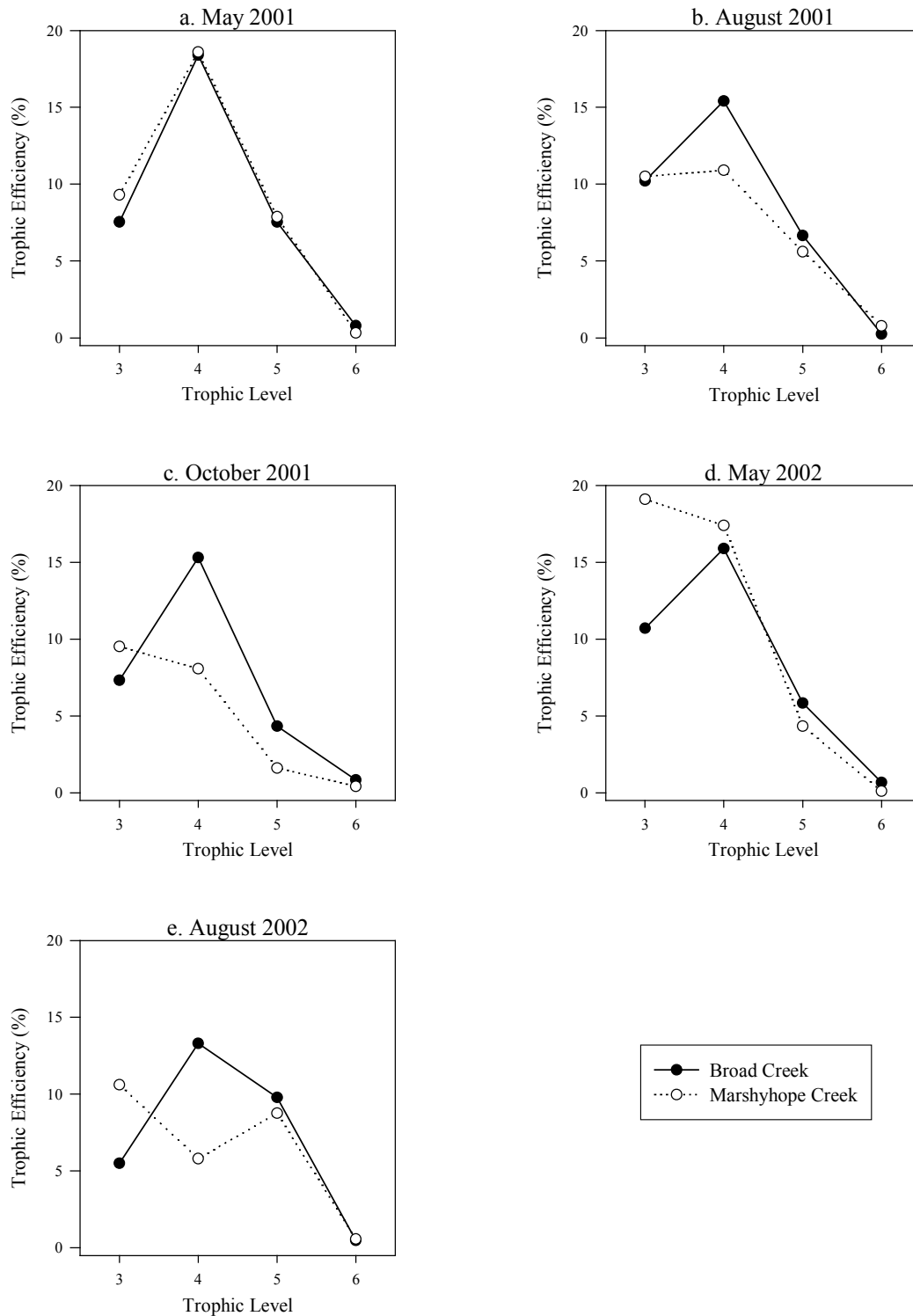
The network measures reflect the significant seasonal variation in the organization and activity of the tidal freshwater marshes. All measures achieved their highest values in May in both years, due to the massive aboveground biomass production of macrophytes (Figures 4.18 a – f). The only notable deviations between the creeks occurred in August 2002, when C increases are reflected in the apparent changes in Φ_I and Φ_E (Figures 4.18 a, e and f – Actual values for all indices appear in Table 4.24). Internal development capacity (C_i) and ascendency (A_i), which only consider the contributions of the internal exchanges among the network compartments, do not distinguish the creeks from each other. Only in 2002 was there a noticeable increasing separation between the two creeks (Figure 4.19).

It is possible that TST can overwhelm interpretation of the absolute values of the network indices, and it is valuable to consider their constituent parts by factoring out TST from the measures of A and Φ and also examining the relative proportions the indices comprise of development capacity. TST provided most of the seasonal fluctuations present in the networks (Figure 4.18a). Broad Creek TST was 3343.1 g carbon m^{-2} y^{-1} in May 2002, fell by about one-third during August and dropped to 830.2 g carbon m^{-2} y^{-1} in October 2001 (Table 4.24). Marshyhope Creek followed the trend almost identically although the magnitudes of TST were usually smaller. Both creeks repeated the pattern the following year through August 2002.

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Figure 4.18 a – f. Network system level indices. The global attributes of each network are plotted out across the time span of the study, tracking changes over time. Developmental capacity is presented first, followed by its five constituent elements: ascendancy, redundancy, and overhead from dissipations, inputs and exports.
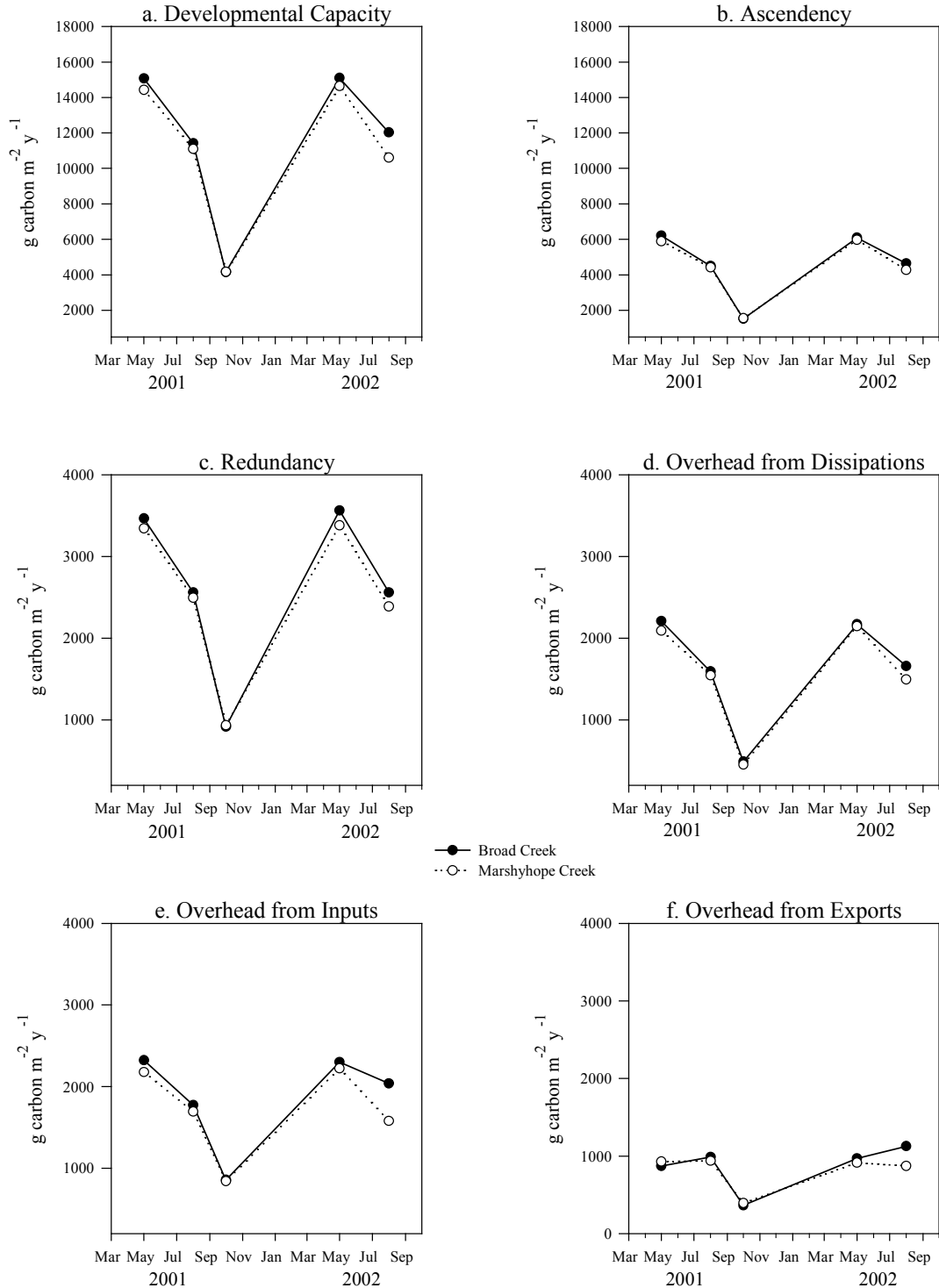
Table 4.24. Network Analysis indices of Broad Creek and Marshyhope Creek (Units for non-ratio terms are g carbon m^{-2} y^{-1}; bits).

Information Index	BCMay01	BCAug01	BCOct01	BCMay02	BCAug02	MCMay01	MCAug01	MCOct01	MCMay02	MCAug02
TOTAL SYSTEM THROUGHPUT	3343.1	2431.2	830.2	3304.3	2459.1	3184.2	2406.2	851.2	3203.9	2327.2
DEVELOPMENT CAPACITY	15075.0	11414.0	4150.5	15092.0	12020.0	14425.0	11090.0	4168.0	14635.0	10601.0
ASCENDENCY	6203.1	4498.7	1524.3	6088.0	4638.0	5886.5	4419.2	1546.3	5971.2	4268.5
OVERHEAD ON IMPORTS	2321.8	1773.5	857.0	2299.7	2038.9	2177.3	1694.5	842.5	2222.5	1578.7
OVERHEAD ON EXPORTS	872.6	987.6	364.4	970.4	1125.6	927.1	938.3	393.9	913.1	871.6
DISSIPATIVE OVERHEAD	2211.0	1593.3	488.8	2170.9	1658.6	2090.8	1544.5	452.3	2146.8	1494.2
REDUNDANCY	3466.0	2561.0	916.1	3563.2	2559.3	3343.1	2493.8	933.1	3381.5	2387.6
AMI	1.855	1.850	1.836	1.842	1.886	1.849	1.837	1.817	1.864	1.834
Φ / TST	2.654	2.844	3.164	2.725	3.002	2.681	2.772	3.080	2.704	2.721
INTERNAL CAPACITY	6513.9	4822.4	1515.4	6696.5	4903.2	6372.1	4660.7	1528.9	6459.6	4486.1
INTERNAL ASCENDENCY	3047.9	2261.4	599.3	3133.4	2344.0	3029.0	2166.9	595.9	3078.1	2098.5
A/C	41.1%	39.4%	36.7%	40.3%	38.6%	40.8%	39.8%	37.1%	40.8%	40.3%
Φ$_I$/C	15.4%	15.5%	20.6%	15.2%	17.0%	15.1%	15.3%	20.2%	15.2%	14.9%
Φ$_E$/C	5.8%	8.7%	8.8%	6.4%	9.4%	6.4%	8.5%	9.5%	6.2%	8.2%
Φ$_D$/C	14.7%	14.0%	11.8%	14.4%	13.8%	14.5%	13.9%	10.9%	14.7%	14.1%
R/C	23.0%	22.4%	22.1%	23.6%	21.3%	23.2%	22.5%	22.4%	23.1%	22.5%
A$_i$/C$_i$	46.8%	46.9%	39.5%	46.8%	47.8%	47.5%	46.5%	39.0%	47.7%	46.8%
R$_i$/C$_i$	53.2%	53.1%	60.5%	53.2%	52.2%	52.5%	53.5%	61.0%	52.3%	53.2%
Other Measures										
OVERALL CONNECTANCE	1.756	1.83	1.79	1.825	1.84	1.793	1.808	1.778	1.796	1.794
INTERCOMPARTMENTAL CONNECTANCE	1.851	1.835	2.395	1.834	1.87	1.795	1.842	2.369	1.813	1.822
FOODWEB CONNECTANCE	2.065	2.133	1.953	2.109	1.91	1.942	2.049	1.956	2.246	1.823
CYCLES	2427	2333	2405	2962	3199	2517	3217	2256	2903	2752
CYCLING INDEX	23.17%	19.88%	2.42%	23.99%	20.32%	24.94%	19.87%	2.24%	25.15%	19.64%

Figure 4.19 a and b. Internal capacity and ascendency. C_i and A_i consider only the internal functioning of the ecosystem, or those parts of capacity and ascendency generated solely by the internal exchanges between the compartments.

a. Internal Capacity (C_i)

b. Internal Ascendency (A_i)
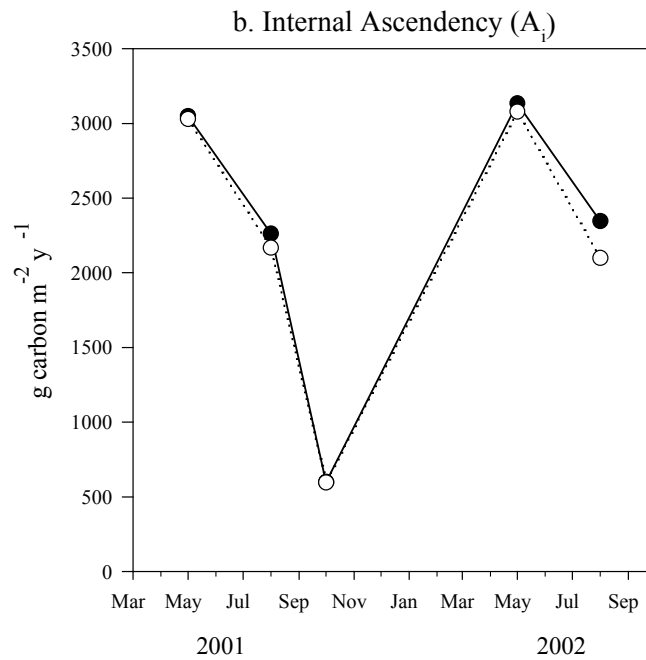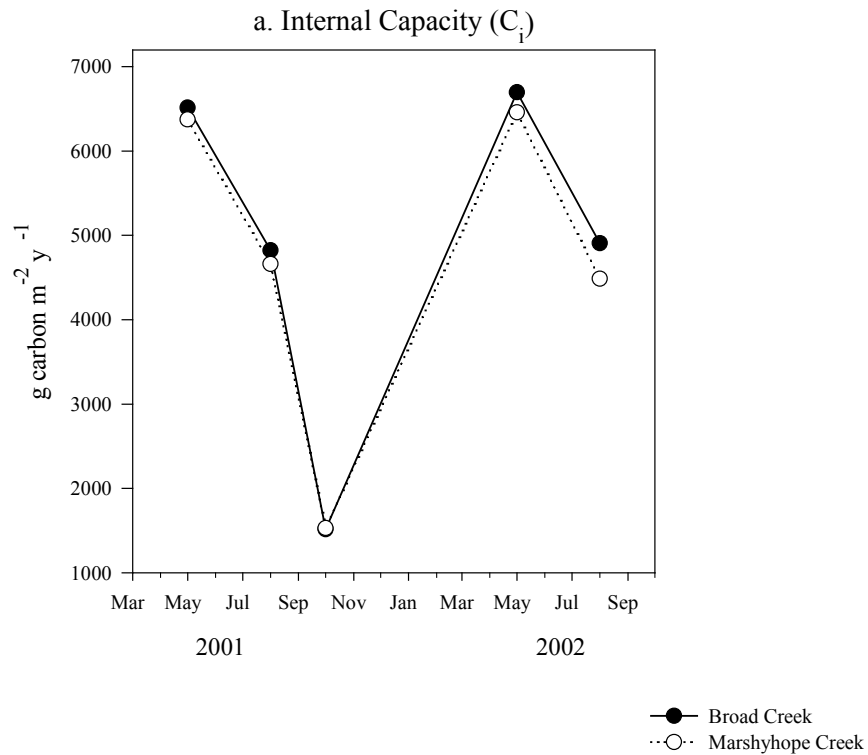
Relative measures of ascendency describe in a simple manner how much of the total system capacity is devoted to its organization and efficiency, removing the influence of the flux in TST. The measures were fairly similar across 2001, although after May 2001, Marshyhope Creek A/C was always greater than that in Broad Creek (Figure 4.20a). The ratios peaked at over 40% in all the May networks and declined through the summer and fall. By 2002, however, the difference between Broad Creek and Marshyhope Creek A/C increased, particularly by August 2002. A_i/C_i also has a seasonal pattern but was more variable with respect to the creek, where Broad Creek deviated from the pattern seen in A/C with the ratio increasing from May to August in both years (Figure 4.20b). R/C has been identified as a measure of an ecosystem's ability to resist further changes in the presence of stress. A rising relative level of R/C is thought to be indicative of increasing resistance (Ulanowicz 2004). R/C, like A/C, was greatest in May in both creeks and declined across the rest of the growing season. Aside from May 2002, R/C was greater in Marshyhope Creek (Figure 4.20c). The fluctuation increased in Broad Creek in 2002, and R/C achieved its highest level in May 2002 and then dropped to its lowest point by August 2002 in Broad Creek.

Once the seasonal magnitudes of TST were factored out of ascendency and overhead, their remaining elements, AMI (A/TST) and H_c (Φ/TST) respectively, showed some differences between the creeks. AMI in Marshyhope Creek was consistently lower than that in Broad Creek with the exception of May 2002 (Figure 4.21b). AMI trajectories diverged after this date, increasing to 1.886 in Broad Creek while falling to 1.834 in Marshyhope (Table 4.24). H_c was almost always greater in Broad Creek and

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Figure 4.20 a – d. Network indices relative to development capacity. All the indices are constituent parts of development capacity, and shifts in their relative proportions may indicate changes in system behavior. Overall ascendency and redundancy are contrasted with the similar ratios for the internal indices.
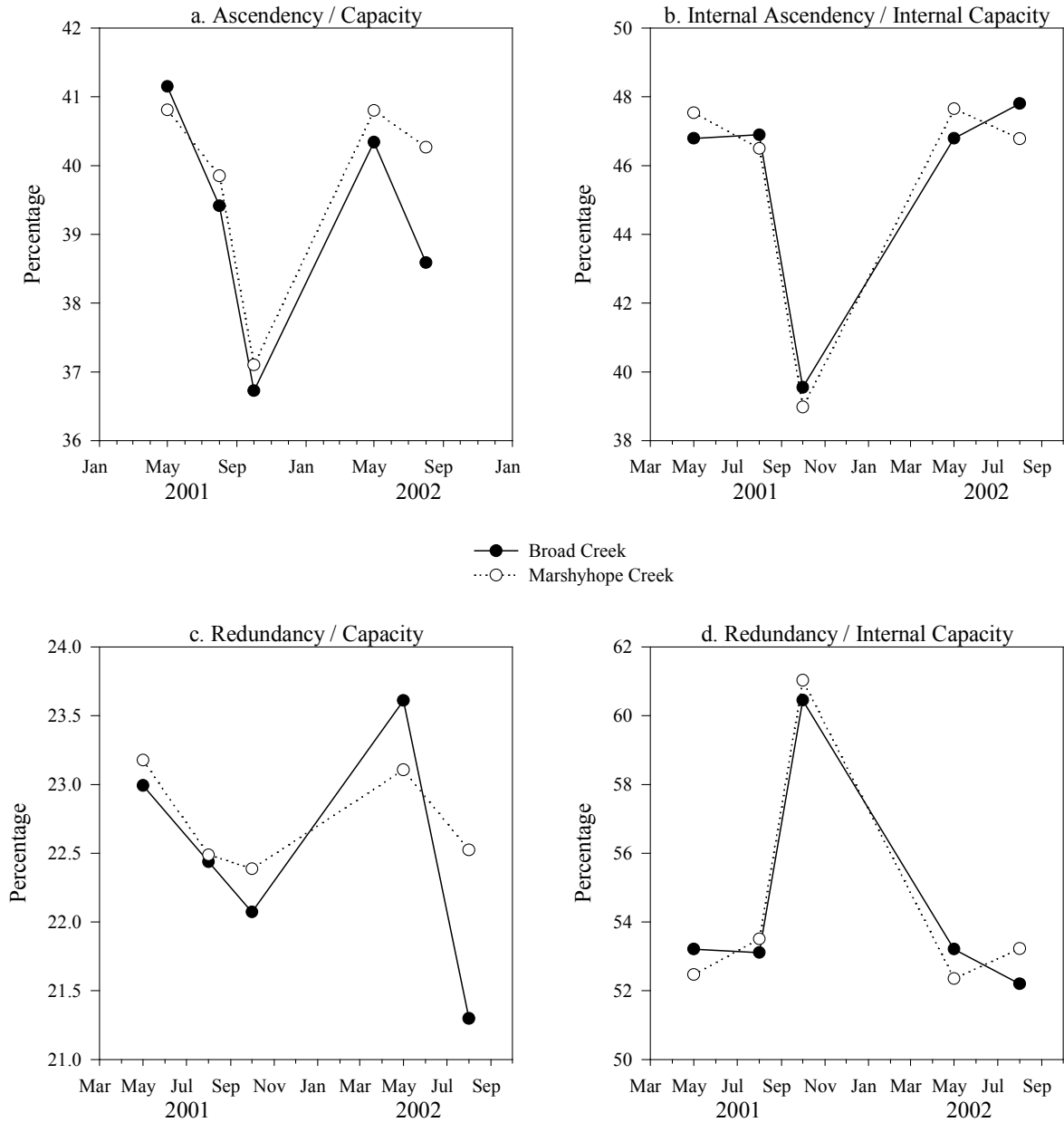
Figure 4.21 a – c. Decomposition of ascendency and overhead. The elements of ascendency and overhead are broken down into their constituent elements. TST is removed from ascendency and overhead, leaving their informational content intact as AMI, the measure of system order, and H_c, the residual system disorder.

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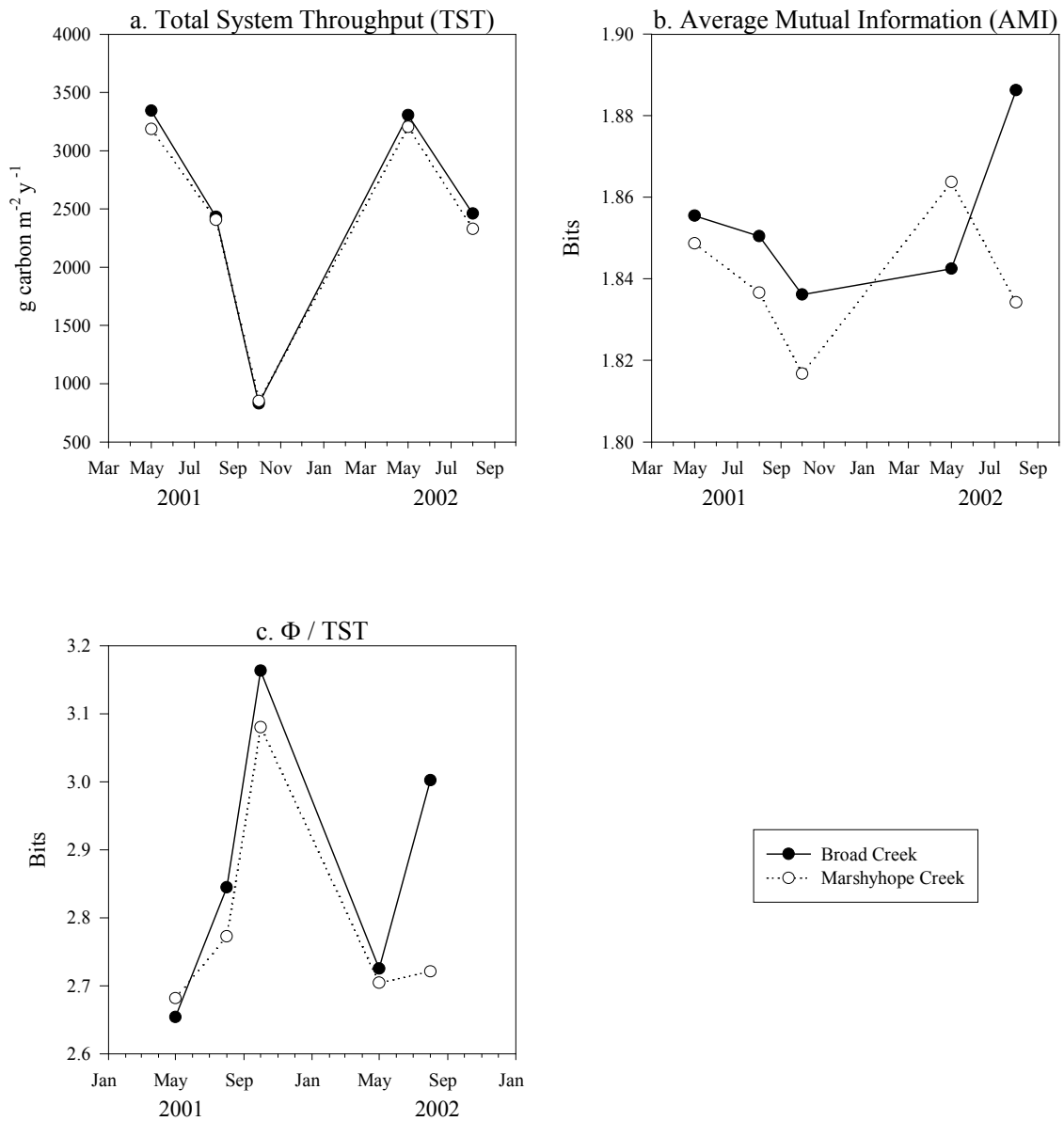
appeared to demonstrate a seasonal habit, rising sharply in both creeks in October 2001 (Figure 4.21c). Its values were similar in both creeks until August 2002 when the residual freedom or disorder rose to 3.002 while remaining nearly static in Marshyhope Creek (Table 4.24).

Cycle Analysis

Marshyhope Creek had the greatest number of cycles in August 2001 at 3217, while Broad Creek reach its maximum number of cycles, 3199, the following August (Table 4.24). Broad Creek had the fewest number of cycles in August 2001 and its total steadily increased through 2002, but the cycles seemed to peak seasonally in Marshyhope Creek (Figure 4.22a). As with the other indices and trophic relationships, seasonal effects appeared to influence the cycling of carbon in the marsh ecosystems. The Finn Cycling Index was annually at its greatest in spring, declining slightly by August and dropping substantially by October as the marshes senesced (Figure 4.22b). Both creeks recycled carbon in similar proportions throughout the span of the study. Most material was cycled over very short pathways, although less so in October in both networks (Table 4.25). In May 2001 and August 2001, Marshyhope proportionally cycled more carbon over longer pathways than Broad Creek, but this pattern reversed in 2002.

DISCUSSION

The two creeks were surprisingly similar in virtually every measure before the salinity pulse began to alter the behavior and function of the tidal freshwater marshes. There was a very strong seasonal pattern to the system-level properties, but this was

Figure 4.22 a – b. Cyclical flow in the networks. Cycle analysis reveals the number of cycles detected in the network (Figure a) and calculates the Finn Cycling Index (Figure b), a measure of the proportion of carbon flowing through the cyclical pathways.
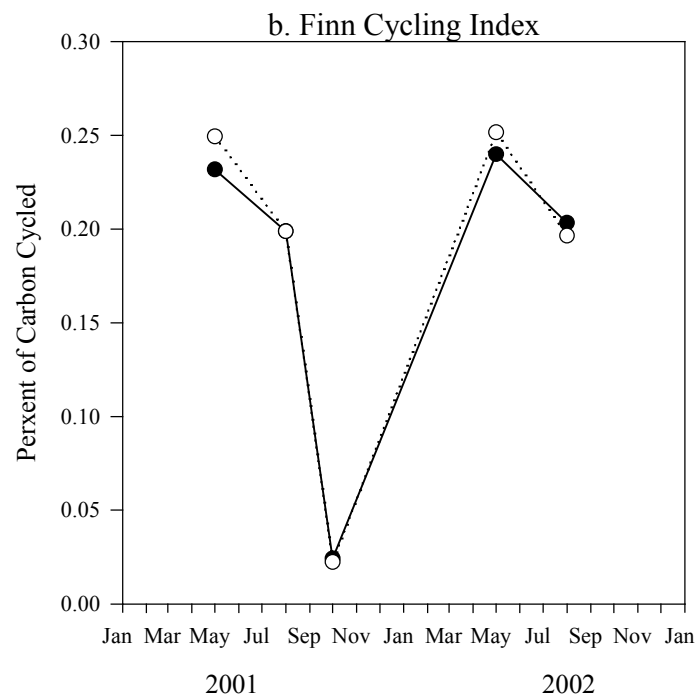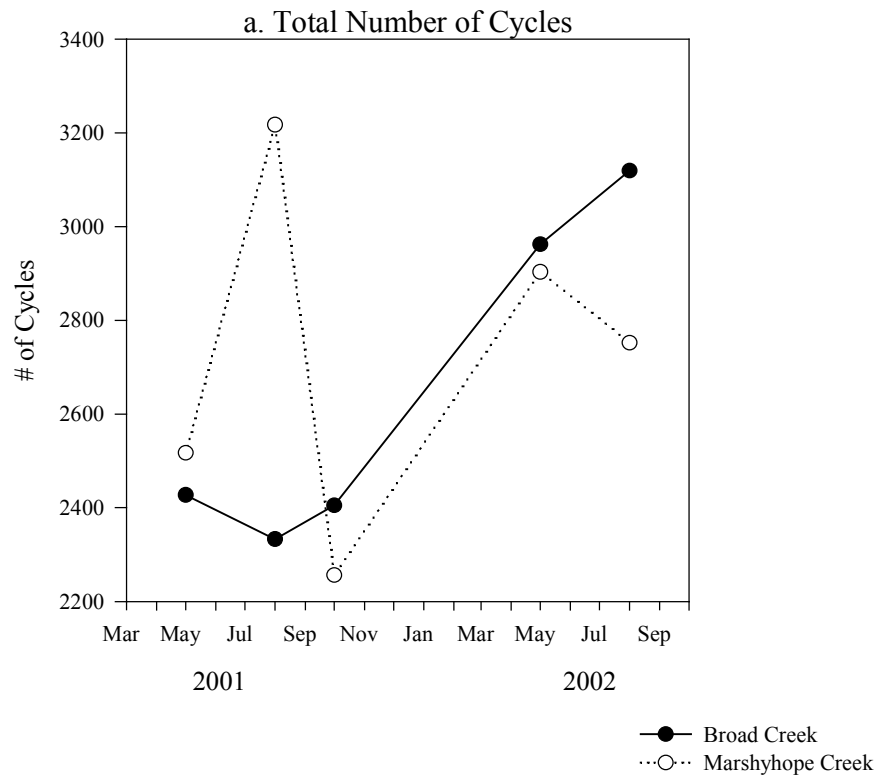
a. Total Number of Cycles

b. Finn Cycling Index

mostly a reflection of overall system activity rather than a fundamental shift in network

structure (Fabiano et al. 2004; Baird and Ulanowicz 1989). Yet several features still stand

out, suggesting some functional differences that may be related to nutrient enrichment

between the marshes of the two creeks. Nevertheless, the effects of the salinity increase

from October 2001 onward significantly affected the comparisons (see Figure 2.7b). In

many cases, trophic behaviors of the consumer organisms were very different from 2001

to 2002. The same sorts of changes appeared in most of the system level indices, with the

greatest separations and trajectory deviations occurring in 2002 when Marshyhope Creek

was borderline oligohaline (e.g., Figure 4.21). Any differences before May 2002 would

more likely be related to the differences in nutrient regimes, while those that are

expressed in 2002 are most likely the result of ecosystem response and compensation to

the salinity increase.

Nutrient Enrichment

Excluding the complications the drought-induced salinity increase introduced to

the comparison of creeks in terms of eutrophication, network analysis should still detect

any differences regarding tidal freshwater marsh behavior in the presence of any stress

imparted by the elevated nutrient inputs. By looking only at the networks from 2001, the

networks offer this glimpse at pre-salinity increase organization and activity.

Indirect Effects

The indirect effects among the compartments do not reveal dramatic differences between the two creeks in 2001, but there are some slight contrasts. Total contributions and dependencies suggest that Broad Creek consumers received more carbon from pelagic primary production than Marshyhope Creek. The majority of fish that were collected in the tidal marshes feed on benthic prey items, and the four fish compartments highlighted earlier (see Figures 4.3 – 4.6) received most of their carbon from benthic sources of secondary production, which in itself is not a remarkable result.

Looking past the direct interactions, however, one notices that throughout 2001 the contribution coefficients for phytoplankton were consistently larger in Broad Creek to the fish than in Marshyhope Creek (Figures 4.3b – 4.6b). Total dependencies suggest these contributions of phytoplankton to these fish are not trivial. For example, *F. diaphanus* > 35 mm TL total dependency on phytoplankton increased from 8 to 14 percent across 2001 in Broad Creek (Tables 4.12 – 4.14), while dependency fell from 7 to 3 percent over the same time span in Marshyhope Creek (Tables 4.17 and 4.19). Phytoplankton biomass was fairly similar in both creeks, but given the substantially greater dependence of the fish on *Corbicula fluminea* in Broad Creek, it makes intuitive sense that phytoplankton would provide more carbon to higher trophic levels there. Actual dependencies on phytoplankton for Corixidae and *Corbicula* confirm this with the Asian clam TDC's typically over 20 percent, while phytoplankton was not even one of the top sources for Corixidae (Figures 4.23 and 4.24).

Figure 4.23 a – f. Dependency coefficients (percentage) for *Corbicula fluminea*. Dependency coefficients estimate the fraction of Asian clam consumption that was mediated by one of these six compartments.
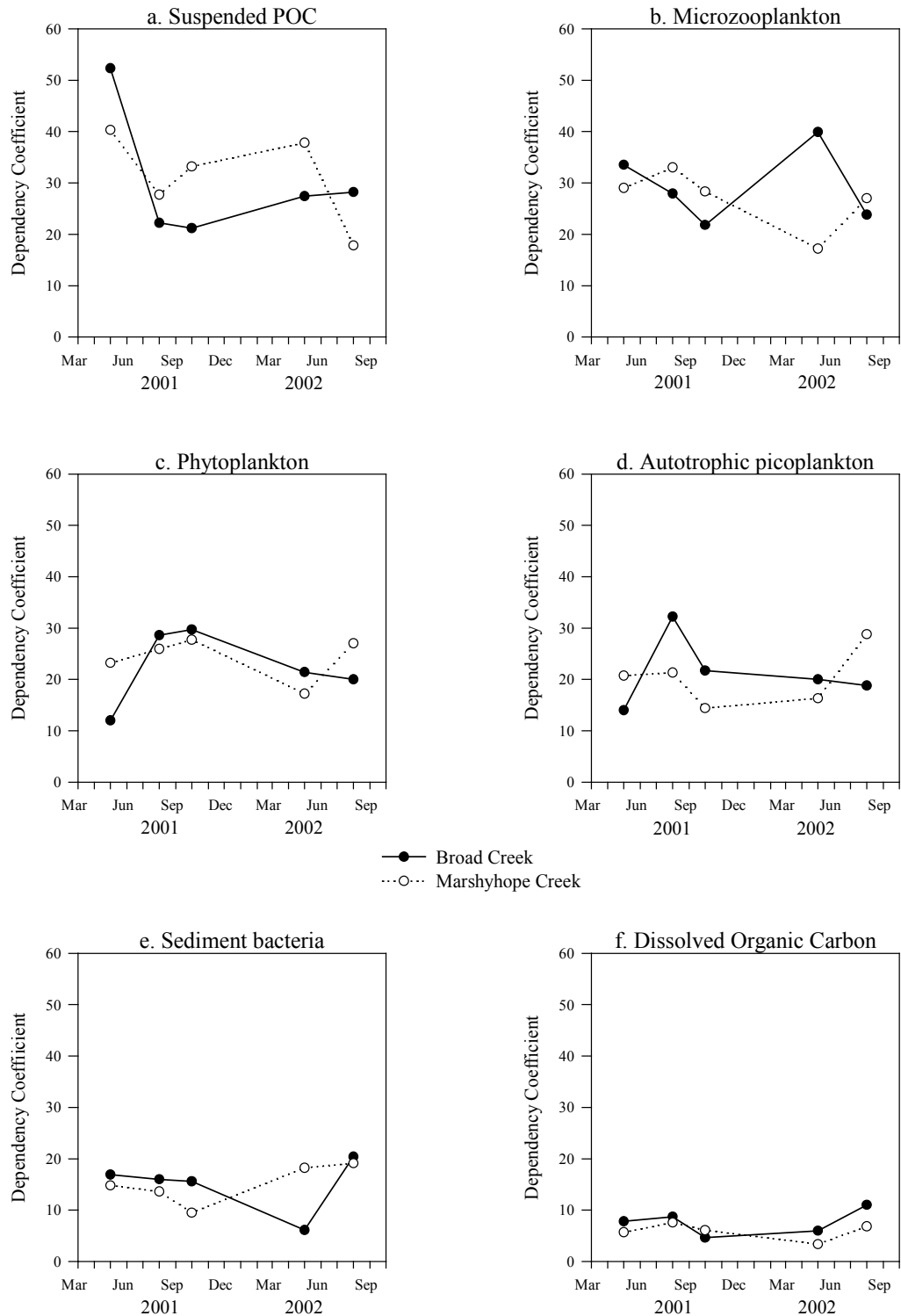
Figure 4.24 a – f. Dependency coefficients (percentage) for Corixidae. Dependency coefficients estimate the fraction of Corixidae consumption that was mediated by one of these six compartments.
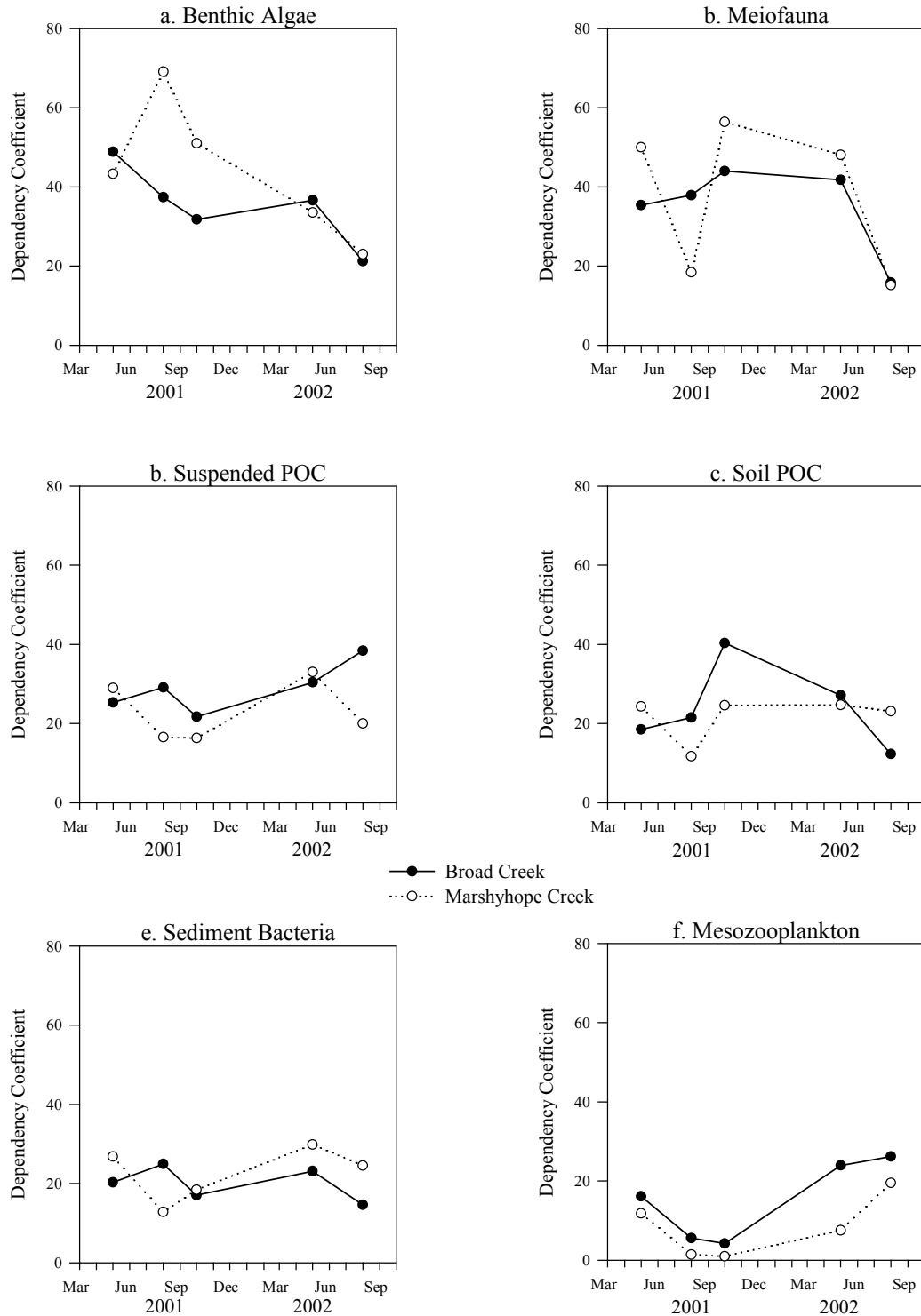
Total dependencies did not uniformly suggest any indirect relationships that identified

differences between the creeks across the higher trophic organisms. The patterns appear

more species specific, although there were some trends that spanned several

compartments. For instance, *Fundulus heteroclitus* in Marshyhope Creek was

consistently more dependent on Benthic Algae while the same compartment in Broad

Creek showed a higher dependency on Suspended POC (Figures 4.9b and c). Similarly,

Fundulus diaphanus > 35 mm TL dependencies on Suspended POC were also higher:

Creek	May 2001	Aug 2001	Oct 2001
Broad Creek	39.1	27.0	24.3
Marshyhope	33.7	16.1	12.4

This trend was not evident in any other compartment that appeared in every network.

Compartments at lower trophic levels had variable dependencies on Suspended POC

(e.g., Figure 4.24c).

Trophic Levels and Trophic Chains

The high level of variability expressed in the average trophic levels is probably

indicative of complexity of trophic responses to sudden shifts in resource availability, and

no compartment ever clearly exhibited different trophic position over prolonged periods

of time. For instance, two of the higher-level consumers, *F. diaphanus* > 35 mm TL and

F. heteroclitus, generally seem to function at higher trophic levels in Marshyhope Creek

than in Broad Creek. But in August 2001, their respective mean trophic level dropped

substantially as one of their primary prey resources, Corixidae, declined even more

precipitously. Corixidae dependencies on Benthic Algae were significantly greater in

August 2001, which largely explains the drop in the trophic position of these three

compartments. This example is probably more indicative of the short-term changes created by fluctuating environmental conditions that affect tidal freshwater marshes. Average trophic position in other systems where the results of ecosystem stress were more apparent also suggest that shifts in individual species are modest at best, and often ambiguous (Ulanowicz 1996).

The trophic chains also did not suggest strong differences between the creeks in 2001 either. The flows between trophic levels do not follow a uniform pattern regarding the magnitudes of flows, and the same holds for trophic efficiencies. The efficiencies of the two creeks were very similar in May 2001, but after this date Broad Creek tended to have higher efficiencies in higher trophic levels than Marshyhope Creek. A comparison of a relatively pristine *Zostera*-dominated seagrass meadow with a strongly eutrophic area where seagrasses were replaced by macroalgae suggested the eutrophic system had fewer trophic levels and greater efficiencies at lower trophic levels (Patrício et al. 2004). The number of trophic levels in the Nanticoke marshes never varied, but interestingly, it was Marshyhope Creek that showed the tendency to have higher efficiencies at lower trophic levels than Broad Creek during 2001.

System Level Functions

The creeks were also remarkably similar throughout 2001, with most system level indices suggesting minimal differences. AMI was greater in Broad Creek throughout 2001, although the magnitude of the difference ranges from 0.01 to 0.02 bits (Table 4.24). It is, nonetheless, a consistent difference. Similar to other systems where seasonal

networks were compared (Baird and Ulanowicz 1989), the tidal freshwater marshes tended to have peak AMI at the height of the growing season and then declined by fall (Figure 4.20b). Yet other comparisons of stressed and pristine systems have not revealed large differences in AMI. Ulanowicz (1996) previously observed nearly identical AMI between the thermally stressed and control ecosystems. The same pattern occurred in comparisons of estuarine ecosystems of differing eutrophic status, where the least- and most-enriched ecosystems had almost identical AMI (Patrício et al. 2004). This suggests that the response of many ecosystems to modest stress is largely an extensive property of system dynamics, affecting overall system activity while internal structure persists (Ulanowicz 1996).

Salinity Increase

The comparison of ecosystem response to nutrient regimes was severely complicated by the drought-induced salinity increase from October 2001 through 2002. The mid-Atlantic region began experiencing widespread rainfall deficits in May 2001, which persisted through early September 2002 (Maryland DNR 2002). At its height in 2002, the drought-severity status was at the maximum possible level across much of the lower Eastern Shore, D4, Exceptional Drought (National Drought Mitigation Center 2002). The effect on the tidal marshes of the Nanticoke in May 2002 and August 2002 was pronounced. While many of the network analysis measures suggested a seasonal pattern to organization, cycling and trophic function in 2001, most of these were very different in 2002.

Indirect Effects

Focusing again on the upper trophic levels, total contribution coefficients indicate that there were widespread changes among sources of carbon. For all four fish species, the patterns of Phytoplankton contributions shifted. *Etheostoma olmstedi*, *F. diaphanus* > 35 mm TL and *F. heroclitus* all saw contributions from Phytoplankton rise, in some cases more than doubling in May and August 2002 (Figures 4.4b – 4.6b). The patterns were different, however, for each species. *F. diaphanus* contributions from Phytoplankton rose through August 2002 in Broad Creek, but declined in Marshyhope from the May level (Figure 4.2b). *F. heroclitus* Phytoplankton contributions peaked in May 2002 and fell in both creeks by August 2002 (Figure 4.5b). *E. olmstedi* had peak contributions in Marshyhope Creek during May 2002, but Broad Creek darters received the highest contributions in August 2002 (Figure 4.6b). Dependency coefficients did not suggest any wholesale shifts in indirect reliance on resource pools, but the TDC's still trended very differently in 2002 than in 2001.

The trophic response of aquatic macrofauna to changes in salinity is obviously species dependent, with their respective physiological abilities to tolerate salt stress dictating where the animals can function (Subrahmanyam and Coultas 1980). But most of the species observed in the Nanticoke marshes are able to tolerate fluctuating salinity (Murdy et al. 1997). It is possible that it is not so much the total increase in salinity that affects the trophic behavior of the aquatic animals, but rather the variability of the changing salinity (Ley et al. 1994). During the drought, salinity increased on the rising tide and declined on the falling tide, exposing the organisms residing in and around the

marshes to a daily range of maximum and minimum salinity exposure. In August 2002, salinity differences between high and low tide at sites along Marshyhope Creek were typically 0.5 ‰. While this magnitude may not seem substantial, it often straddled the freshwater/oligohaline boundary. In addition, the associated changes in conductivity were quite large, which was more sensitive to changes in ionic concentrations in the water column than my measure of salinity (at one site, it dropped from 2387 to 918 μS cm^{-1} in about three hours). The ensuing physiological stress probably changes animal behavior and reduces benthic secondary production (Montague and Ley 1993). For example, in the Nanticoke marshes, *Gammarus* spp. were relatively abundant benthic primary consumers, but by August 2002 they were entirely absent from both creeks (Figure 4.8f). Total dependencies of fish species on other organisms associated with freshwater environments, such as *Corbicula fluminea* and Corixidae, also declined in August 2002, (Figures 4.8 a and b).

Trophic Levels and Trophic Chains

The trophic position of five of the six most common animal species changed abruptly in August 2002 (Figure 4.11). *E. olmstedi* increased from an average trophic position of 3.12 to 3.47 in Broad Creek, while falling in Marshyhope Creek from 3.23 to 3.14 (Table 4.22). This pattern is repeated in both *F. diaphanus* compartments and *F. heteroclitus*. Ley and Montague (1994) suggested that secondary consumers in stressful environments consume more low-quality food items, and this may be what occurred on Marshyhope Creek in August 2002. The rise in Broad Creek contradicts this notion, since the increase in osmotic stress resulted in feeding at higher trophic levels. It is possible

that the responses of the fish and macroinvertebrates is not linear, and that the slight increase in ionic concentrations may encourage shifts in trophic behavior in the lower-order consumers without impacting their ability to produce an adequate resource pool for the fish.

The trophic chains do not respond in any obvious way to the rising salinity. Trophic efficiencies were very similar between the creeks (Table 4.23), and the magnitudes of flows do not present any shifting patterns of carbon flow. It is possible that while there were some behavioral shifts in trophic behavior among the consumer organisms, the overall effect on system behavior was mitigated by compensation from other species. When, for example, *Gammarus* spp. disappeared from the marshes in August 2002, small individuals of *Palaemonetes pugio* were more frequently collected. In fact, the average trophic position of the grass shrimp is almost identical to that of the amphipod, both within the range of 2.47 – 2.50 (Table 4.22).

System Level Functions

Before the drought affected the tidal marshes, most of the variability in the network indices resided in the seasonal dynamics of the marshes. In 2002, after several months of steadily rising salinity, the magnitudes of network indices began to show increased divergence. By August 2002, development capacity in Marshyhope Creek was 1419 g carbon m^{-2} y^{-1} lower than in Broad Creek. The previous August, the difference was only 324 g carbon m^{-2} y^{-1} (Table 4.24). The measures of overhead for exports and imports deviate by the greatest proportion in August 2002. The growing difference

between Φ_I in the creeks reflects the decline in macrophyte production in Marshyhope

Creek by August 2002 (see Figure 2.8b). By August 2002, the salt stress was noticeably

affecting the quality of the macrophyte vegetation in Marshyhope Creek, especially at the

downstream sampling sites. As was the case in the high marsh, low marsh plant biomass

had also declined in August 2002 to fall-like levels observed during October 2001 (see

Figure 2.9). Dieback of *Nuphar lutea*, the dominant low marsh plant species, was

widespread in the lower intertidal zone in August 2002, responding in a manner similar to

other broadleaf, soft-stemmed marsh plants observed enduring salt stress (Howard and

Mendelssohn 1999).

Freshwater marsh response to increased salinity largely depends on the tolerance

limits of the dominant species and the duration of the increase. If they can survive the

saltwater influx, the marsh plant community should be able to survive (McKee and

Mendelssohn 1989). Near-term recovery of marsh vegetation is affected by the residual

changes in interstitial salinity, reduced soil conditions and sulfide concentrations. The

longer these persist at elevated levels, the more likely the marsh will continue to suffer a

decline in aboveground biomass and species richness (Flynn et al. 1995). The return in

September 2002 to more normal rainfall conditions across the Eastern Shore ended the

salinity increases, but soil interstitial salinity declines lagged behind river water,

suggesting a residual stress that remained after open water ionic concentrations reverted

to freshwater conditions (personal observation). Frequent and longer-term exposure to

salinity pulses could eventually result in species replacements as freshwater plant species

suffer from the physiological stress and lose their competitive advantages over rival

saltwater-tolerant species (Crain et al. 2004; Howard and Mendelssohn 2000). If species replacements ultimately occurred due to an increase in salinity fluctuations and the marshes take on a more oligohaline character, marsh loss may even become an issue, as is the case further downstream in the Nanticoke (Kearney et al. 1988).

In August 2002, Φ/TST, the residual disorder in the system, in both creeks was also quite different than in the previous year. Broad Creek increased from 2.725 to 3.002 bits, while the increase in Marshyhope Creek was only 0.019 bits over the same time span (Table 4.24). In the previous year in both creeks, the ratios increased from 0.1 to 0.2 bits from May to August, before rising by approximately 0.3 bits in October. One would expect that since the macrophyte biomass had declined significantly in the Marshyhope marshes by August 2002, that Φ/TST in this creek should be rising faster than in Broad Creek. But the opposite trend occurred. The difference seems to reside in the portion of overhead contributed by system inputs. Relative Φ_I increased slightly between May and August 2001 in both creeks (Table 4.24). But in 2002, relative Φ_I increased by 11.2 percent in Broad Creek, while Marshyhope declined by two percent.

This difference between the creeks is most apparent in the relative amount of redundancy in the marsh systems. Increasing salinity was first detected in Marshyhope Creek in October 2001; by May 2002, mean salinity in Marshyhope Creek was already over 0.25 ‰, but August 2002 was the first time conductivity appreciably rose in Broad Creek. While the changes appear modest, the increase in ionic concentration was probably sufficient for *Palaemonetes pugio* to become relatively common in these

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marshes for the first time and to affect *Gammarus* spp. abundance adversely. It has been predicted that perturbation would increase R/C as the ecosystem becomes more resistant to further perturbation (Ulanowicz 2004), and this phenomenon has been observed in some systems (Patrício et al. 2004). In this study, however, R/C declined by over two percentage points in Broad Creek after the salinity stress was first observed (Figure 4.21c). The likely explanation for this contradiction is that the underlying seasonal behavior is so strong that both A/C and R/C decline as the overhead related to exogenous inputs and outputs (Φ_I and Φ_E) increase as the growing season progresses, as the systems become more "pass-through" instead of "accumulative" (Table 4.24).

It remains important to note that all these differences between Marshyhope and Broad Creek are relatively small compared to other ecosystems. Patricio et al. (2004) detected much larger differences in A/C and R/C in their comparisons of eutrophic and pristine ecosystems. Their measure of relative ascendency was almost 14 percent lower in the stressed estuary while R/C was over 30 percent greater in the stressed system. The overall impact of salinity does not produce nearly as pronounced a response in the tidal freshwater marshes of the Nanticoke. The lack of distinction may be the due to the degree of difference in the comparison. It is possible that the creeks, in reality, are too similar, and their high level of shared common features are hindering the detection of meaningful differences. The previous chapters likewise noted similarly modest contrasts between the creeks, but did not observe a clear-cut pattern of difference between the creeks.

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<u>Conclusions</u>

Nutrient enrichment and the rise in salinity in the tidal freshwater marshes suggest a great deal about the immediacy and intensity of a given environmental stress. The effects of the high levels of nutrient inputs into the Nanticoke River watershed are long term and relatively consistent. It would be hard to consider, at this point, that the marshes are undergoing any sort of press perturbation (sensu Bender et al. 1984); the species composition has probably arrived at some sort of relative stasis in response to the long-term excessive nutrient loads the river receives. The constancy of the altered nutrient regime may minimize the practicality of using these two creeks as a space-for-time substitution to observe the effects of nutrient enrichment (McClelland et al. 1997). Nevertheless, certain results did suggest that nutrient enrichment, in the network analysis sense, is occurring in the Broad Creek marshes. Aside from October 2001 when both systems are undergoing seasonal collapse, Broad Creek had higher total system activity than Marshyhope Creek without a corresponding loss of organization. This meets the network analysis definition of enrichment, but falls short of the hypothesized consequences of eutrophication, which would entail degraded organization (Ulanowicz 1997). The higher nitrogen load associated with Broad Creek has probably ratcheted up the activity of this creek system, but it has not compromised its organizational integrity relative to Marshyhope Creek. Because the comparative "baseline" creek is also exposed to a similarly large macronutrient input, the effectiveness of the comparison is probably limited.

All the differences discussed for the pre-drought period focus on separations that are very small compared to other similar analyses (e.g., Patrício et al. 2004). The Nanticoke River is persistently phosphorus-limited in the tidal freshwater zone, yet some tributaries, like the Patuxent River, experience frequent nitrogen limitation in similar habitats (Maryland DNR 2004). More appropriate comparisons in the future may be possible by expanding the scope of comparison by including trophic networks of tidal freshwater marshes located in other tributaries of the Chesapeake.

Arrival of the drought-induced salinity increase forced an ecosystem response. If 2001 is assumed to be the baseline, situation-normal pattern of seasonal activity and organization, then the behavior in 2002 indicates the marshes were enduring a significant stress event. Broad Creek was not exposed to the changes in the ionic concentrations in the river water until August 2002, but the response was sometimes very similar to that of Marshyhope Creek in May 2002. These changes, though, were largely limited to the direct and indirect relationships among the compartments, such as the sequential spikes in contributions of Phytoplankton to *E. olmstedi* in May and August 2002 (Figure 4.6b). The initial responses to the salinity increase were seen in the shifting biomasses of the mobile organisms, which can easily escape any stress imparted by fluctuations in environmental conditions. Since the macrophyte production accounts for such a large part of total system throughput, however, any small changes among the linkages among the consumer organisms probably were dwarfed by these relatively massive flows. August 2002 was the first time that the macrophyte community appeared to be suffering from the salinity increase, but as the magnitudes of the indices suggest, this still did not present a large

difference between the creeks typically seen in other comparative network analyses (Almunia et al. 1999). The decomposition of ascendency and overhead indicated that ecosystem responses in the two creeks deviated in August 2002, as AMI and Φ/TST both increased in Broad Creek while in Marshyhope Creek the indices either declined (AMI) or remained nearly static (Φ/TST) (Figure 4.20). These differences are also apparent in the relative measures of capacity and ascendency, but the resultant changes are only differences of about two percentage points (Figure 4.21).

Even with all these equivocal results, the tidal marshes of the Nanticoke River still offer a comprehensive look at these ecosystems, something that has not been done before. They also present a picture of ecosystem response to environmental stress. For example, systems with high A_i/C_i are considered to be well-organized and probably are resistant to environmental stress. Conversely, these systems tend to have low redundancy and thus are not very resilient (Baird et al. 1991). The Nanticoke marshes appear to have a well-developed internal structure as indicated by A_i/C_I, and correspondingly lack resilience as measured by redundancy (Figure 4.21). In comparison, highly stressed aquatic ecosystems appear to maintain higher levels of redundancy than the tidal freshwater marshes. Studies of estuarine systems that were significantly impacted by human activities all maintained R/C_i over 60 percent, while these tidal marshes only reach those levels during periods of high senescence (Baird et al. 1991). The tidal marshes also cycle carbon at a comparatively high rate, similar to aquatic coastal systems impacted by pollutants, while more pristine systems tend to have relatively low Finn Cycling Indices (Baird and Ulanowicz 1993).

The comparisons with aquatic systems, however, are somewhat limited given the differences in biomass production and storage between terrestrial and aquatic systems (Baird et al. 1991). Yet there are very few studies that used network analysis to investigate ecosystem properties in wetland systems that might provide a more apt comparison. Fortunately, several large ecological network analyses were performed on cypress, gramminoid and mangrove wetland ecosystems in south Florida (Ulanowicz et al. 1997; Ulanowicz et al. 1999; Ulanowicz et al. 2000). The most appropriate of these three for comparison with the Nanticoke marshes is the freshwater gramminoid ecosystem of the Everglades. In this similarly macrophyte-dominated wetland type, A/C was estimated to be 52.5 percent, about 10 percentage points greater than in the Nanticoke marshes. This difference may be due in large part to the carbon subsidy from upstream sources and subsequent flushing that the tidal marsh receives. This is reflected in the overheads on imports and exports in the two ecosystems, which are typically five to ten percentage points greater in the Nanticoke than in the sawgrass ecosystem (9.1 and 1.5 percent, respectively; see Table 4.24 for Nanticoke values). Interestingly, A_i/C_i is similar between the two systems, averaging nearly 47 percent in the high growing season in the tidal freshwater marshes and 46.3 percent in the sawgrass marshes of the Everglades. This indicates a fairly rigid internal organizational structure in both marsh ecosystems (Heymans et al. 2002). Heymans et al. (2002) suggested that the Florida marsh ecosystems are fairly fragile given the relatively small number of linkages between primary producers and heterotrophic organisms, which may also be the case in the Nanticoke tidal marshes.

The relative lack of change in the tidal freshwater marshes after the salinity increase suggests that the marsh ecosystem is fairly resistant to stress. The higher-level consumers, for the most part, exhibit a fairly wide range of salinity tolerance. The plant community also appears fairly robust to the stress imparted by brackish waters, as it took at least three months of exposure to the steadily rising salinity before macrophyte biomass production was noticeably impacted. The marshes appear to be well organized relative to the stresses of the intertidal zone, although it is surprising that these systems adapted to stressful environments may lack resilience given their low level of redundancy. Marshyhope Creek appears slightly more resistant, given its relative lack of significant change during the exposure to the salinity increase. Species losses and declines here seem to have been supplemented by similarly functioning replacements. Broad Creek, on the other hand, exposed less frequently to the salinity stress, showed greater declines in organization and the network measures of resilience at the peak of the drought, although the declines were not precipitous, compared to other ecosystems.

CHAPTER 5

ISOTOPIC RATIOS OF NITROGEN IN THE NANTICOKE RIVER: LAND-USE LINKAGES TO MARSH COMMUNITY STRUCTURE

INTRODUCTION

Eutrophication is a significant threat to the health of coastal ecosystems (Driscoll et al. 2003; Carpenter et al. 1998; Boesch 1996). The cascading effects of excess nutrients have been well documented, and their presence, particularly nitrogen, can lead to shifts in the sources of primary productivity as aquatic ecosystems become more eutrophic. This often happens in estuaries when phytoplankton production increases so dramatically that aquatic macrophytes are extirpated by the shading effects created by these massive algal and periphyton blooms which are generated by the increase in available macronutrients (Hauxwell et al. 2003; Kemp et al. 1983). The respiratory demands of the abundant phytoplankton in turn deprive the waters of oxygen, creating "dead zones" of extreme hypoxic, and even anoxic, conditions in coastal estuaries (Hagy et al. 2004; Chesapeake Bay Program 2004d). These shifts among the primary producers affect the resources available to consumer organisms within the system and can eliminate significant pathways of material and energy transport within and between ecosystems (McClelland and Valiela 1998b).

The Chesapeake Bay has been a focal point in the struggle to find practical strategies to minimize and mitigate nutrient enrichment in estuaries. For over 20 years, collaborative efforts on the part of various state and federal government agencies have been attempting to determine the sources and behavior of excess nutrients in the Bay (Chesapeake Bay Program 2003b; Horton 2003). Inputs from point sources have been greatly minimized, but most of the excess nutrients in the Bay come from non-point sources, most often agricultural in origin and which tend to travel via groundwater (Staver and Brinsfield 2001; Speiran et al. 1997; McFarland 1995). In 2002 it was estimated that 117 million pounds of nitrogen, 38 percent of the total nitrogen load, the greatest single source, came from agricultural sources (Horton 2003).

The Nanticoke River

The Delmarva Peninsula is part of the Coastal Plain, a region characterized by low elevations and little topological relief, where most uplands are never more than 80 feet above sea level. The Nanticoke River flows from northeast to southwest across the Delmarva Peninsula, issuing into Fishing Bay on the eastern side of the Chesapeake Bay. The freshwater portion Nanticoke River watershed spans three different hydrogeomorphic regions: well-drained uplands (water table >10 ft below surface), poorly drained uplands (water table < 10 ft below surface), and poorly drained lowlands (shallow water table and flat water table gradients). Most of the main branch of the river is contained within a region of well-drained uplands characterized by permeable soils, relatively deeply incised streams and longer water flow paths, while its major tributaries stretch across mostly poorly drained uplands (Hamilton et al. 1993). While approximately

48 percent of the land surface in the entire Eastern Shore is devoted to agricultural land

use, the Nanticoke River watershed average is higher at over 50 percent, and it's two

largest sub-watersheds, Marshyhope Creek and Broad Creek, are even greater (Table

5.1). This is much higher than the proportion of total Chesapeake Bay watershed land-use

that is devoted to agriculture, measured at 16 percent in 1990 (Shenk and Linker 2000).

Table 5.1 Land Use in Broad Creek and Marhsyhope Creek (CBP 2003a).

Land Cover Category	Marhsyhope Creek Area (sq mi.)	Pct.	Broad Creek Area (sq.mi.)	Pct.
Developed	2	0.009	3	0.024
Agriculture	120	0.543	66	0.537
Forested	59	0.267	44	0.358
Open Water	2	0.009	1	0.008
Wetland	35	0.158	8	0.065
Barren	2	0.009	0	0.000
Total	221		123	

The majority of the Nanticoke watershed's agricultural croplands consist of small

grains, corn and soybeans used as feed sources for the poultry industry. In 2003, 73.8

million bushels of soybeans and 55.6 million bushels of corn were produced and fed to

poultry on the entire Eastern Shore (Delmarva Poultry Industry 2005). In the four

counties that the Nanticoke River passes through, Wicomico, Dorchester and Caroline

Counties in Maryland and Sussex County in Delaware, over 320 million chickens were

reared in 1997 alone (Delmarva Poultry Industry 2005). Poultry waste is typically

recycled back into the crop fields as a fertilizer, providing very high concentrations of

macronutrients. Total application rates of nitrogen alone in the Pocomoke River watershed, for example, have been estimated to average nearly six million pounds on an annual basis (Ator et al. 2004). Excess nutrients not utilized by the crop plants often passes into the ground water or gets transported to streams via overland runoff during storm events.

Below the Delmarva Peninsula are a series of contained aquifers, stacked upon each other and separated by confining units of varying thickness. These aquifers slope downward, shallower in the north than in the southern half of the peninsula, while the depth to the interface between fresh and saline water gradually rises toward the south. A surficial aquifer rests atop these confined aquifers whose upper bound ranges from less than 10 feet below the ground surface in poorly drained uplands down to 40 feet in the well-drained uplands (Hamilton et al. 1993). Most of the land surface of the Eastern Shore serves as the recharge area for surfical aquifer, which in turn would eventually (i.e., over geologic time) recharge the confined aquifers below. The groundwater in the surficial aquifer also discharges into streams, freshwater ponds, wetlands, tidal marshes, bays and the Atlantic Ocean (Speiran et al. 1997). This discharge is a major source of the Chesapeake Bay's water, accounting for approximately 27 billion of the 50 billion gallons of annual streamflow in the entire Chesapeake watershed (Phillips et al. 1999).

Nitrogen

The sources of nitrogen in ground water are varied, including atmospheric deposition to soils and seepage of organic nitrogen from residential septic systems, but on

the Eastern Shore, approximately 95 percent of the nutrient load comes from manure and inorganic fertilizer (Denver et al. 2004). High levels of nitrogen have been consistently detected in groundwater on the Eastern Shore, particularly near agricultural lands (Hamilton et al. 1993). The organic forms of nitrogen found in the poultry waste applied to the croplands either volatize out of the system (as NH_3) or are mineralized to form NH_4^+ (McFarland 1995). Ammonium is water soluble and percolates into the soil water, where it is either adsorbed to solid particles or, with sufficient oxygen, is transformed into nitrite (NO_2^-) and nitrate (NO_3^-) (Mitsch and Gosselink 2000). Nitrate is highly mobile and is readily transported by the movements of groundwater. Depending on the trajectory of the groundwater, the nitrate can end up in deeper portions of the surficial aquifer or can be transported to discharge areas in times ranging from a matter of days to decades. Groundwater dating in the Coastal Plain springs suggests that the average below-ground residence time of most discharged water is six to ten years (Phillips et al. 1999).

Dissolved forms of nitrogen from the landscape can be transported by water to streams in several ways. Overland surface flow occurs during storm events with high rates of precipitation and nutrients can be transported in the runoff. Soil water percolates downward to the water table, but it can discharge to creeks before it enters the groundwater, typically during and after storms (Figure 5.1). But the most significant source of dissolved nitrogen is via groundwater. Groundwater contributes approximately 48 percent of the total nitrogen load to streams in the Chesapeake Bay watershed,

Figure 5.1. Pathways of waterflow in coastal landscapes. All white arrows indicate potential pathways for nutrient flows into coastal waterways (image from Phillips et al. 1999).
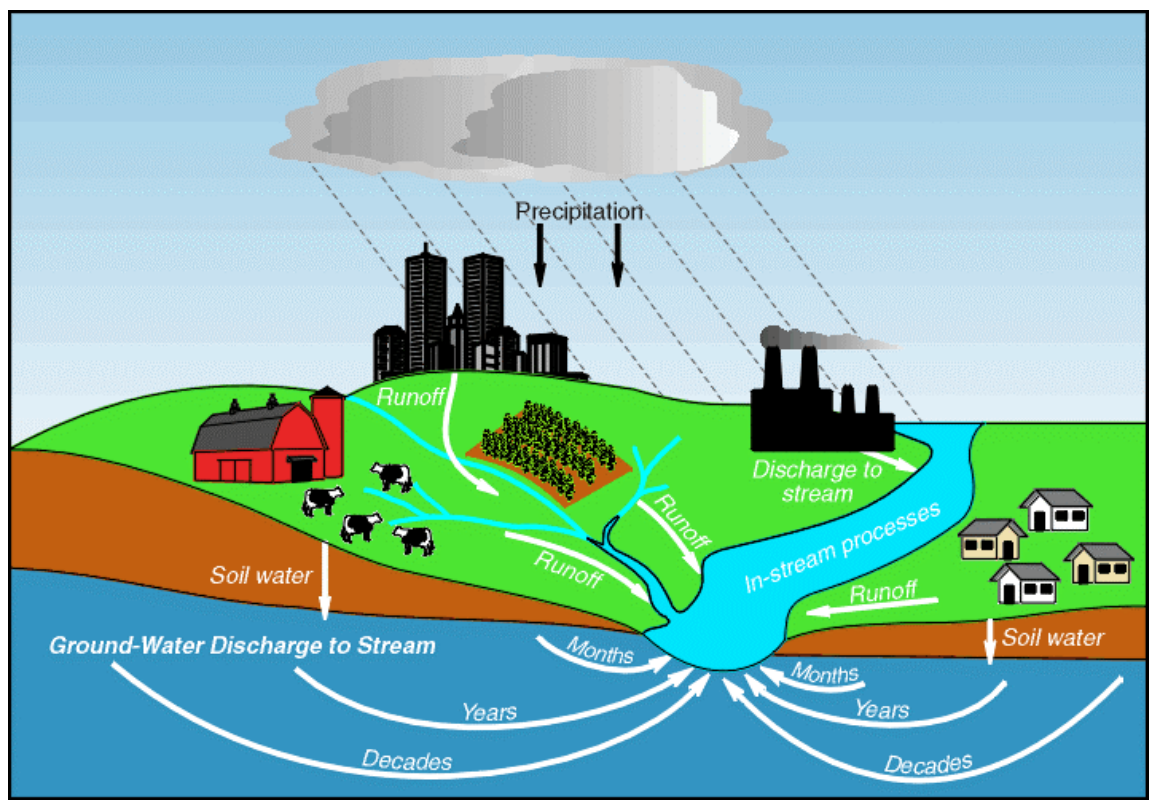
although the proportion of nitrogen from groundwater in individual streams ranges from 17 to 80 percent (Phillips et al. 1999).

Over the past 10 years, the United States Geological Survey has constructed a series of models estimating nutrient loads contributed to stream water from watersheds around the United States. These models, named SPAtially-Referenced Regressions On Watershed attributes (SPARROW), have been used to relate water quality to various sources of nutrients and the processes that affect their transport (Smith et al. 1997). The most detailed implementation of these models has been applied to the Chesapeake Bay watershed, where estimates of nitrogen and phosphorus loads were compiled for more than 1600 unique upland "stream reaches," which consist of distinct sub-watershed and drainage units (Brakebill and Preston 2003). The models simultaneously consider upstream nutrient-loading rates and localized land-surface characteristics that affect the delivery of the nutrients to the stream water. The Chesapeake Bay model considered the following sources of nutrients in each stream reach: point sources (municipal and commercial), urban, agricultural (fertilizer and manure) and atmospheric deposition (Preston and Brakebill 1999). These estimates identify the amount of nitrogen that each stream reach produces and passes on to the next stream segment or the Bay itself. Thus, it is possible with this model to estimate the amount of nutrients that enter both Broad Creek and Marshyhope Creek and quantify the contributions from various sources. Yet this information alone is not enough to identify any effects of nutrient enrichment in the tidal freshwater marshes. It is necessary to determine to what extent the excess nitrogen load affects these ecosystems.

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Marshes are considered ideal locations for fostering nitrogen transformations. The close proximity of an often-present thin aerobic soil layer on top of a much larger anaerobic soil matrix permits both the oxidation and reduction of nitrogen into different forms, and, most importantly, is responsible for high levels of denitrification (Mitsch and Gosselink 2000). These transformations are often complicated, and depend on multiple factors, both chemical and physical, in the marsh itself. The rate of nitrification in the soils is often fairly low, but is likely faster in less water logged soils (Bowden 1986). The process may also be encouraged by the presence of oxidized rhizospheres around wetland plant roots (Howes et al. 1981). Pore water ammonia concentrations are often hundreds of times higher in the wetlands than in their surficial waters, yet there may still be a net flow of ammonium into the marshes, probably due to microbial demand in the plant litter layer (Bowden 1986). The plant litter layer may also be creating anaerobic surficial microzones where much of the net nitrate input is denitrified (Bowden et al. 1991). Marshes also tend to accumulate nitrogen during the growing season as the nutrient is temporarily sequestered in aboveground plant biomass production (Klopatek 1978). Upon senescence, however, up to 80 percent of this nitrogen can be lost within one month, often accompanied by increased algal production within the marshes (Simpson et al. 1978). Most of the nitrate entering tidal freshwater marshes likely comes from river water inputs, and these marshes appear to be sinks for NO_3-. Ammonium produced by organic matter mineralization appears to be removed via coupled nitrification-denitrification reactions (Anderson et al. 1998), but also tends to be produced in amounts sufficient to support plant production (Bowden et al. 1991). Most stored nitrogen is found in peaty

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materials, and the proportional size of this nitrogen pool is dependent upon the age of the marsh (Bowden 1987).

<u>Stable Isotopes</u>

Stable nitrogen isotope ratios have recently been used to identify sources of nutrients in aquatic and terrestrial ecosystems (McClelland et al. 1997; Erskine et al. 1998; Karr et al. 2001). Nitrogen sources in nature often have distinctive signatures that are created by both physical and biological processes, and in locations where animals contribute the majority of nitrogen to the ecosystems (via animal waste), the nitrogen pool has more nitrogen-15. While the absolute differences between the various source pools are very small, the standardized differences seen in the isotopic ratios distinctly identify them (Peterson and Fry 1987).

Approximately 99.63 percent of all nitrogen is ^{14}N, while only 0.37 percent is ^{15}N (Ehleringer and Rundel 1989). Estimates of stable isotope abundance, however, are not measured in absolute terms. Instead, they are expressed as a ratio between the sample specimen and internationally accepted standard (Peterson and Fry 1987). The isotopic composition is expressed in terms of δ, which are parts per thousand differences from a standard:

$$\delta = [(R_{sample} / R_{standard}) - 1] * 1000$$

where R is the ratio of rare to abundant isotopes, and R_{sample} and $R_{standard}$ are the ratios of the sample and standard, respectively. Positive values indicate enrichment, or that the sample has more of the rare species than the standard, while negative values mean the

sample has less of the rare isotope than the standard, otherwise know as depletion (Dawson and Brooks 2001).

Groundwater is a major conduit for nitrogen to coastal waters, and the isotopic signature of this nitrogen, mostly in the form of NO_3^-, can suggest where it is coming from. Groundwater containing NO_3^- derived from atmospheric deposition has $\delta^{15}N$ values ranging from +2 to +8 ‰, and nitrate from synthetic fertilizer is typically between –3 and +3 ‰. Nitrate that comes from animal-derived sources, however, is often substantially more enriched. Nitrate in ground water coming from wastewater and animal manure ranges from +10 to +20 ‰ (McClelland et al. 1997). The signature of animal-derived nitrogen is enriched largely due to volatilization of ammonia that occurs in animal manure while it is being stored or applied to fields. Volatilization preferentially removes ^{14}N, and the residual nitrogen is mineralized into NH_4^+ enriched with ^{15}N (Karr et al. 2001). The process of nitrification converts the ammonium into nitrite and nitrate, which is readily mobile in groundwater, and the animal-derived nitrogen freely moves toward deeper aquifers or to discharge areas. Groundwater containing high levels of nitrate that was processed by animals (e.g., sewage or manure) will have elevated ^{15}N signatures (Kreitler et al. 1978; Kreitler and Browning 1983). Groundwater is a major contributor of both water and nitrate to the Chesapeake Bay and its tributaries (Bachman et al. 1998). Therefore, the observation of ^{15}N enrichment in nitrogen pools in coastal ecosystems can be interpreted as evidence linking land-use practices with these systems (McClelland and Valiela 1998a).

This chapter investigates implications of the isotopic signatures of nitrogen found in the flora and fauna in the two major tributaries of the Nanticoke River and how they could be related to nutrient sources. Enriched nitrogen signatures should correspond to locations with nutrient loads with larger contributions from animal-derived nitrogen. Earlier in Chapter One, I noted that estimates of nitrogen inputs from animal waste indicated larger loading rates in Broad Creek than in Marshyhope Creek (Chesapeake Bay Foundation 1996). Furthermore, another study on the Nanticoke River has observed higher nitrate levels in the soils of tidal freshwater marshes and swamps on this same creek (Figure 1.2a). Yet the analysis presented in this chapter was not the primary purpose intended for the isotopic analyses, which actually were analyzed to assess trophic relations among the plant and animal taxa of the marshes. However, the patterns revealed by the isotopic ratios of the dominant taxa in conjunction with the model-based description of nutrient dynamics offer further evidence that the land-use practices are affecting coastal wetland food webs of the Chesapeake Bay.

RESEARCH METHODS

This section will only describe in detail the processing and analysis of samples used in the stable isotope analysis. Specific information about sample sites and sampling protocols are briefly described in Chapter Two, while a thorough explanation of all collection methods is presented in Appendix I.

<u>Sample Preparation</u>

The size of the sample pool for stable isotope analysis was limited due to financial constraints. Therefore, I looked only at the dominant taxa from two sampling events, May 2001 and October 2001. These dates represent the largest time interval between sample dates within one growing season that I collected. I chose these dates because analysis of samples from two widely separated dates should identify any seasonal shifts in isotopic composition that has been documented in some plant species (Boon and Bunn 1994). Other research suggested that four to six replicates per taxon per date would adequately account for the variation in isotopic levels (Keough et al. 1998; McClelland et al. 1997; Boon and Bunn 1994). Sample materials and preliminary preparation for the isotope samples varied based on taxon, specimen size and specimen morphology (Table 5.2).

Table 5.2. Source material for isotope samples. These headings represent the major taxa that were prepared for isotopic analysis.

Sample Type	Material Used
Fish	White muscle tissue, dorsal and posterior to pectoral fins
Macroinverts	*Varies by taxa*
Palaemonetes	Muscle tissue from abdomen
Corbicula	Soft body tissue
All others	Entire organism
Plants	Homogenized aboveground tissue
Soil	Homogenized combined material

The isotopic samples were prepared for analysis at two facilities at the University of Maryland. Initial specimen preparation was performed at the Wetland Ecology and Engineering Laboratory, while the weighing and sample packaging occurred at the University's Insect Ecology Laboratory. The samples were sent to a third party for the

actual isotope analysis procedure at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University. Only natural levels of isotopes were observed; this was not an enrichment study (i.e., where the fate of artificially elevated isotope signatures is tracked).

Given the limited number of samples I could analyze due to budgetary constraints (per sample cost of $10 with a $2500 budget), I aggregated soil samples by marsh type and site. I combined each site's soil into high and low community marsh samples so that each date was reduced to six samples, three of each marsh type (12 total per date, 24 total).

Specimens of the vascular *Acorus calamus* (sweetflag), *Impatiens capensis* (jewelweed), *Polygonum arifolium* (halberd-leafed tearthumb), *Schoenoplectus fluviatilis* (river bulrush) and *Peltandra virginica* (Arrow arum) were randomly selected for the isotopic analysis. I ground each sample to a fine powder in a Cyclotech 1093 sample mill with a 0.75 mm screen over the discharge vent from the grinder chamber. This screen size ensured a complete pulverization of the dried plant material. After each sample was ground, the mill was cleaned with high-pressure air and then rinsed with deionized water and allowed to air dry before the next sample was processed. The ground material was then stored in airtight containers before final sample processing.

Animal specimens were chosen similarly to the plants. Unlike the plants, however, specimens came from individual animals rather than entire samples. All fish

samples consisted of white muscle tissue dissected from the dorsal region of the fish posterior to the pectoral fins. Most invertebrates were too small to dissect out specific tissue, so many of these samples consist of entire individuals. Bivalve and decapod tissue, however, was extractable and was used to avoid carbon contamination from the carbonate in the shell material (Table 5.2). The dissected tissue and animal samples were dried in an oven at 80° C for 48 hours. The dried specimens were stored in airtight containers until final processing.

At the Insect Ecology Laboratory, I performed the final preparatory work on each sample. Regardless of previous preparation, all the specimens were ground with a 50 ml 99.5% Alumina mortar and pestle (Coors, U.S.A.). I placed this powdered material into small 4 x 6 mm or 6 x 10 mm low-blank tin cups (Costech Analytical, Inc.), using a Mettler-Toledo MX series microbalance, weighing the samples to the nearest 0.001 mg. The tins filled with soils had approximately 7.000 mg of material, while those with animal and plant tissue contained roughly 1.000 mg and 3.500 mg, respectively. These sample masses were sufficiently large enough to contain detectable amounts of C and N, yet small enough to not saturate the mass spectrometer's detectors. After the cup was filled, I crimped them shut using two pairs of forceps, folding the top down like a lunch bag. This eliminated any potential contamination from contact with my hands or lab bench surfaces. The mortar, pestle and forceps were cleaned with deionized water, isopropyl-alcohol and acetone between each sample packing process to prevent cross-contamination. The crimped sample capsule was re-weighed to account for any material that may have been lost during the crimping and then placed in its own cell in a clear

polystyrene 96-well plate (B-D Falcon). Twenty of the cells in each well plate accounted

for bypass, blank, standard and duplicate samples required by the mass spectrometer

during the analysis, all of which help assess and maintain the precision of the isotope

analyses.

Sample Analysis

The Colorado Stable Isotope Laboratory, Northern Arizona University, performed

the actual stable isotope analysis. They used a Finnigan Delta Plus XL mass spectrometer

configured for continuous flow analysis of organic samples after Dumas combustion.

Each sample was simultaneously analyzed for carbon and nitrogen. This process provided

data about isotopic ratios for N and also C, which were also used to determine percent N

and C and C/N of each sample. This chapter only considers the nitrogen data.

Carbon ratios were determined using an internal working standard (peach tissue)

calibrated against an internationally accepted reference standard. Atmospheric nitrogen

was the standard used for the N analysis. During the analyses, every tenth sample was

replicated to estimate the precision of isotopic ratio. The replicates were within ±0.1 ‰

for carbon and ±0.2 ‰ for nitrogen.

Data Analysis

Differences in isotopic ratios between the two dates were evaluated to see if the

signatures differed between the seasons for selected abundant species. Each selected

taxon was separated by creek, and then the mean signatures of N were compared using

independent sample t-tests between the dates. Levene's Test for Equal Variance was used to determine what variance assumptions were required for the t-test, and the appropriate analysis was selected for each comparison. Each comparison was treated independently since physico-chemical processes, feeding behaviors and nitrogen assimilation vary across the selected taxa and suggest independent species responses to the nitrogen species. If the seasonal differences were not significant, the data were combined to produce an overall mean isotopic ratio for the given taxon. If the ratios were significantly different between seasons, then the samples were not combined and treated individually in subsequent analyses.

The experimental design established for the sampling protocols precluded the use of parametric statistical analysis to compare the ratios of both creeks. The marsh sites were the true replicate units throughout the study. Given the number of specimens needed for each species, I could not estimate mean isotopic ratios for each species at each of the three sample sites within each creek – the isotope sample units are sub-samples within the replicate units. While the various source materials were randomly selected from the entire pool of collected specimens, there is no way to account properly for variability expressed by differences among the marsh sites within the creeks. In a statistical sense, any comparison would only be comparing two different creeks that presumably could occupy different points along a gradient of isotopic ratios for similar systems. The data can be used, however, to identify the overall trends in isotopic ratios between the two creeks. Graphical comparisons of nitrogen are presented for all major taxa. These trends,

combined with other evidence related to nutrient loading in the two sub-watersheds, will be used to describe a larger context of nutrient enrichment in the Nanticoke River system.

RESULTS

<u>Isotopic Ratios</u>

Only two taxa exceeded the critical values in the examination of differences between seasons for the nitrogen isotopes (Table 5.3a). Low Marsh Soil and *Gammarus* sp. both had p-values less than 0.05 (p = 0.0199 and p = 0.0205, respectively). *Gammarus* sp. δ^{15}N declined between June and October 2001 from 11.12 to 10.47. The measured enrichment of Low Marsh Soil increased across this time period, from 5.35 ‰ in June to 5.95 ‰ in October. Otherwise, all other taxa demonstrated no difference between the two seasons. In the analysis of percent nitrogen, five taxa showed a significant decrease in nitrogen content of more than 1.5 percent between June and October 2001. These species were *Fundulus diaphanus*, *Fundulus heteroclitus, Schoenoplectus fluviatilis, Etheostoma olmstedi* and Corixidae (Table 5.3b).

All the animal species and soils in Broad Creek had more enriched nitrogen than their corresponding representatives in Marshyhope Creek (Figure 5.2a). The taxa were sorted by approximate trophic position with the soil materials at the bottom, and the highest order consumers at the top (ranking based on results presented in Table 4.22).

Table 5.3 a and b. Results of t-tests comparing isotopic signatures of selected samples between dates. Table a. presents the p-values from the t-tests determining whether there is a seasonal difference in $\delta^{15}N$. Table b. depicts the same analysis for $\delta^{13}C$. The t-test p-value is compared to the Hochberg (1988) experiment-wide test of significance. Only values that are less than their corresponding Hochberg alpha level suggest that the means are significantly different.

a. $\delta^{15}N$

Taxon	d15N p-value
Low Marsh Soil	**0.0066**
***Gammarus* sp.**	**0.0205**
High Marsh Soil	0.2348
Corixidae	0.2489
Notropis hudsonius	0.3360
Impatiens capensis	0.5044
Fundulus diaphanus (L)	0.5102
Etheostoma olmstedi	0.5230
Fundulus heteroclitus	0.8080
Schoenoplectus fluviatilis	0.8836
Acorus calamus	0.9838

b. Percent nitrogen

Taxon	Pct. N p-value
Fundulus diaphanus (L)	**<0.0001**
Corixidae	**<0.0001**
Fundulus heteroclitus	**0.0018**
Schoenoplectus fluviatilis	**0.0108**
Etheostoma olmstedi	**0.0280**
High Marsh Soil	0.2813
Impatiens capensis	0.2954
Gammarus sp.	0.3304
Notropis hudsonius	0.3883
Low Marsh Soil	0.8268
Acorus calamus	0.8995

Figure 5.3 a and b. Nitrogen content of plant, animal and soil taxa and in Broad Creek and Marshyhope Creek. Figure a. presents mean $\delta^{15}N$, and figure b. depicts percent nitrogen. Error terms are standard errors of the means. **Fish taxa codes**: ANMI: *Anchoa mitchilli*, NOHU: *Notropis hudsonius*, ETOL: *Etheostoma olmstedi*, FUDI-L: *Fudnulus diaphanous* > 35mm TL, FUHE: *Fundulus heteroclitus*, FUDI: *Fundulus diaphanous* < 35mm TL. **Invertebrates:** COSP: Corixidae sp., GASP: *Gammarus* sp.. **Plants**: POAR: *Polygonum arifolium*, ACCA: *Acorus calmus*, LEOR: *Leersia oryzoides*, SCFL: *Schoenoplectus fluviatilis*, IMCA: *Impatiens capensis*, PEVI: *Peltandra virginica*. **Soils**: HM SOIL: Soils from high marsh zone at collection sites, LM SOIL: Soils from low marsh zone at collection sites.

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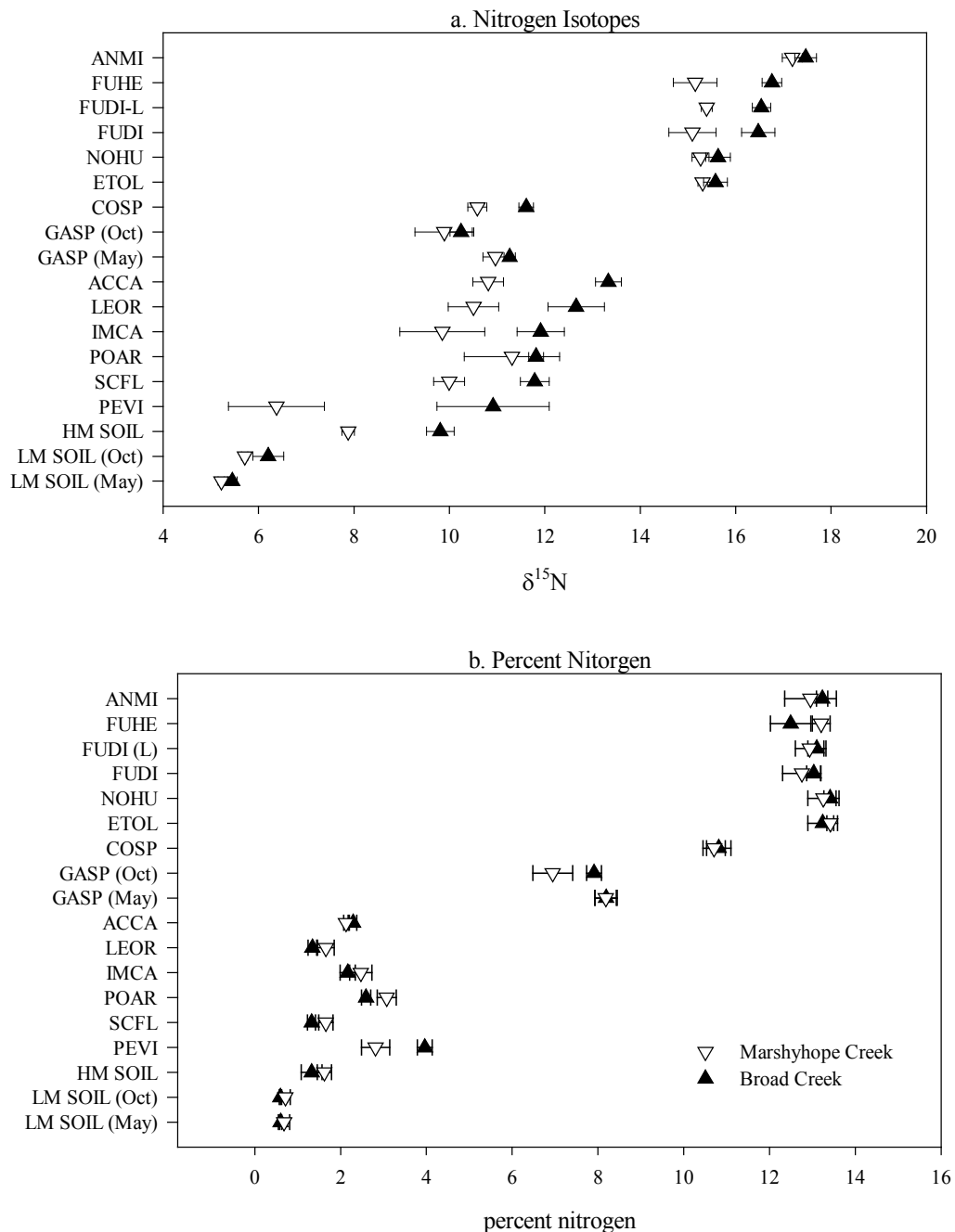
The isotopic ratios of plants typically mirror their nitrogen source with very low

fractionation rates (Dawson et al. 2002). The plant species in Marshyhope Creek ranged

in δ^{15}N from 6.5 to 11.5 ‰, while the same species in Broad Creek ranged from 9.5 to

13.5 ‰. This suggests that the nitrogen sources in Broad Creek are more enriched with

nitrogen-15 compared to Marshyhope Creek. The trend extends into higher trophic

positions also. In each taxa, δ^{15}N values were greater in Broad Creek than in Marshyhope

Creek. In half of the taxa, there is a clear separation between the samples obtained in each

creek, while those taxa with overlapping error bars, nonetheless, still have more depleted

δ^{15}N in Marshhyope Creek. As a point of contrast, percent nitrogen values for the same

taxa are presented to show the more random pattern of distribution seen in the nitrogen

content of the taxa (Figure 5.2b). The randomness of percent nitrogen in conjunction with

the uniform pattern of enriched nitrogen in Broad Creek suggests that the distribution of

nitrogen isotopic ratios is not a chance pattern determined by the availability of nitrogen.

Nitrogen isotopes can also supply information about trophic position of

organisms, particularly when used in conjunction with other isotope ratios. In this study,

carbon isotopes were also measured for each sample simultaneously with the nitrogen. As

reported in many studies, consumer organisms typically have δ^{15}N 3-5 parts per thousand

more enriched than their prey species, while δ^{13}C shifts to a smaller extent of about one

part per thousand (Vander Zanden and Rasmussen 2001; Keough et al. 1996; Cifuentes et

al. 1988; Schroeder 1982). Slight differences in the mass of molecules can affect the rate

of biochemical reactions, resulting in what is called isotopic fractionation where one

isotope becomes slightly more abundant than the other as a result of the reaction.

Nitrogen is affected to a larger degree than carbon, especially in trophic transfers (Peterson and Fry 1987). The fish and invertebrates of the Nanticoke River's tidal freshwater marshes roughly represent two separate trophic levels according to the isotopic ratios (Figure 5.2a). In both creeks, higher-order consumers like *Fundulus diaphanus*, *F. heteroclitus* and *Notropis hudsonius* are approximately five parts per thousand more enriched than the dominant aquatic invertebrate taxa. The stomachs of the fish typically contained remnant pieces of both Gammarid amphipods and Corixid waterboatmen. The invertebrates possess similar nitrogen signatures to the macrophytes, suggesting that the invertebrates are not utilizing macrophyte production.

Nitrogen Sources

The SPARROW model presents nitrogen and phosphorus yield data for three dates, with 1997 being the most recent. Since nitrogen is widely considered to be the limiting nutrient in freshwater wetlands (Bedford et al. 1999), it alone will be presented here. Marshyhope Creek is contained entirely within stream-reach segment in the SPARROW model (3595). Broad Creek is divided into three segments (3585, 3586 and 3587) (Brakebill and Preston 2004). All of the collection sites were located within the most downstream segment of Broad Creek (3585). Of the three measures the model provides, Total Yield is the most appropriate since it factors in both upstream contributions to the reach plus the sources in the stream reach's watershed (Brakebill and Preston 2003; John Brakebill, U.S. Geological Survey, personal communication).

Point sources, urban run-off and atmospheric deposition all averaged less than one kg ha^{-1} y^{-1} in both creeks, while agricultural sources dominated the total yield of nitrogen.

The point sources within each creek are located near urbanized areas in Federalsburg,

Maryland, in the Marshyhope Creek watershed and in Laurel, Delaware, in Broad Creek.

The total nitrogen yield is greater in Marshyhope Creek than in Broad Creek, with the

contribution of commercial fertilizer accounting for a 1.5 kg ha^{-1} y^{-1} difference (Table

5.4a).

Table 5.4 a and b. Total nitrogen yield and relative contribution of primary nitrogen
sources in Broad Creek and Marshyhope Creek (Brakebill and Preston 2004).

a. Total yield of nitrogen sources for stream segments (N kg ha^{-1} y^{-1})

	Total Yield	Point Source	Urban Sources	Atmospheric Deposition	Commercial Fertilizer	Manure Fertilizer
Broad Creek	10.211	0.373	0.126	0.309	7.945	1.458
Marshyhope Creek	11.434	0.867	0.057	0.323	9.522	0.665

b.Relative contribution of nitrogen sources

	Point Source	Urban Sources	Atmospheric Deposition	Commercial Fertilizer	Manure Fertilizer
Broad Creek	3.65%	1.23%	3.03%	77.81%	14.28%
Marshyhope Creek	7.59%	0.49%	2.83%	83.28%	5.82%

Yet in proportional terms, the overall contribution of commercial fertilizer is very

similar, approximately 80 percent of all nitrogen, for both creeks (Table 5.4b). The

largest difference in relative terms is in the contribution that manure provides to the

nitrogen yield. More than 14 percent of Broad Creek's nitrogen yield comes from

manure, while less than five percent of Marshyhope Creek's load comes from the same

source.

DISCUSSION

The isotopic ratios indicate that nitrogen in Broad Creek is more enriched with ^{15}N, while the percent nitrogen of the samples suggest there is no pattern to the availability of nitrogen that might affect these ratios. The higher trophic levels reflect the enriched source as both primary and secondary consumer organisms demonstrate predicted patterns of increases in δ^{15}N. The most recent SPARROW model of Chesapeake Bay nutrient-loading rates estimated that Marshyhope Creek receives a substantially smaller percentage of nitrogen derived from animal waste than Broad Creek (Brakebill and Preston 2004). While the most recent estimates of total yield of nitrogen are now slightly greater in Marshyhope Creek than in Broad Creek, there is a major difference in nitrogen sources as Broad Creek receives 0.739 kg N ha^{-1} y^{-1} more nitrogen from animal manure than does Marshyhope Creek. The enrichment in isotopic signatures also appears in higher trophic levels where both aquatic invertebrates and small fish also have higher δ^{15}N in Broad Creek than in Marshyhope Creek.

Nitrogen

Earlier versions of the SPARROW model suggested that Broad Creek had substantially higher total nitrogen yields than Marshyhope Creek before 1997, and that manure applications accounted for the majority of agriculturally produced nitrogen in both creeks, but substantially more so in Broad Creek (Table 5.5). Since the mid-1990s, however, the overall contribution of manure to groundwater nitrate has fallen dramatically across the Delmarva Peninsula. Estimates of total manure contribution to nitrogen on the Eastern Shore have fallen steadily since 1987 from a peninsula-wide total

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of approximately 125 million pounds per year to 75 million pounds (Denver et al. 2004).

Nevertheless, the amount of dissolved inorganic nitrogen has remained very steady since

1988 in the Nanticoke River (Figure 5.3). During the height of the growing season, this

nitrogen declines to an average of less than one mg L^{-1} while during the winter months it

Table 5.5 a and b. SPARROW model estimates of actual and relative total yield of nitrogen in Broad and Marshyhope Creeks, 1987 and 1992.(Brakebill and Preston 2003).

a. Delivered yield of nitrogen (kg N ha^{-1} y^{-1})

	Total Yield	Point Source	Commercial Fertilizer	Applied Manure	Atmospheric Deposition
Broad Creek 1987	24.16	0	4.49	18.52	0.98
Marshyhope 1987	13.35	0.28	4.46	7.66	0.87
Broad Creek 1992	23.31	0	4.3	17.78	0.96
Marshyhope 1992	10.61	0.23	3.55	6.09	0.7

b. Relative yield of nitrogen from primary sources

	Point Source	Commercial Fertilizer	Manure Fertilizer	Atmospheric Deposition
Broad Creek 1987	0.0%	18.6%	76.7%	4.1%
Marshyhope 1987	2.1%	33.4%	57.4%	6.5%
Broad Creek 1992	0.0%	18.5%	76.3%	4.1%
Marshyhope 1992	2.1%	33.5%	57.4%	6.6%

typically rises to more than four mg L^{-1}. In fact, the relative contribution of manure-

derived nitrogen is still much larger in Broad Creek than in Marshyhope Creek. Yet given

the large contributions of nitrogen from groundwater to the Bay and the fairly long

residence time of groundwater (Phillips et al. 1999), past agricultural practices are still

likely influencing current ecological plant and animal communities as the nitrate-laden

water is slowly released to the streams.

Figure 5.3. Dissolved inorganic nitrogen in the Nanticoke River, 1988 – 2002. These data are actual measures of dissolved inorganic nitrogen content of the river water sampled near Sharptown, Maryland (USGS station ET6.1). The oscillating pattern reflects the annual growing season demand of organisms for nitrogen. Samples were collected monthly by Maryland Department of Natural Resources (Chesapeake Bay Program 2005).
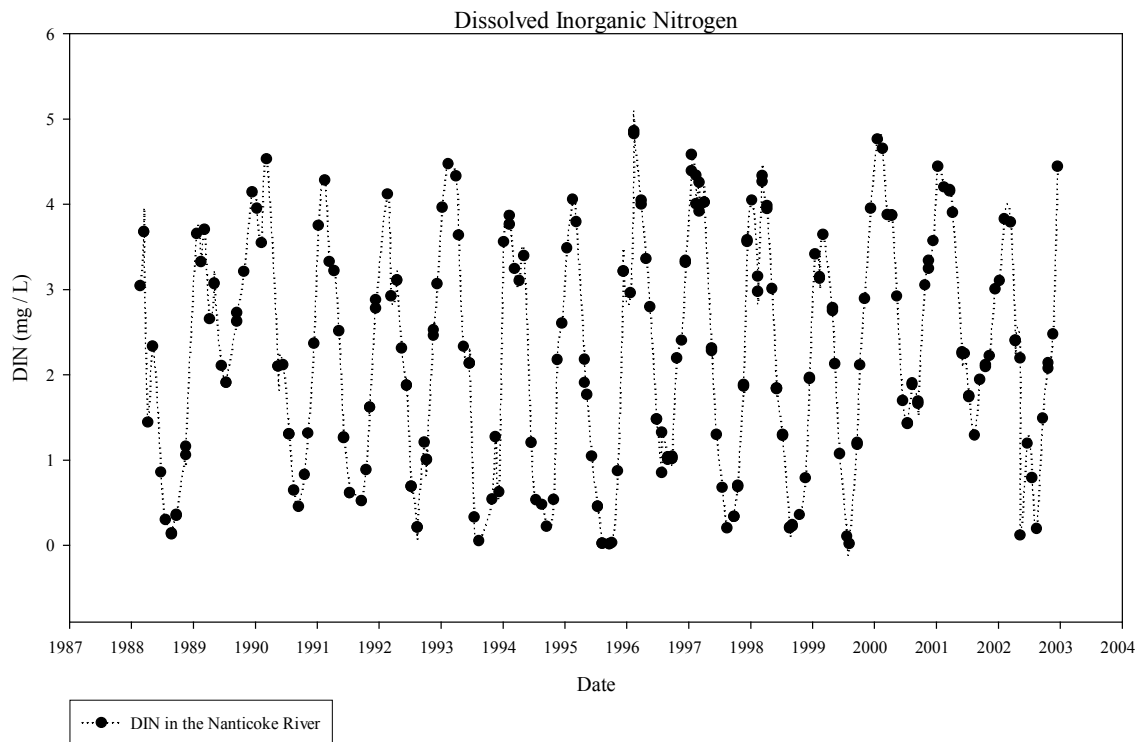
In addition to the contributions from manure applied to agricultural fields and storage to the pool of available nitrogen, there are other potential sources of animal-derived nitrogen on the Eastern Shore, specifically from septic systems. The Chesapeake Bay Program constructed the Chesapeake Bay Watershed Model (an application of the CBP's Hydrologic Simulation Program – Fortran) that identifies the potential contributions of both nitrogen and phosphorus based on land use (Chesapeake Bay Program 2005d). The available model output offers nutrient load estimates for all major watershed units located within the Chesapeake Bay drainage basin, including the Nanticoke River over four dates: 1985, 2000, 2001 and 2003 (Unfortunately, model resolution does not distinguish among the sub-watersheds of the Nanticoke. 2000 census data indicates that the human population in Broad Creek's watershed was 15,143, while the nearly twice as large Marshyhope Creek watershed has 17,100 people living within its boundaries). Using information on land use in 1985, the baseline year, the model estimated that the entire Nanticoke River delivered 154,043 pounds of nitrogen from septic output to the Chesapeake Bay. By 2000, the estimates of the amount of nitrogen coming from septic sources had risen to 183,688 pounds and by 2003 the estimate jumped to 222,944 pounds of nitrogen per year (Chesapeake Bay Program 2005d). Like animal manure, much of this nitrogen is already enriched from fractionation during trophic level transfers, and the subsequent volatilization of the ammonia found in the waste further enriches the nitrogen.

There are also strikingly different land-use characteristics between the two watersheds that also suggest that Broad Creek should be receiving both a more enriched

load and a larger nitrogen load than Marshyhope Creek. The Broad Creek watershed is home to over 250 animal production facilities, while Marshyhope Creek only has about 65 (Chesapeake Bay Foundation 1996). The entire area of the Broad Creek watershed is 97 square miles smaller than Marshyhope's, which only serves to concentrate the animal waste production in the smaller area. Marshyhope Creek also has proportionally more wetlands that could enhance the buffering between the upland agricultural areas and stream systems (Table 5.1). Sixteen percent of the Marshyhope watershed is covered by marsh and swamp, while wetlands only cover 6.5 percent of Broad Creek. The Marshyhope Creek watershed also has 15 percentage points more forested land cover than Broad Creek.

Buffers between agricultural areas and waterways are believed to facilitate nitrogen removal processes through denitrification. The buffer's width serves as an area where both vegetation uptake and other nitrogen removal processes can minimize the amount of nutrients passing from uplands into adjacent waterways (Lowrance et al. 1997). It appears, however, that the width required to treat run-off adequately may be greater than expected. In North Carolina evidence suggests that the state's mandated width for riparian buffers may not be sufficient to reduce nitrogen loads substantially derived from animal waste (Karr et al. 2002). The state requires that buffers be at least 25 feet wide between wastewater treatment sites at concentrated animal feeding operations (CAFO) and streams receiving discharge. Yet in swine waste lagoons adjacent to riparian buffers direct measures of dissolved nitrogen in the water suggested that $\delta^{15}N$ was approximately 15.4‰, while water entering creeks ostensibly protected by the riparian

buffers contained nitrate enriched almost to the same level at 15.3‰ (Karr et al. 2001).

This suggests that the narrow riparian buffer's capacity to remove nitrogen is quickly

saturated by the sheer volume of nitrogen-laden groundwater emanating from the

treatment facilities. In the Nanticoke River, therefore, the more expansive coverage of

land surface by wetlands and forest in Marshyhope Creek may further enhance the

watershed's ability to reduce the amount of nitrogen derived from animal waste from

appearing in its wetland and aquatic ecosystems.

Plant and Animal Community Responses

The consequences of the proportionally greater nitrogen yield rate from animal

wastes are not entirely clear in any of the previous chapters. Any possible linkage to

nutrient enrichment effects was likely marginalized by the increase in salinity that caused

substantial changes in the vegetation and aquatic macrofauna. But again, there are some

more pieces of evidence emerging that suggest that differences between the creeks may

be related to nutrient load. The simultaneous comparisons of carbon and nitrogen isotope

ratios suggested that coarse trophic structure was not substantially affected by the

differences in nitrogen yield (Figure 5.4). But the macrophytes indicated that the quality

of nitrogen between the nitrogen source material in both creeks did differ (Figure 5.2). It

is the consumer organisms that could show differences in material and energy flow

pathways. The higher-order consumers in both creeks still appear to rely on similar

sources of production as only the nitrogen ratio seems to have shifted, which the

comparison of carbon and nitrogen isotopes also confirms. Both Broad Creek and

Marshyhope Creek data suggest that the small fish are feeding on aquatic invertebrates.

Fractionation during assimilation can occur for both carbon and nitrogen, with the offsets between trophic levels being 0 – 1.5‰ for carbon and 3 – 5‰ for nitrogen (Peterson and Fry 1987), similar to what is being seen in the two creeks.

In both creeks, the small invertebrate consumers (Corixidae, *Gammarus* sp. and Coenagrionidae) are within the ranges of the carbon and nitrogen offsets, indicating that they are a likely food source for fish, a result confirmed by stomach-content analysis (Figure 5.4). There is a block of small fish species in the middle of both graphs, and the relative position of the species is nearly identical between the two creeks, with only the small *Fundulus diaphanus* moving. The patterns to the differences probably suggest subtle differences in dietary preferences between the killifish species and *Etheostoma olmstedi* and *Notropis hudsonius*. *Anchoa mitchilli* is not clustered together with the other fish in either graph. This fish feeds pelagically on zooplankton unlike the other species that appear to be preying upon the small macroinvertebrates. Other than these small contrasts between the consumer organisms, pathways of energy and material flow appear similar in the two creeks.

Some research in this area suggests that the isotopic signatures of coastal aquatic organisms can serve as an early warning system for changes in nutrient load regimes. In Waquiot Bay, Massachusetts, human-derived nitrogen has been linked to shifts in primary consumer consumption from seagrasses to algal-dominated communities. Subwatersheds of Waquiot Bay with high nitrogen loads from anthropogenic sources (i.e., septic system output) had substantially more enriched nitrogen in primary producers

Figure 5.4. Carbon and nitrogen stable isotopes of consumer organisms in Broad Creek and Marshyhope Creek. The combination of $\delta^{13}C$ and $\delta^{15}N$ can be used to estimate trophic relationships and trophic position. Species codes are used as labels to identify the mean $\delta^{13}C$ and $\delta^{15}N$ values for each of the major animal taxa that were analyzed. COSP: Corixidae, COEN: Coenagrionidae, GASP: *Gammarus* sp., ANMI: *Anchoa mitchilli*, NOHU: *Notropis hudsonius*, ETOL: *Etheostoma olmstedi*, FUDI-L: *Fudnulus diaphanous* > 35mm TL, FUHE: *Fundulus heteroclitus*, FUDI: *Fundulus diaphanous* < 35mm TL.

a. Broad Creek Consumer Organisms

b. Marshyhope Creek Consumer Organisms
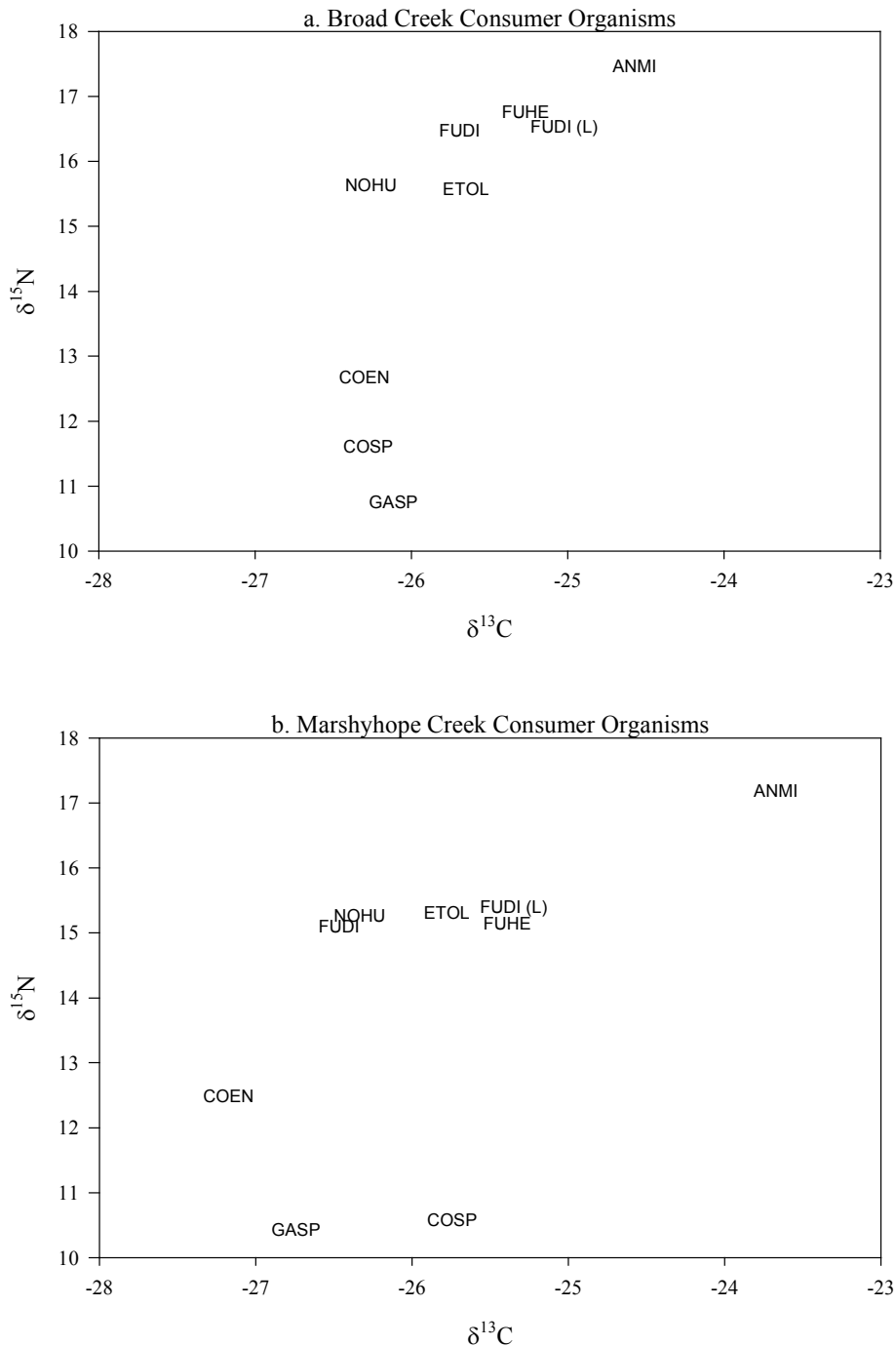
than sites with little or no human activity impacting groundwater quality (McClelland et al. 1997). In sites with low nitrogen loads, eelgrass can consist of up to 16 percent of the primary consumer organism's diets, while in the areas with very high nitrogen loads, the only resources available for these small organisms are phytoplankton and attached algae. The differences in the variation in $\delta^{15}N$ between the sites at the producer level also appeared in higher trophic levels, implying that the shift in nitrogen sources cascades throughout the entire local food web (McClelland and Valiela 1998b). Studies of groundwater nitrogen confirmed the earlier results that those sites located near concentrated human activities always had higher $\delta^{15}N$ than those that were considered more pristine (McClelland and Valiela 1998a). Valiela et al. (2000) suggested that local abundance of seagrasses, phytoplankton and macroalgae could serve as measurement points that would accurately estimate the nitrogen loading rates.

Several studies set in tidal freshwater marshes have looked at plant community responses to nutrient additions. In marshes along the Hudson River, New York, increases in nitrogen load have been linked to the success of invasive species that can sequester more nitrogen than native species (Otto et al. 1999). Invasive species, particularly *Phragmites australis*, affect local nitrogen dynamics primarily through their ability to produce greater biomass per unit area (and hence more sequestration of nitrogen) than indigenous dominant species. The plant appears to have the ability to substantially reduce local availability of NH_4^+ as compared to marshes without *Phragmites* and thus out-compete other plant species, as the plant sequesters the nitrogen in stored biomass (Meyerson et al. 1999).

The effect of these invasive plants can be seen on multiple levels in the affected system. Resident nekton must adjust to changes in plant stem density, quality and quantity of detritus and physical structure of the marshes. *Phragmites*-related effects, in particular, have been studied a great deal over the past few years in salt marshes. In tidal mesohaline marshes in the Delaware River estuary, *Fundulus heteroclitus,* the mummichog, was observed to switch from a diet low in material derived from *Spartina alterniflora* to a diet where over 70 percent of secondary production originated in *Phragmites* (Wainright et al. 2000). It has also been suggested that *Phragmites*-dominated marshes will result in less diverse nekton assemblages (Weinstein and Balletto 1999). There is empirical evidence suggesting shifts in patterns of nekton use based on differences in vegetation (Posey et al. 2003; Chick and McIvor 1997; Rader and Richardson 1994). Other research, however, has indicated virtually no difference in faunal species assemblages between the altered and unaltered systems (Meyerson et al. 2000; Meyer et al. 2001; Weis and Weis 2000).

The tidal freshwater marshes of the Nanticoke River have not undergone the widespread plant species replacements that other research in tidal wetlands has studied. What appears to be the case in these wetlands are more subtle, localized shifts in plant community composition and expression. Total plant biomass and plant species richness differ between Broad Creek and Marshyhope Creek (Figures 2.8 a and b), with each difference suggesting higher nutrient loads in Broad Creek. This supposition is supported

by the presence of more enriched nitrogen signatures and the historically greater nitrogen load Broad Creek has received.

Small fish and aquatic invertebrates have demonstrated well-defined responses to similar changes in macrophyte abundance and quality in tidal habitats on the Potomac River, Virginia. Observed fish density in SAV was often at its greatest in densely vegetated beds while adjacent beds with lower plant density have fewer fish in the early growing season (Killgore et al. 1989). Removal of plant material from these SAV beds, reducing physical structure available for small fish, has led to temporary shifts from demersal fish to pelagic species (Serafy et al. 1994). The effect of changes in plant community composition and structure are even more pronounced in other marsh systems. Increases in macroinverebrates and small fish density and species richness in the Water Conservation Areas of the Everglades have been related to the increase of *Typha latifolia* abundance in nutrient enriched locations (Rader and Richardson 1994). Small fish in these habitats have also been observed to exhibit selective prefererences for specific plant species when seeking cover from predators (Chick and McIvor 1997). Small fish density often seems to be higher in more densely vegetated marsh habitat, although it is not a universal behavior across species (Jordan et al. 1998). The comparison of plant biomass to group characteristics in Chapter Three do not overwhelmingly support this relationship. In the marshes of the Nanticoke, no measure of plant community biomass strongly correlated with any of the ordination axes describing nekton abundance (Figures 3.3 and 3.5). Some of the ordination sample units related to animal density did appear related to plant species richnessm but there was no clear pattern of either creek or site

affiliation with this trend (Figure 3.5). Thus, it is impossible to directly link the pattern seen at the Nanticoke sites to the those observed in other research.

The results of the isotopic analysis of these two tributaries of the Nanticoke River obviously lead to further questions about the presence and effect of enriched nitrogen in the coastal river systems of the Chesapeake Bay on several levels. The applicability of these results is limited because of the geographic scope of the study. All the sites are located within a single watershed feeding the Chesapeake. The SPARROW model estimates nutrient yields provided by over 1600 stream segments in the entire Chesapeake watershed. More of these units could be sampled in order to explore the relationship between nitrogen isotope ratios and the proportion of nitrogen load attributed to animal-derived sources.

The study would have been further enhanced by direct measures of groundwater nitrogen. While it is fairly clear from the results of this analysis and the supporting evidence regarding land-use and nitrogen loads that the groundwater contains nitrate with highly enriched nitrogen, it does not provide a direct link between the wetland ecosystems and the surrounding uplands. McClelland and Valiela (1998a) confirmed that the signatures in the biota of the estuary they studied were directly related to the quality of the groundwater by observing the groundwater's δ^{15}N ratio. The expansion in sources sampled should also expand to cover phytoplankton and attached algae, organisms that also directly utilize the nitrogen discharged by the groundwater

Regardless of these limitations, the evidence contained in the isotopic data strongly suggests a link between the quality of the nitrogen in plant and animal tissue in relation to local upland land uses and upstream sources. As seen in other coastal ecosystems, proximity to animal-derived nitrogen sources results in enriched nitrogen signatures in the biota. The widespread use of manure as a crop fertilizer on the Eastern Shore produces high levels of nitrate in the groundwater. Since groundwater is the primary source of water for coastal stream baseflow, it is highly likely that these signatures are the result of manure-derived nitrogen infiltrating the tidal freshwater wetlands.

CHAPTER SIX

SUMMARY OF THE PATTERNS IN PLANT AND ANIMAL COMMUNITY ASSEMBLAGE AND ECOSYSTEM STRUCTURE IN TIDAL FRESHWATER MARSHES OF THE NANTICOKE RIVER

The tidal freshwater wetlands of the Nanticoke River exist at the interface between landscapes, one dominated by urbanized and agricultural activities, the other being the highly variable estuarine environment. Straddling this interface, the wetlands are exposed to multiple environmental stressors. This includes elevated nutrient inputs from the upstream sources and frequent, yet intermittent, salinity pulses from the mesohaline regions downstream. This dissertation looked at multiple levels of ecological organization as it probed the basic question, how are the structure and composition of the plant and aquatic animal communities related to these various environmental factors.

The extended Nanticoke River watershed, including the Marshyhope Creek, Broad Creek and Deep Creek sub-watersheds, covers 822 square miles on the lower Eastern Shore in Maryland and Delaware (Chesapeake Bay Program 2003a). The watershed has the highest percentage of wetlands associated with any Chesapeake tributary, and tidal freshwater wetlands make up a very large portion of the watershed's total wetland coverage (Tiner 2005). In 1991, the river system was identified as both a Last Great Place and a Bioreserve by The Nature Conservancy (The Nature Conservancy 1998). Yet the Nanticoke River is facing a number of environmental threats, ranging from shoreline erosion from boat traffic to increased nutrient loads from human activities.

Given the aquatic nature of many of these problems, the river's tidal wetlands are one of the most endangered ecosystems in the watershed, and may be particularly threatened by the altered nutrient dynamics (The Nature Conservancy 1998).

The coastal landscape of the Chesapeake Bay has been affected by human activity for over three hundred years (Cooper 1995). Steadily increasing human populations within coastal watersheds across the United States have caused changes in the patterns of water, sediment and nutrient delivery in every major coastal system (Kiddon et al. 2003; Boesch 1996). Yet the effects of the nutrient enrichment on other ecosystems in the Chesapeake Bay's watershed are not as well understood, particularly for tidal wetlands. These ecosystems are certainly not immune to the effects of eutrophication. They are routinely cited as ideal natural systems for removing excess nutrients from coastal waters, particularly nitrogen (Kadlec and Knight 1996). This constant pressure from anthropogenic stressors ought to heighten the curiosity of ecologists and conservationists and encourage further study of these wetlands. Bay-wide monitoring efforts, however, acknowledge that evaluating the health of coastal wetlands of the bay region will be extremely difficult given the financial limitations of the restoration plans (Chesapeake Bay Program 2006). Efforts are underway to better identify the services wetlands provide, but these efforts focus more on their roles within the entire watershed landscape (Tiner 2005). Only one study ever directly looked at the effects of elevated nutrient inputs in tidal freshwater marshes, but it has been over 25 years since it was published (Whigham et al. 1980). Nutrient enrichment in ecosystems results in complex system responses, with effects often propagate throughout the higher trophic levels as the system,

as the components compensate for these changing environmental conditions (Carpenter et al. 1985; Vanni et al. 1997; Schindler et al. 1997; Lavrentyev et al. 1997). But there has never been a comprehensive effort to assess the consequences of nutrient enrichment in multiple trophic levels in tidal freshwater wetlands.

Also affecting the tidal freshwater marshes are frequent salinity pulses induced by long-term weather patterns. Prolonged droughts over the past fifteen years have resulted in at least five episodes where, well within the tidal freshwater zone, salinity rises above 0.5 parts per thousand for several months (Figure 4.1). The implications of salt water intrusions are not very well understood for freshwater fish, and the responses probably occur on multiple levels (Peterson and Meador 1994). Most of the species, even those that declined once the salinity reached its highest levels, exhibit fairly high levels of tolerance (Murdy et al. 1997). Any shifts in animal density are likely a consequence of species replacements as the range of species pools associated with downstream osmotic conditions eventually extended into the tidal freshwater marshes (Wagner and Austin 1999). In the plant community, Freshwater marsh plant response to increased salinity largely depends on the tolerance limits of the dominant species and the duration of the increase. If they can survive the saltwater influx, the marsh plant community should be able to survive (McKee and Mendelssohn 1989). Near term recovery of marsh vegetation is affected by the residual changes in interstitial salinity, reduced soil conditions and sulfide concentrations. The longer these persist at elevated levels, the more likely the marsh will continue to suffer a decline in aboveground biomass and species richness (Flynn et al. 1995).

In this study, the original research questions were framed around the issue of nutrient enrichment, and how it related to the two major tributaries of the Nanticoke River, Marshyhope Creek and Broad Creek (Figure 1.1). The Marshyhope Creek watershed covers 221square miles in both Maryland and Delaware, while that of Broad Creek spans across 123 square miles in Delaware. Further differentiating these two sub-watersheds are their respective patterns of land cover and use. Wetlands cover about 18.6 percent of the Marshyhope landscape, while Broad Creek's watershed contains only 6.5 percent. Proportionally, Broad Creek also has more than twice as much developed land than Marshyhope, 2.4 percent versus 0.9 percent (Chesapeake Bay Program 2003a). Even more significantly, though, the smaller Broad Creek watershed contains over 280 animal production facilities, while Marshyhope Creek has only 60 within its landscape (Chesapeake Bay Foundation 1996). As a possible consequence of this agricultural activity, the Broad Creek watershed has averaged about 265 – 1040 lbs/acre/year of nitrogen input derived from animal waste. The average manure-based nitrogen load in the Marshyhope watershed appears to be somewhat lower, with most areas ranging between 170 – 265 lbs/acre/year (Chesapeake Bay Foundation 1996). These differences suggest that the tidal freshwater marshes, as well as the other ecosystem types found in Broad Creek, have potentially been exposed to substantially higher nutrient loads than those in Marshyhope Creek have.

But in 2001, I began to notice that salinity was increasing at the downstream-most marsh sites. Beginning in October 2001, a prolonged drought began in the mid-Atlantic

region and persisted until the following September (National Drought Mitigation Center 2002). The consequence of the drought was a steady increase in the salinity of the river waters that flooded the marshes. This salinity change obviously had consequences for the distribution of both plants and animals in the marshes. Aquatic macrofauna responded immediately to changes, and the most dramatic effects appeared to occur within conditions considered freshwater, although measures of water conductivity indicated a fairly larger gradient of changes in the ionic concentration in the river water. The marsh plant community responded more slowly, but nonetheless, by August 2002, even the marsh plants began to show symptoms of the effects of salinity increases.

This chapter will highlight the major findings of each of the four principal sections of this dissertation. First, I will discuss the findings of the creek-wise comparisons of community level variables and individual species. This will focus on two questions: Are the creeks different from each other with respect to the plant and aquatic macrofauna communities, and whether or not fish and aquatic invertebrate abundance are related to plant community abundance. Second, I will discuss the results of ordination analysis in Chapter Three, addressing the following questions: Do plant and animal species assemblages in a predictable manner along the longitudinal river transect, and do the animal assemblages show any sort of relationship to plant community composition and abundance. In the third section, I will describe the results of Chapter Four where I presented a trophic network analysis comparison of the two creeks, hypothesizing that Broad Creek was more impacted by nutrient enrichment and should show more symptoms of eutrophication at the ecosystem level than Marshyhope Creek. Fourth, I will

conclude with a presentation of the principal results of Chapter Five, where I ask whether or not the elevated nutrient load and higher proportion of nitrogen originating from animal wastes in Broad Creek has resulted in significantly elevated nitrogen isotope ratios in the flora and fauna of this creek. Lastly, I will provide a brief synthesis of these results in the context of nutrient enrichment within a rapidly changing environment.

Comparison of Broad Creek and Marshyhope Marsh Communities

Several distinct differences emerged from this study that distinguish the creeks from each other. The differences in the plant community strongly suggest that there is a response to nutrient enrichment in Broad Creek, with more macrophyte biomass production than Marshyhope Creek yet fewer species per unit area (Figure 2.8). The difference in total species richness within the two creeks indicating fewer species in Broad Creek also corroborates the species density data (Table 2.7). Total nekton biomass was typically greater in Marshyhope, as was total animal density and species density in both trapping methods (Figures 2.10-2.12 and 2.14-2.16). These results combine to suggest that prolonged increases in the density of emergent marsh vegetation may lead to decreased aquatic macrofauna abundance. Given the fact that Broad Creek has a historically higher nitrogen load than Marshyhope Creek, the differences in nekton abundance may be an indirect consequence of this nutrient enrichment.

Yet this conclusion is by no means overwhelmingly supported by the results. The plant and animal communities offered some tempting differences, but the statistical comparisons generally did not support widespread differences between the two creeks. I

hypothesized that differences in plant species biomass and composition would result in an alteration of aquatic macrofauna abundance between the creeks. These mixed results corroborate similar research that looked at how aquatic animals were responding as plant community composition is changed. These studies suggested that plant species invasions in tidal marshes, particularly that of *Phragmites australis*, would create a less beneficial physical environment for nekton (Weinstein and Balletto 1999). My study approached this question from a different perspective. Species invasions resulting in complete species replacement are not the only way marsh vegetation can be affected by external events. Other more subtle changes can alter the characteristics of a plant assembly, the effects of which could cascade into the consumer organisms that depend on the structural benefits of the vegetation (Livingston 1984). Therefore, I wanted to identify if differences existed between presumably similar plant communities and, if they existed, to see if they were related to differences in aquatic macrofauna densities. Any conclusions drawn by this study, however, were complicated by uncontrollable environmental factors that had far-ranging effects on the flora and fauna tidal freshwater marshes. The consequence of the drought was a steady increase in the salinity of the river waters that flooded the marshes. Salinity changes likely explain why some differences appeared to not be significant, particularly in regard to animal abundance.

Landscape Level Patterns of Plant and Animal Species Assemblages

The ordination analysis of the plant and animal communities suggested that multiple environmental factors appeared to be related to the community structure and composition of both the plants and animals. Especially among the nekton, community

composition seemed to vary across the longitudinal river distance gradient. But seasonal patterns in plant community composition and structure overwhelmingly determined how the sample units in the vegetation-based ordination were distributed. The ordination of animal biomass did not reveal any well-defined groups and did have relatively high stress, but it did suggest that there was a certain level of segregation of sample units based on creek identity of the sample units. Animal density indicated that both seasonal patterns and affinity to marsh site both influenced the ordination of sample units. The ordinations of animal community characteristics indicated that many species tended to ordinate along axes associated with salinity and conductivity, which are a surrogate measure for distance upstream of each marsh. Among the animal community, however, there was not much evidence that patterns of plant species richness and community biomass (a measure of physical structure) were related to the distribution and abundance of the animals.

Marsh Ecosystem Response to Nutrient Enrichment and Salinity Stress

The two creeks were surprisingly similar in virtually every network analysis measure before the salinity pulse began to alter the behavior and function of the tidal freshwater marshes. There was a very strong seasonal pattern to the system level properties, but this was mostly a reflection of overall system activity rather than a fundamental shift in network structure (Fabiano et al. 2004; Baird and Ulanowicz 1989). Yet several features still stand out suggesting some functional differences that may be related to nutrient enrichment between the marshes of the two creeks. In many cases, trophic behaviors of the consumer organisms were very different from 2001 to 2002. The

same sorts of changes appeared in most of the system level indices, with the greatest

separations and trajectory deviations occurring in 2002 when Marshyhope Creek was

borderline oligohaline (e.g., Figure 4.21). Any differences before May 2002 would more

likely be related to the differences in nutrient regimes, while those that are expressed in

2002 are most likely the result of ecosystem response and compensation to the salinity

increase.

Nutrient enrichment and the rise in salinity in the tidal freshwater marshes suggest

a great deal about the immediacy and intensity of a given environmental stress. The

effects of the high levels of nutrient inputs into the Nanticoke River watershed are long

term and relatively consistent. It would be hard to consider, at this point, that the marshes

are undergoing any sort of press perturbation; the species composition has probably

arrived at some sort of relative stasis in response to the long-term excessive nutrient loads

the river receives (Bender et al. 1984). The constancy and uniformity of the nutrient

regime may minimize the practicality of using these two creeks as a space-for-time

substitution to observe the effects of nutrient enrichment (McClelland et al. 1997).

Nevertheless, certain results did suggest that nutrient enrichment, in the network analysis

sense, is occurring in the Broad Creek marshes. Aside from October 2001 when both

systems are undergoing seasonal collapse, Broad Creek had higher total system activity

than Marshyhope Creek, without a corresponding loss of organization. This meets the

network analysis definition of enrichment, but falls short of the hypothesized

consequences of eutrophication which would entail degraded organization (Ulanowicz

1997). The higher nitrogen load associated with Broad Creek has probably ratcheted up

the activity of this creek system, but it has not compromised its organizational integrity relative to Marshyhope Creek. Because the comparative "baseline" creek is also exposed to a similarly large macronutrient input, the effectiveness of the comparison is probably limited.

Nitrogen Isotopes and Nitrogen Sources in the Nanticoke River

The isotopic ratios indicate that nitrogen in Broad Creek is more enriched with ^{15}N, while the percent nitrogen content of the samples suggest there is no pattern to the availability of nitrogen that might affect these ratios. The higher trophic levels reflect the enriched source as both primary and secondary consumer organisms demonstrate predicted patterns of increases in δ^{15}N. The most recent SPARROW model of Chesapeake Bay nutrient loading rates estimated that Marshyhope Creek receives a substantially smaller percentage of nitrogen derived from animal waste than Broad Creek (Brakebill and Preston 2004). While the most recent estimates of total yield of nitrogen are now slightly greater in Marshyhope Creek than in Broad Creek, there is a major difference in nitrogen sources as Broad Creek receives 0.739 kg N ha^{-1} y^{-1} more nitrogen from animal manure than does Marshyhope Creek. The enrichment in isotopic signatures also appears in higher trophic levels where both aquatic invertebrates and small fish also have higher δ^{15}N in Broad Creek than in Marshyhope Creek.

Ecosystem Structure and Function of Tidal Freshwater Marshes

This study identified responses at multiple hierarchical levels of tidal freshwater marshes to both the long-term differences in nutrient loads in the two creeks and the gradually rising salinity stress. The creek-wise comparison of Chapter One suggested that

the plant communities of the localized sub-watersheds differ with respect to total community biomass, a likely consequence of nutrient enrichment. Yet the aquatic animal community did not seem to respond to this pattern of vegetative expression. As the analysis expanded to a larger scale in the ordinations included in Chapter Three, it became very apparent that in the case of the aquatic macrofauna, it was proximity to the downstream estuarine environment that clearly influenced the species assemblages along the longitudinal gradient. This effect was reinforced by the network analyses where it became clear that the effect of the differences in nutrient load had resulted in modest differences between the creeks. The species assemblages, as indicated by Sørensen's Similarity Index, were fairly similar between the creeks, especially before the drought. Thus, the network analysis measures indicated subtle differences between the creeks relative to nutrient enrichment. It was only after the decomposition of the measures of ascendency that the underlying pattern of organization suggested that Broad Creek had both a higher level of organization in conjunction with greater total system throughput. This is symptomatic of ecosystems enduring nutrient enrichment, but relative to Marshyhope Creek, it does not seem that the higher nutrient load in Broad Creek has resulted in large-scale functional changes in its marshes. The relative lack of change in the tidal freshwater marshes after the salinity increase suggests that the marsh ecosystem is fairly resistant to stress. The higher-level consumers, for the most part, exhibit a fairly wide range salinity tolerance. The plant community also appears fairly robust to the stress imparted by brackish waters, as it took at least three months of exposure to the steadily rising salinity before macrophyte biomass production was noticeably impacted. The marshes appear to be well organized relative to the stresses of the intertidal zone,

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although it is surprising that these systems adapted to stressful environments may lack resilience. Marshyhope Creek appears slightly more resistant, given its relative lack of significant change during the exposure to the salinity increase. Species losses and declines here seem to have been supplemented by similarly functioning replacements. Broad Creek, on the other hand, exposed less frequently to the salinity stress, showed greater declines in organization and the network measures of resilience at the peak of the drought, although the declines were not precipitous, compared to other ecosystems. Yet the concluding chapter indicated that long-term exposure to relatively higher loading rates of nitrogen from animal derived sources, namely poultry waste, has altered the quality of nitrogen in Broad Creek, again relative to Marshyhope Creek.

The lack of distinction may be the due to the degree of difference in the basic comparison. It is possible that the creeks, in reality, are too similar, and their high level of shared common features are hindering the detection of widespread meaningful differences relative to nutrient enrichment. Both creeks exist in a region of the Chesapeake Bay watershed with some of the highest nutrient loading rates. Both creeks have presumably come to some sort of equilibrium in terms of species assemblage and abundance with respect to the high levels of nutrient enrichment. Thus the relative lack of difference between the creeks in terms of community level properties and even ecosystem level function before the drought. It was not until the salinity increase arrived that both the species assemblages and ecosystem properties showed demonstrable responses. In the ordinations, there is a clear distinction between downstream and upstream nekton

assemblages. The ecosystem functions of the marshes also diverged as the drought continued.

Future efforts to examine how tidal freshwater marsh plant and animal communities respond to nutrient enrichment should consider looking at sites in more river systems. The Nanticoke River receives very high nutrient loads, but there are other rivers receiving higher inputs of nutrients. Sampling marshes across a gradient of nutrient enrichment would likely provide a better picture of how the tidal freshwater marsh ecosystems are responding to differing levels of enrichment.

APPENDIX I

ELABORATION OF FIELD COLLECTION AND LABORATORY METHODOLOGIES

RESEARCH METHODS

I collected soil, plant, macroinvertebrate and small fish samples from the six study sites from August 2000 through August 2002. Only the throw trap, water quality and low marsh vegetation data were collected in 2000. From May 2001 until the conclusion of field activities in August 2002, all sampling protocols described hereafter were performed at every site on each date. Sampling activities were confined to the growing season since these months are when animal species richness is at its maximum and aboveground vegetation is at its most complex levels of development.

Soil Sampling

Soils were collected from May 2001 through August 2002. The primary purpose for collecting the soils was for stable isotope analysis to identify the potential sources of material and energy in these ecosystems. I also looked at organic matter, carbon and nitrogen content of the soils. At each site, three low marsh samples and three high marsh samples were collected using a bulb planter to extract approximately the top 10 cm of soil material. Each sample trip produced nine high marsh and nine low marsh samples per creek. The samples were stored in airtight bags and kept in refrigeration until they were processed.

Upon return to the laboratory, the samples were placed into aluminum tins and were dried in an environmental chamber set at 116° F and 7 percent relative humidity for at least seven days. The dried samples were broken by hand and then milled to a powder using Cyclotech 1093 sample mill with a 0.75 mm screen over the discharge vent. This screen size was sufficiently small enough to produce a finely pulverized powder of sample material (grain size <0.1 mm diameter). The powdered soil was stored in airtight containers until used for further analysis.

Soil Organic Matter Content

Each sample's organic matter content was estimated using a standard loss-on-ignition technique (Nelson and Sommers 1996). Samples were placed in crucibles that were pre-heated for two hours in a 400° C Fisher Scientific Isotemp muffle furnace. Soil sample material was placed into the prepared crucibles, weighed to the nearest 0.0001 g and heated at 105° C for 24 hours. The samples were placed in a dessicator over $CaCl_2$ to cool and then reweighed to the nearest 0.0001 g. The samples were returned to the muffle furnace, set at 400° C, for 16 hours to ignite the organic material. The crucibles were allowed to cool and then weighed a final time. LOI content was calculated as:

$$\%LOI = (Weight_{105} - Weight_{400} / Weight_{105}) \times 100$$

where $Weight_{105}$ is the soil mass after the initial muffle furnace treatment and $Weight_{400}$ is the soil mass after the ignition stage.

Soil Nitrogen and Carbon Content

Percent nitrogen and carbon in the marsh soil samples was estimated during stable isotope analysis. Samples were sent to the Colorado Plateau Stable Isotope Laboratory where they were analyzed with a Finnigan Delta Plus XL mass spectrometer configured for continuous flow analysis of organic samples after Dumas combustion. Each sample was simultaneously analyzed for carbon and nitrogen. This process provided data about isotopic ratios for C and N, percent C and N and C/N. The sample processing and analysis techniques are fully described in Chapter Four.

Plant Samples

I collected plants in both high and low marsh habitats. Low marsh sampling began in August 2000 in conjunction with my throw trapping efforts to collect fish and aquatic macroinvertebrates. High marsh vegetation sampling began in May 2001. Both sampling efforts concluded in August 2002.

In both the high and low marsh, a 0.25 m^2 PVC square quadrat was used to define an area of aboveground biomass that was harvested by cutting the plant stems at ground level with a knife. The high marsh samples were located haphazardly by pitching the quadrat onto the marsh surface and then working it down to the ground through the dense vegetation. These were collected from the same general areas within each high marsh site on each sampling date. The low marsh collections, on the other hand, were taken from within the quadrat placed in a randomly chosen corner of the throw trap after it was

deployed. The aboveground vegetation that was rooted within the square was removed and placed into separate containers and returned to the University of Maryland Wetland Ecology and Engineering Laboratory for subsequent sorting and identification.

Plant Sample Processing

The samples were sorted down to the species level (Crow and Hellquist 2000a; Crow and Hellquist 2000b; Tiner 1993). After sorting, each species was placed into a separate paper bag labeled by species name, sample date and location. The contents of the bags were then dried in an environmental chamber set at 116° F and 7 percent relative humidity for at least seven days. Following this initial drying period, the samples were placed into a Yamoto DX 600 Drying Oven at 80° C for 48 hours. After this second drying period, the plant material was weighed on a Mettler PM34-K DeltaRange balance to determine the dry weight of the plant tissue to the nearest 0.1 g.

<u>Throw Traps</u>

Throw trapping is an active technique used in shallow aquatic and inundated wetland habitats to provide density estimates of animal populations (Kushlan 1981). Its most effective use, however, is limited to sampling macroinvertebrates (e.g., snails, shrimps, crayfish and insect larvae) and small fish in shallow water since it samples such a small area (Jordan et al. 1997; Turner and Trexler 1997; Chick et al. 1992; Whiteside and Lindegaard 1980). The construction of this device is very simple; it is a 1 m by 1 m cube-shaped frame lined with barrier material on the sides. Both the top and bottom are open. The trappers toss the device a short distance from themselves, and then quickly

approach it and press on the top to secure the edges down into the underlying substrate, trapping all mobile organisms within its walls. Once the trap is secured, the plant material is thinned out in order to create working room for sweepnets to be able to pass back and forth through the water column to collect the animals.

Trap Design

The throw trap I constructed possessed a more reinforced and rigid design than those described by other researchers. Some researchers using throw traps have alluded to the fragility of the standard design rod frame and mesh walled throw traps versus portability trade-offs with more heavy-duty construction (Kushlan 1981). The marsh sample sites I was working in consisted of mostly unconsolidated substrates interlaced with dense *Nuphar lutea* rhizomes just below the surface. It was clear that I needed a trap that would endure a substantial amount of wear and tear from both transport and deployment. The frame I designed consisted of two 2 m by 0.6 m 1/8-inch thick aluminum sheets folded to form a 90° angle. Each sheet formed two sides of the throw trap. The two halves were welded together to complete the cube, and aluminum angle was riveted to the welded joints for additional strength. Additional bands of aluminum angle were pop-riveted to the sides and welded together at the corners 15 cm from the bottom and along the top of the trap to provide lateral reinforcement to the trap frame (Figure 2.2).

Sampling Techniques

The traps were deployed haphazardly along the low water edge of the low marsh habitat in water of depths between 5 cm and 45 cm. In order to minimize the effects of tidal stage on faunal distributions, I only collected samples as the tide was falling. By obeying this protocol, I could only complete five to seven samples per tidal cycle before the river water receded to my sample cutoff point – the subtidal mudflats below the low marsh edge.

The low marsh substrate of the sample sites was very mucky and unconsolidated and prevented me from effectively deploying the traps anywhere but from the stable surface of a boat deck. The traps were cast from the reinforced bow decking of a 17' Princecraft Holiday DLX BT utility boat. In order to minimize the effect of the presence of the boat in the marsh, approximately five minutes were allowed to pass once the boat was in position and the trap caster was stationed on the bow. My own observations of the fish in the marshes indicated that the small aquatic macrofauna seemed to adjust to the boat's presence in less than a minute, but I settled on five minutes to make sure that as many organisms as possible were no longer disturbed by my presence. This time duration was also short enough to allow me to safely perform at least six traps per falling tide.

Once the trap was cast, it was immediately secured on all four sides by pressing the trap walls down into the substrate. After the trap was thoroughly anchored, I measured the following environmental variables: water depth, water temperature, salinity, conductivity, and dissolved oxygen. Water depth was estimated by averaging two depth

readings taken with a meter stick just resting on the substrate, one taken near the inshore-most part of the trap and the other from the part of the trap nearest to the main channel. Salinity (ppt) and conductivity (μS cm^{-1}) were measured with an YSI-30 salinity/conductivity meter in 2001 and 2002. In 2000, salinity was estimated using a refractometer, and conductivity was not measured. Dissolved oxygen (mg L^{-1}) was measured in 2000 with an Orion Model 810 Dissolved Oxygen Meter and in 2001-2002 with an YSI-55 instrument. Water temperature was recorded on three different devices over the span of the study. In 2000, I used the Orion Model 810 to measure water temperature. In 2001 and 2002, I used both an YSI-30 meter and YSI-55 meter to record water temperature. While the readings never varied more than a few tenths of a degree, I averaged the two temperature readings from both YSI devices in 2001 and 2002 before performing any comparative data analysis with the flora and fauna.

Once physical parameters had been estimated, the trap area was visually surveyed and a stem density estimate was determined. Density categories ranged from 0 implying no vegetative cover to 5 indicating "very high" coverage that would impede access to all but small aquatic macrofaunal organisms. When the trap caster exited the boat and secured the trap, he or she would identify the trap corner for vegetation sampling. Since the securing process involved several arbitrary circuits around the trap to anchor it, the corner of the trap the caster ended up nearest to was designated the vegetation sample location. Plants were then sampled as described above (Section 3.2). The aboveground vegetation in the remaining area of the trap was also removed to permit the sweep net to

pass through the trap without obstruction. All plant material was visually inspected for attached organisms before it was collected or discarded.

After the trap area was clear, a sweep net was passed through the water column to collect all fauna contained within the trap. The sweep net consisted of one inch diameter PVC pipes connected together to form a frame ~1 m wide by 0.6 m high. This 0.6 m x 1 m space was covered with standard door screen (mesh openings measured 1/16-inch across) fastened to the frame with cable ties. I attached two 0.4 m arms to the top so the person sweeping had a place to hold it. The trap was swept with the net in two opposite directions to make sure that any potential refuge area near the sweep net's insertion point on one side of the trap was adequately cleared by the passes from the opposite direction. At least five sweep net passes were taken in every trap. If animals were collected in sweep four or five, passes continued until there were no animals collected on two consecutive sweeps.

In 2000, all specimens were euthanized in the field using a lethal concentration of Tricaine-MS. The specimens were then temporarily preserved using a 10 percent Formalin solution. They were transferred to a 70 percent solution of ethanol within two weeks for long-term storage. In 2001 and 2002, I collected tissue samples from the animals for stable isotope analysis and could not use any preservatives that might alter the C and N signatures of the specimens. All captured animals, therefore, were immediately placed in an ice-water bath to reduce metabolic activity before euthanization. Following the University of Maryland's Institutional Animal Care and

Uses Committee (IACUC) approved protocols, the vertebrates were euthanized by inserting a scalpel blade through the skull into the brain. All specimens, both invertebrates and fish, were then frozen for transport and storage.

Animals were identified to the lowest possible taxon. For the fish, I was able to identify all specimens to species level (Murdy et al. 1997; Lippson and Lippson 1997; Rohde et al. 1994; Wang and Kernehan 1979; Lippson and Moran 1974). Invertebrates were identified to species level at best, or to a functional taxonomic group at the least (Voshell 2002; Jessup et al. 1999; McCafferty 1988; White 1989; Pennak 1978). The fish were measured for total length in millimeters, and all individual animal mass (g wet weight) were measured on a Metler AG204 DeltaRange balance.

I collected approximately six throw trap samples at each marsh site on each research trip. I began throw trapping in May 2000 and concluded the sampling in August 2002. I collected a total of 245 throw trap samples over the duration of the study.

Flume Traps

I used my own variation of the flume trap along the high marsh/low marsh transition areas based on the classic design of the same name (McIvor and Odum 1986; McIvor and Odum 1985). Fish are more mobile than the macroinvertebrates in these marsh communities, so this method offered an additional measure of fish abundance that might identify any biases in the throw trap and whether or not larger fish moved into the shallower waters of the low marsh/high marsh transition zone.

The flume trap is used to capture aquatic animals as they enter the high marsh when tidewaters rise. It consists of two parallel barriers spaced 1.5 m apart and perpendicular to the river's edge, open at the deepwater end. As the tide rises and fish move into the marsh, they are confined within the walls of the barrier as they follow the rising waters and enter the high marsh. At slack high tide, another net is anchored at the deepwater end that will collect the retreating fish as the waters exit the marsh. Once the tide has fallen, the trapping net is removed and the specimens can be cleared from the trap (McIvor and Odum 1986).

Trap Design

My flume traps consisted of two separate components: the permanent parallel barriers installed in the marsh and the detachable trapping portion of the assemblage. The permanent barriers could not capture fish without the trap net, so they posed no risk to the fauna of the marsh when no sampling activities were occurring.

I placed two 12 meter-long nets 1.5 m apart, parallel to each other and perpendicular to the water's edge over the high marsh/low marsh transition zone to make the permanent barriers. Half of the net was in the low marsh zone, and half in the high marsh zone. I used 1/8-inch plastic netting (Nylon Net Company) attached to one-inch PVC pipe anchor poles to construct these barriers (Figure 2.3). The deep-water end of the barrier wall averaged about 1.25 meters high, while the inland barrier height was closer to 0.6 meters. This height ensured that the top of the net was always higher than

the maximum water depth at high tide. The barrier net was also buried 20 cm deep into the substrate to prevent animal escape.

The trapping portion of the flumes consisted of mini-trawl nets made of 1/32-inch delta knotless netting attached to aluminum frames. This netting is non-abrasive and animals cannot become entangled in it, which simplified the trap-clearing process. The mini-trawls themselves were 1.5 m wide by 0.4 m high. The net tapered down from this opening to a cod-end that could be cinched shut. The mini-trawl nets were manufactured by the Nylon Net Company, Memphis, Tennessee.

The frame that the mini-trawl was attached to consisted of two 1.6 m long side supports, a 1.5 m sloped plate along the bottom and two 1.5 m center support bars holding the sides together, one at the top and one 40 cm from the bottom. All these components were welded together forming a frame 1.5 m wide by 1.6 m high (Figure 2.4). The mini-trawl nets were attached to the lower opening in the frame while the upper opening of the frame was covered with more 1/32-inch knotless netting to complete the barrier. The netting was attached to the frame by sandwiching it between the welded frame and small aluminum strips. The strips, netting and frame were fastened together with stainless steel hex bolts, nuts, washers and lock washers spaced every four inches along the frame. On the leading edge of the trap, I attached two one-inch PVC guide poles spaced 0.75 cm off the frame so that the PVC piping was not directly touching the poles. These poles served as the anchor points for the detachable trap to the barrier nets.

The guide poles on the mini-trawl frame slid into end-anchors on the barrier nets. Two-inch PVC poles with a 1.5 cm wide vertical channel routed into it served as the end-anchors. They were affixed to the deepwater ends of the barrier nets with the channel facing outward. To deploy the trap, the guide poles were slid inside the anchor poles and the entire frame was firmly pressed to the substrate, which securely attached the trap net assemblage to the barrier nets.

Two permanent stations (i.e., the barrier nets) were located at each site. I constructed six of these trap nets for this study, which enabled me to sample all six stations on either creek simultaneously.

Collection Techniques

An individual sample collection consisted of three steps: trap deployment, a passive collection period and, finally, trap removal and clearing. At slack high tide, we approached the sample station by boat to attach the mini-trawl collection nets (we used a 17" Princecraft Holiday DLX BT utility boat). The process required two people, one to insert the trap net and one to guide the boat. As we approached the barrier nets at the station, the boat operator would cut the engine and slip overboard into the shallows to maneuver the boat quietly by hand toward the trap opening. The installer would stand upon the bow decking holding the trap net. Once the boat was next to the barrier opening, the installer would quickly place the guide poles into the slots along the permanent anchor poles and slide the trap net down to the marsh surface. Approach and deployment

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optimally took less than one minute. The trawl net, with its cod-end closed, was then stretched out to its fullest extent and anchored to the ground.

Once the tide waters had fallen below the mouth of the mini-trawl nets, we would remove the trap net and empty its contents. I only collected fish and what I called "charismatic" macroinvertebrates (e.g., shrimps and crabs) from the flume traps. The throw trap samples sufficiently described macroinvertebrate community characteristics in more density-specific terms, so these species were not collected here to minimize the number of organisms destructively sampled (Chick et al. 1992). Animals were preserved, sorted and processed in the same manner as described for the throw traps.

I began using the flume traps in May 2001, and I continued deploying them through August 2002. Due to some mechanical defects in the guide pole design, only six total samples were collected in May 2001. In the remaining four sample events, I attempted to collect three samples per station per trip. This would ideally produce six samples per marsh site per trip, or 18 samples per creek per trip. Across all dates, I collected 136 flume samples. On most occasions, irreparable damage to either the trap frame (October 2001 and May/June 2002) or to the mini-trawls (August 2002) limited the total number of samples.

Data Analysis

The data sets from field observation have let me look for ecological trends and relationships in several different ways, ranging from simple correlation analyses to more

complex multivariate analyses. While I was able to perform comparisons within specific data sets, I was, more importantly, also able to aggregate data for each site on each date. This allowed me to examine data across observational data sets to develop a better picture of the relationships among the multiple variables I observed.

There were several variable descriptions that were common to most field samples. Both faunal trapping techniques produced data about animal abundance, biomass and in the case of fish, total length. These data were either aggregated to assess variables at the community level, like species richness and total biomass, or individually for each species, such as numerical abundance and biomass of specific species. For the throw trap samples, each biological variable had a corresponding measure of salinity, conductivity, dissolved oxygen, water temperature, water depth, plant stem density and plant biomass.

Vegetation samples produced fewer community variables. Since samples were identified to species level and then weighed, the only measure of abundance was biomass – individual stems were not counted. Therefore, only species richness, total biomass and individual species biomasses are available for the plants. Soil data is limited to percent total carbon, percent total nitrogen and organic matter content, all of which are presented for both low and high marsh soils for each site.

When it was deemed necessary, data were transformed ($\ln (x+1)$) to minimize any issues with non-normality to proceed with parametric statistical evaluations. All

transformations were done before any data reductions were performed (i.e.,

transformations occurred before any site means were calculated).

Comparison of Animal Trapping Methods

Two different trapping techniques were used to characterize the aquatic

macrofauna in tidal freshwater marshes to account for any unexpected biases in either of

the trapping methods. It was impossible to compare the numerical or biomass catches of

each trap directly since the resultant totals are not in compatible terms. The throw trap is

an active trap that estimates density per unit area, while the flume trap is a passive device

where collections occur over a prolonged period of time and span an undefined area. If,

however, the data are relativized to the proportion each species contributes to the total

abundance, then I can directly compare how similar the two trapping methods are.

I compared these proportions using a paired sample t-test for each species using

SPSS 10 to compute the test statistics (SPSS Inc. 1999). The proportion of total

abundance for each species found in the throw and flume traps were paired based on

sample date and creek, which provided 28 pairs of data for each variable. I only

compared the 12 most abundant animal species across the five sample dates for both

numerical density and biomass, omitting those that occurred in less than five percent of

the samples. To evaluate the significance of the t-test results, I used the Hochberg

experimental-wise error to test significance of each comparison. This sequential method

is considered more powerful than other Bonferoni experiment-wise tests of significance

(Quinn and Keough 2002). After the t-tests were performed, the p-values were ranked

from greatest to smallest. The largest p-value was compared to α, the second largest to $\alpha/2$, the third largest to $\alpha/3$, and so on (in these analyses, $\alpha = 0.05$). Whenever a calculated p-value was less than its paired critical value, it and all other p-values less than or equal to that value are considered to be significant (Hochberg 1988).

Correlation Analysis

The throw trap data set has habitat data directly associated with each sample unit. Therefore, it was possible to examine these data to identify if any of the measured water quality and associated vegetation variables were correlated with the fish and invertebrate assemblages. Pearson correlation coefficients are present in three matrices, one for all samples combined, and then one for each creek. The correlation matrices present the strength of the relationship, direction of the relationship and the statistical significance of the relationship. SPSS was used to calculate the Pearson correlation (SPSS Inc. 1999).

Analysis of Variance

Analysis of Variance (ANOVA) was performed on all the community level variables and for density and biomass for selected dominant species. Site means for each sample date were compiled from each of the original data sets consisting of the individual samples. This step was necessary since the individual samples at each site do not represent true replicates. The replicates in this study are the sites, where each collection (i.e., individual throw trap sample, high marsh plant quadrat, etc.) represents a subsample within each site.

Creek, date and their interaction were used as independent factors for the vegetation, throw trap, flume trap, and soil data. The sites were sampled repeatedly over time, introducing the likelihood that the data were temporally correlated. I used a repeated measures analysis design to deal with this concern. Three different models were initially used, one assuming homogenous variance for the target variable, and two assuming heterogeneous variances resulting either from creek or date. If model fit was better in either of the partitioned variance models, then heterogeneous variances were assumed. Different covariance matrix structures were then evaluated to produce the model with best fit for each dependent variable, using either homogenous or heterogeneous covariance matrix structures based on the results of the partitioning (Larry Douglass, Biometrics Program, University of Maryland, personal communication).

Six covariates were additionally included in the ANOVA models of the throw trap data. Higher order interactions among covariates and factors, however, were not considered in the models. Inclusion of these interactions consumed too many degrees of freedom to perform meaningful ANOVA. Non-significant covariates ($p < 0.1$) were removed from these models. PROC MIXED was used for all ANOVA (SAS Institute 2003).

Sorensen's Similarity Index

I used Sorenson's Similarity Index to further assess the similarity of the creeks. The index uses presence and absence of species to calculate a value between 0 and 1 that measures similarity between communities, in this case, measuring the degree of similarity

between Broad and Marshyhope Creeks (Sørensen 1948). The closer the number is to one, the more similar the creeks will be. The data was compiled in two different ways to look at the patterns in similarity over time. First, vegetation and animal species were combined to develop a comprehensive list of what species were present and in which sites they were occurred. In this case, the index should reflect the variation among the sites within each creek. The second data set discounted the effect of site and only identified presence or absence by creek. If the sites are highly variable, then this calculation should result in a higher value, or greater similarity, for the index.

APPENDIX II

SUMMARY OF DATA FOR BROAD CREEK AND MARSHYHOPE CREEK

This appendix presents a summary of the raw data collected at the research sites from August 2000 through August 2002. The inclusion of this data presentation in earlier chapters was not vital to their content. Most of this data presented here was either graphically represented earlier or did not add any meaningful context to the comparisons of the two creek systems.

I wanted to provide a source for future researchers who might be interested in the biomass and numerical densities of organisms in tidal freshwater marshes. I am speaking specifically of scientists in the modeling community, who often are looking for data to either provide an estimate of standing stocks or evidence that supports their assumptions about plant and animal distributions. For those engaged in network analysis, in particular, the availability of organism densities per unit area is critical for establishing the baseline characteristics of a network. Finding biomass estimates for target species can sometimes feel like winning the lottery.

The means in the following tables are often the arithmetic means of the raw data and may be different than those discussed in earlier chapters. They may also be different from means presented elsewhere, especially for data that was detransformed for graphical presentations. Table A2.1 presents grand means for the aquatic macrofauna collected in both flume and throw traps. These data are presented in their transformed values (ln

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(x+1)), since the detransformed error estimates are assymetrical. Tables A2.2 and A2.3 present the means for these organisms spread across all dates between the creeks for both the throw traps and flume traps, and they are likewise presented as the transformed values. The next four tables (A2.4 through A2.7) present both animal abundance and biomass estimates of every species for both the throw trap and the flume trap. These are followed by presentations of mean plant biomass for each species on both creeks (Table A2.8 and A2.9) and the measures of water quality and habitat characteristics (Table A2.10). The last data presentation summarizes all the estimates associated with stable isotope analysis, many of which were not explicitly discussed in this dissertation (Tables A2.11 and A2.12).

Table A2.1. Community level variable grand means from throw and flume traps for Broad Creek and Marshyhope Creek. Units for density are number of individuals, biomasses are grams wet weight, and species densities are number of species. Measurement scales differ between the methods. Throw traps are m^{-1}, while flume traps are $trap^{-1}$. Standard errors of the means are presented within parentheses following the mean values. Density and biomass numbers remain in transformed format (ln (x+1)).

Throw Traps	Broad Creek	Marshyhope Creek
Total Density	2.4633 (0.385)	2.7702 (0.385)
Total Biomass	0.9456 (0.114)	1.5368 (0.124)
Total Species Density	2.8532 (0.275)	3.3297 (0.275)
Fish Density	1.5045 (0.146)	1.6359 (0.146)
Fish Biomass	0.8652 (0.107)	1.4196 (0.118)
Fish Species Density	1.1104 (0.072)	1.6903 (0.079)
Invertebrate Density	1.6917 (0.256)	1.9403 (0.375)
Invertebrate Biomass	0.1030 (0.015)	0.2450 (0.057)
Invertebrate Species Density	1.5688 (0.373)	2.1319 (0.375)

Flume Traps		
Total Density	1.8384 (0.260)	2.4937 (0.260)
Total Biomass	1.9414 (0.175)	2.8034 (0.175)
Total Species Density	2.0278 (0.246)	3.0486 (0.246)
Fish Density	1.8659 (0.271)	2.4070 (0.271)
Fish Biomass	1.9106 (0.285)	2.4929 (0.285)
Fish Species Density	1.8882 (0.305)	2.6491 (0.247)

Table A2.2. Community level variable means on each sample date in Broad Creek and Marshyhope Creek. Units for density are number of individuals m^{-1}, biomasses are grams wet weight m^{-1}, and species densities are number of species m^{-1}. Standard errors of the means are presented within parentheses following the means. Density and biomass numbers remain in transformed format (ln $(x+1)$).

Broad Creek	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Total Density	3.1527 (0.420)	2.9965 (0.390)	2.1850 (0.201)	2.3129 (0.209)	2.1389 (0.133)	2.4427 (0.148)	2.1925 (0.191)
Total Biomass	0.7705 (0.269)	0.8199 (0.273)	0.7559 (0.240)	1.0073 (0.233)	0.8574 (0.189)	1.3766 (0.270)	1.5186 (0.272)
Total Species Density	2.9375 (0.433)	1.8889 (0.254)	2.6875 (0.362)	3.0000 (0.404)	3.2778 (0.331)	3.2222 (0.250)	3.0556 (0.328)
Fish Density	2.8074 (0.434)	1.3243 (0.370)	1.0564 (0.209)	1.0668 (0.243)	0.7931 (0.202)	1.8890 (0.249)	1.6808 (0.258)
Fish Biomass	0.6698 (0.272)	0.7304 (0.275)	0.7194 (0.244)	0.9083 (0.247)	0.7890 (0.199)	1.3545 (0.274)	1.4795 (0.280)
Fish Species Density	0.8889 (0.193)	0.6667 (0.140)	0.9375 (0.193)	1.0556 (0.249)	0.7778 (0.191)	1.7778 (0.207)	2.0556 (0.338)
Invertebrate Density	1.6890 (0.322)	2.5426 (0.422)	1.7586 (0.249)	1.8676 (0.236)	1.7726 (0.182)	1.1943 (0.193)	1.0173 (0.188)
Invertebrate Biomass	0.1966 (0.052)	0.1698 (0.058)	0.0671 (0.017)	0.1338 (0.043)	0.1095 (0.026)	0.0413 (0.011)	0.0782 (0.015)
Invertebrate Species Density	2.0000 (0.329)	1.2222 (0.207)	1.7500 (0.296)	1.9444 (0.308)	2.5000 (0.345)	1.3889 (0.257)	1.0000 (0.162)

Broad Creek	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Total Density	2.7692 (0.296)	2.0014 (0.232)	2.5486 (0.265)	3.1274 (0.399)	2.7604 (0.508)	3.2747 (0.392)	2.8053 (0.221)
Total Biomass	1.1236 (0.225)	1.0458 (0.177)	1.4670 (0.272)	1.9334 (0.350)	1.3264 (0.269)	1.2692 (0.242)	1.8446 (0.268)
Total Species Density	3.2500 (0.233)	2.1111 (0.241)	3.6875 (0.506)	3.3333 (0.396)	2.3158 (0.242)	4.8333 (0.638)	3.8333 (0.305)
Fish Density	1.9541 (0.382)	1.2361 (0.202)	1.7838 (0.207)	1.8832 (0.295)	1.2072 (0.261)	1.1312 (0.193)	2.1920 (0.285)
Fish Biomass	1.0426 (0.239)	1.0379 (0.178)	1.4317 (0.278)	1.7924 (0.377)	1.0230 (0.245)	1.0460 (0.273)	1.6954 (0.286)
Fish Species Density	1.1875 (0.136)	1.0000 (0.114)	2.3750 (0.375)	1.8333 (0.294)	0.9474 (0.179)	1.5556 (0.345)	2.2778 (0.211)
Invertebrate Density	1.8365 (0.260)	1.1852 (0.254)	1.6314 (0.354)	2.0513 (0.514)	2.0956 (0.576)	2.9336 (0.459)	1.8481 (0.205)
Invertebrate Biomass	0.1456 (0.029)	0.0226 (0.006)	0.0809 (0.026)	0.2148 (0.085)	0.3964 (0.205)	0.3130 (0.072)	0.4461 (0.117)
Invertebrate Species Density	2.0625 (0.266)	1.0556 (0.206)	1.3125 (0.299)	1.5000 (0.345)	1.3684 (0.256)	3.6111 (0.572)	1.5556 (0.185)

Table A2.3. Community level variable means on each sample date in flume traps in Broad Creek and Marshyhope Creek. Units for density are number of individuals trap^{-1}, biomasses are grams wet weight trap^{-1}, and species densities are number of species trap^{-1}. Standard errors of the means are presented within parentheses following the means. Density and biomass numbers remain in transformed format (ln (x+1)).

Broad Creek	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Total Density	.	.	1.4256 (0.542)	2.0143 (0.220)	2.0395 (0.267)	2.5785 (0.175)	2.2352 (0.265)
Total Biomass	.	.	1.9279 (0.420)	2.1658 (0.265)	2.2428 (0.289)	2.5879 (0.265)	2.9875 (0.312)
Total Species Density	.	.	1.6667 (0.333)	2.1111 (0.279)	2.4167 (0.452)	2.3889 (0.216)	2.800 (0.509)
Fish Density	.	.	1.4256 (0.542)	2.0111 (0.219)	2.0222 (0.263)	2.5785 (0.175)	2.217 (0.266)
Fish Biomass	.	.	1.9279 (0.420)	2.1645 (0.265)	2.2417 (0.289)	2.5879 (0.265)	2.7190 (0.265)
Fish Species Density	.	.	1.6667 (0.333)	2.0556 (0.286)	2.3333 (0.414)	2.3889 (0.216)	2.2667 (0.492)

Marshyhope Creek	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Total Density	.	.	1.6060 (0.206)	1.8631 (0.172)	2.3092 (0.301)	1.7078 (0.169)	3.2972 (0.263)
Total Biomass	.	.	1.3072 (0.267)	2.0627 (0.364)	3.5568 (0.261)	1.5969 (0.245)	3.1307 (0.372)
Total Species Density	.	.	1.5000 (0.146)	2.1176 (0.373)	2.3333 (0.333)	1.7500 (0.194)	5.1333 (0.413)
Fish Density	.	.	1.5657 (0.208)	1.8603 (0.171)	2.3092 (0.301)	1.6337 (0.195)	3.1270 (0.260)
Fish Biomass	.	.	1.1733 (0.266)	2.0625 (0.364)	3.5568 (0.261)	1.5832 (0.249)	2.8255 (0.327)
Fish Species Density	.	.	1.4444 (0.145)	1.9412 (0.348)	2.3333 (0.333)	1.5625 (0.203)	4.0000 (0.378)

Table A2.4. Animal densities in throw traps in both creek systems presented as mean abundance (numbers m^{-1}) and standard error of the mean (value within parentheses). Species with less than five total occurrences are aggregated in the "Other" categories.

a. Broad Creek

Species List	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	0	0	0	0	0
Etheostoma olmstedi	0	0	0.31 (0.31)	0.11 (0.11)	0	1.22 (0.61)	0.06 (0.06)
Fundulus diaphanus	9.50 (4.66)	13.50 (6.37)	1.94 (0.90)	3.33 (1.69)	1.56 (0.71)	1.94 (1.09)	3.67 (1.82)
Fundulus heteroclitus	0.06 (0.06)	0	0.13 (0.09)	0	0.11 (0.08)	0.61 (0.56)	0.17 (0.12)
Gambusia holbrooki	1.00 (0.66)	0.06 (0.06)	0.13 (0.13)	0	0.39 (0.39)	0.22 (0.13)	1.00 (0.83)
Gobiosoma bosc	0	0	0	0	0	0	0
Lepomis macrochirus	0	0	0	0.72 (0.23)	0.17 (0.12)	0.11 (0.08)	0.11 (0.08)
Menidia beryllina	0	0	0	0	0	0	0
Morone americana	0	0	0.06 (0.06)	0	0	1.78 (0.97)	0
Notropis hudsonius	0	0	0.12 (0.12)	0	0	3.28 (1.47)	0
Trinectes maculatus	0	0	0	0	0	0	2.50 (0.84)
Other Fish	0	0	0.25 (0.17)	0.06 (0.06)	0.06 (0.06)	0.06 (0.06)	0.89 (0.66)
Calinetes sapidus	0	0	0	0	0	0	0
Coenagrionidae	0.37 (0.18)	0.28 (0.19)	0.25 (0.14)	0.39 (0.29)	0.44 (0.16)	0	0
Cordulidae	0.19 (0.10)	0	0.06 (0.06)	0.06 (0.06)	0.28 (0.14)	0.06 (0.06)	0.06 (0.06)
Corixia sp.	47.56 (17.08)	40.22 (13.51)	5.69 (3.77)	3.39 (0.96)	2.33 (0.90)	0	0.89 (0.78)
Gammarus sp.	0.81 (0.44)	0.61 (0.51)	2.25 (1.01)	3.44 (1.59)	1.72 (0.89)	2.11 (0.60)	0
Palaemonetes pugio	0.19 (0.10)	0	0	0	0	0	0.33 (0.16)
Physia gyrina	0	0.06 (0.06)	0.19 (0.10)	0.17 (0.17)	0.39 (0.14)	0.17 (0.12)	0.06 (0.06)
Other Invertebrates	0	0.67 (0.33)	0.50 (0.27)	1.17 (0.43)	1.44 (0.42)	1.00 (0.35)	1.50 (0.54)

b. Marshyhope Creek

Species List	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	0	0	1.42 (1.42)	0	3.11 (2.30)
Etheostoma olmstedi	0	0.06 (0.06)	0.63 (0.27)	0.06 (0.06)	0	0.83 (0.46)	0.17 (0.09)
Fundulus diaphanus	4.88 (1.36)	3.94 (1.26)	0.75 (0.28)	6.00 (2.09)	3.32 (1.22)	0.61 (0.20)	7.56 (3.33)
Fundulus heteroclitus	0.19 (0.10)	0	0.88 (0.42)	4.83 (4.26)	0.37 (0.23)	1.00 (0.45)	0.22 (0.13)
Gambusia holbrooki	5.69 (5.24)	0	0.31 (0.15)	1.28 (0.74)	0	0.44 (0.39)	4.78 (2.50)
Gobiosoma bosc	0	0	0	0	0	0	0.78 (0.29)
Lepomis macrochirus	0	0	0	0.17 (0.12)	0	0	0
Menidia beryllina	0	0	0	0	0	0	0
Morone americana	0	0	0.94 (0.41)	0.06 (0.06)	0.05 (0.05)	0.11 (0.08)	0.11 (0.11)
Notropis hudsonius	0	0.06 (0.06)	3.56 (1.67)	0.11 (0.08)	0.21 (0.12)	0.22 (0.22)	0
Trinectes maculatus	0.06 (0.06)	0	0	0.06 (0.06)	0	0	0.39 (0.18)
Other Fish	0	0	0.06 (0.06)	0.11 (0.08)	0	0	0
Calinetes sapidus	0	0	0	0	0	0	0.11 (0.08)
Coenagrionidae	0.19 (0.14)	0.94 (0.32)	0	0.06 (0.06)	0.16 (0.12)	0	0
Cordulidae	0	0	0	0.22 (0.13)	0	0.06 (0.06)	0.11 (0.08)
Corixia sp.	24.50 (13.92)	3.50 (1.84)	8.38 (5.53)	98.28 (75.19)	889.05 (858.23)	51.28 (22.84)	2.06 (1.11)
Gammarus sp.	0.38 (0.26)	0.39 (0.23)	3.75 (1.58)	1.00 (0.73)	0.21 (0.09)	11.78 (3.85)	0
Palaemonetes pugio	0.31 (0.15)	0	0	0.06 (0.06)	0.58 (0.25)	0	5.33 (1.99)
Physia gyrina	0.07 (0.07)	0	0.06 (0.06)	0.11 (0.08)	0.26 (0.13)	0.28 (0.14)	0.06 (0.06)
Other Invertebrates	0	0.94 (0.32)	0.63 (0.44)	0.56 (0.22)	0.32 (0.19)	8.89 (2.75)	0.39 (0.14)

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Table A2.5. Animal biomass in throw traps in both creek systems presented as mean wet weight (g m^{-1}) and standard error of the mean (value within parenthesis). Species with less than five total occurrences are aggregated in the "Other" categories.

a. Broad Creek

Species List	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	0	0	0	0	0
Etheostoma olmstedi	0	0	0.009 (0.009)	0.28 (0.28)	0	0.23 (0.15)	0.10 (0.10)
Fundulus diaphanus	3.64 (2.68)	4.34 (2.50)	1.87 (1.16)	2.48 (0.93)	1.11 (0.56)	2.91 (1.59)	3.95 (2.54)
Fundulus heteroclitus	0.10 (0.10)	0	0.51 (0.37)	0	0.32 (0.25)	1.19 (1.04)	0.19 (0.14)
Gambusia holbrooki	0.05 (0.03)	0.01 (0.01)	0.001 (0.001)	0	0.12 (0.12)	0.21 (0.19)	0.17 (0.16)
Gobiosoma bosc	0	0	0	0	0	0	0
Lepomis macrochirus	0	0	0	0.63 (0.21)	0.48 (0.36)	1.34 (1.24)	0.13 (0.09)
Menidia beryllina	0	0	0	0	0	0	0
Morone americana	0	0	0.06 (0.06)	0	0	0.26 (0.14)	0
Notropis hudsonius	0	0	0	0	0	0.10 (0.05)	0
Trinectes maculatus	0	0	0	0	0	0	1.25 (0.41)
Other Fish	0	0	0.08 (0.08)	0.07 (0.07)	0.10 (0.10)	0.15 (0.15)	1.92 (1.13)
Calinetes sapidus	0	0	0	0	0	0	0
Coenagrionidae	0.01 (0.01)	0.003 (0.002)	0.004 (0.003)	0.001 (0.0007)	0.003 (0.001)	0	0
Cordulidae	0.003 (0.002)	0	0.006 (0.006)	0.0002 (0.0002)	0.01 (0.005)	0.002 (0.002)	0.002 (0.002)
Corixia sp.	0.17 (0.06)	0.16 (0.06)	0.02 (0.01)	0.06 (0.54)	0.01 (0.003)	0	0.004 (0.003)
Gammarus spp.	0.01 (0.007)	0.004 (0.002)	0.01 (0.004)	0.03 (0.02)	0.01 (0.005)	0.02 (0.005)	0
Palaemonetes pugio	0.01 (0.008)	0	0	0	0	0	0.02 (0.01)
Physia gyrina	0	0.001 (0.001)	0.005 (0.003)	0.01 (0.01)	0.04 (0.02)	0.006 (0.004)	0.003 (0.003)
Other Invertebrates	0	0.06 (0.05)	0.02 (0.01)	0.06 (0.03)	0.05 (0.02)	0.02 (0.01)	0.05 (0.02)

b. Marshyhope Creek

Species List	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	0	0	0.62 (0.62)	0	0.43 (0.37)
Etheostoma olmstedi	0	0.13 (0.13)	0.10 (0.05)	0.12 (0.12)	0	0.17 (0.14)	0.35 (0.20)
Fundulus diaphanus	2.38 (1.04)	2.46 (0.72)	1.28 (0.51)	6.02 (3.10)	1.32 (0.53)	0.55 (0.28)	6.79 (3.09)
Fundulus heteroclitus	0.52 (0.35)	0	2.39 (1.22)	16.23 (14.62)	0.91 (0.54)	3.18 (1.64)	0.38 (0.29)
Gambusia holbrooki	0.50 (0.48)	0	0.09 (0.07)	0.10 (0.05)	0	0.70 (0.64)	0.53 (0.25)
Gobiosoma bosc	0	0	0	0	0	0	0.21 (0.07)
Lepomis macrochirus	0	0	0	0.42 (0.34)	0	0	0
Menidia beryllina	0	0	0	0	0	0	0
Morone americana	0	0	3.19 (3.06)	0.13 (0.13)	0.71 (0.71)	0.02 (0.01)	1.24 (1.24)
Notropis hudsonius	0	0.19 (0.19)	0	0.03 (0.03)	0.48 (0.34)	0.008 (0.008)	0
Trinectes maculatus	0.003 (0.003)	0	0	0.02 (0.02)	0	0	0.07 (0.03)
Other Fish	0	0	0.02 (0.02)	1.00 (0.92)	0	0	0
Calinetes sapidus	0	0	0	0	0	0	0.08 (0.07)
Coenagrionidae	0.002 (0.001)	0.01 (0.003)	0	0.0001 (0.001)	0.001 (0.0009)	0	0
Cordulidae	0	0	0	0.005 (0.003)	0	0.007 (0.007)	0.005 (0.003)
Corixia sp.	0.06 (0.03)	0.01 (0.006)	0.03 (0.02)	0.28 (0.21)	2.82 (2.72)	0.17 (0.07)	0.01 (0.004)
Gammarus spp.	0.003 (0.001)	0.003 (0.002)	0.03 (0.01)	0.006 (0.005)	0.001 (0.0007)	0.07 (0.02)	0
Palaemonetes pugio	0.02 (0.01)	0	0	0.007 (0.007)	0.12 (0.05)	0	0.67 (0.24)
Physia gyrina	0.01 (0.01)	0	0.002 (0.002)	0.02 (0.01)	0.01 (0.008)	0.01 (0.005)	0.0002 (0.0002)
Other Invertebrates	0	0.008 (0.003)	0.03 (0.02)	0.04 (0.02)	0.007 (0.005)	0.18 (0.07)	0.04 (0.02)

Table A2.6. Animal density in flume traps in both creek systems presented as mean abundance (numbers m^{-1}) and standard error of the mean (value within parenthesis). Species with less than five total occurrences are aggregated in the "Other" categories. Fish species are presented first, followed by invertebrates.

a. Broad Creek

Species List	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	1.39 (0.92)	0.12 (0.12)	0.17 (0.17)
Etheostoma olmstedi	0	0.06 (0.06)	0	0.06 (0.06)	0
Fundulus diaphanus	3.33 (2.85)	3.83 (1.01)	5.89 (1.92)	3.53 (0.74)	6.58 (2.33)
Fundulus heteroclitus	1.33 (0.33)	0.50 (0.50)	1.67 (0.80)	2.18 (0.63)	0.50 (0.29)
Gambusia holbrooki	0	1.28 (0.51)	0.17 (0.12)	0.47 (0.33)	1.33 (0.60)
Gobiosoma bosc	0	0	0	0	0
Lepomis macrochirus	0	0.17 (0.12)	0.61 (0.34)	0.18 (0.09)	0.25 (0.13)
Menidia beryllina	0	0	0	0	0
Morone americana	0	0	0	0.06 (0.06)	0.08 (0.08)
Notropis hudsonius	0	0	0.22 (0.10)	0.41 (0.31)	0.25 (0.18)
Trinectes maculatus	0	0	0	0	0
Other Fish	0	0	0.06 (0.06)	0	0.50 (0.50)
Calinetes sapidus	0	0	0	0	0
Palaemonetes pugio	0	0	0	0	0.25 (0.25)
Physia gyrina	0	0	0.06 (0.06)	0.06 (0.06)	0
Other Invertebrates	0	0.06 (0.06)	0	0	0

b. Marshyhope Creek

Species List	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	0.13 (0.13)	0.06 (0.06)	10.47 (5.89)
Etheostoma olmstedi	0	0.05 (0.05)	0.13 (0.08)	0.38 (0.22)	0.20 (0.11)
Fundulus diaphanus	3.67 (1.76)	9.94 (1.99)	4.13 (0.78)	3.00 (1.12)	9.33 (3.18)
Fundulus heteroclitus	6.00 (1.73)	0.89 (0.41)	1.25 (0.53)	5.88 (1.33)	8.47 (3.52)
Gambusia holbrooki	0	3.94 (1.54)	0	0.88 (0.44)	3.13 (1.34)
Gobiosoma bosc	0	0	0	0	1.07 (0.53)
Lepomis macrochirus	0	0	0	0	0
Menidia beryllina	0	0	0	0	0.40 (0.21)
Morone americana	0	0.22 (0.10)	0	1.25 (0.81)	0.60 (0.24)
Notropis hudsonius	0.33 (0.33)	0.61 (0.36)	0	1.25 (0.63)	0
Trinectes maculatus	0	0.17 (0.12)	0	0	0.20 (0.14)
Other Fish	0	0.06 (0.06)	0	0.06 (0.06)	0.07 (0.07)
Calinetes sapidus	0	0	0	0.06 (0.06)	1.07 (0.41)
Palaemonetes pugio	0	0	0.19 (0.10)	0	5.73 (2.98)
Physia gyrina	0	0	0	0.06 (0.06)	0
Other Invertebrates	0	0	0	0	0.07 (0.07)

Table A2.7. Animal biomass in flume traps in both creek systems presented as mean wet weight (g m^{-1}) and standard error of the mean (value within parenthesis). Species with less than five total occurrences are aggregated in the "Other" categories. Fish species are presented first, followed by invertebrates.

a. Broad Creek

Species List	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	0.65 (0.48)	0.03 (0.03)	0.03 (0.03)
Etheostoma olmstedi	0	0.08 (0.08)	0	0.01 (0.01)	0
Fundulus diaphanus	3.57 (2.65)	3.01 (1.33)	4.55 (1.49)	5.70 (2.02)	3.82 (1.06)
Fundulus heteroclitus	3.74 (1.26)	0.52 (0.52)	2.22 (1.03)	4.57 (1.37)	0.72 (0.41)
Gambusia holbrooki	0	0.17 (0.08)	0.03 (0.02)	0.14 (0.10)	0.19 (0.12)
Gobiosoma bosc	0	0	0	0	0
Lepomis macrochirus	0	1.63 (1.26)	4.49 (2.08)	8.99 (6.96)	5.15 (3.13)
Menidia beryllina	0	0	0	0	0
Morone americana	0	0	0	2.3 (2.36)	1.00 (1.00)
Notropis hudsonius	0	0	1.09 (0.51)	0.02 (0.01)	1.09 (0.76)
Trinectes maculatus	0	0	0	0	0
Other Fish	0	0	0.23 (0.23)	0	0.75 (0.75)
Calinetes sapidus	0	0	0	0	0
Palaemonetes pugio	0	0	0	0	0.01 (0.01)
Physia gyrina	0	0	0.01 (0.01)	0.02 (0.02)	0
Other Invertebrates	0	0.61 (0.61)	0	0	0

b. Marshyhope Creek

Species List	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Anchoa mitchilli	0	0	0.04 (0.04)	0.01 (0.01)	1.84 (0.99)
Etheostoma olmstedi	0	0.12 (0.12)	0.38 (0.26)	1.40 (0.78)	0.27 (0.15)
Fundulus diaphanus	8.65 (5.05)	7.91 (2.57)	2.29 (0.57)	5.19 (2.10)	7.53 (3.26)
Fundulus heteroclitus	24.03 (7.63)	2.98 (1.52)	3.85 (1.53)	14.66 (3.51)	7.72 (2.78)
Gambusia holbrooki	0	0.47 (0.19)	0	0.58 (0.23)	0.40 (0.16)
Gobiosoma bosc	0	0	0	0	0.33 (0.15)
Lepomis macrochirus	0	0	0	0	0
Menidia beryllina	0	0	0	0	0.17 (0.09)
Morone americana	0	4.78 (2.57)	0	0.12 (0.08)	8.23 (3.53)
Notropis hudsonius	0	4.07 (2.27)	0	5.15 (2.84)	0
Trinectes maculatus	0	0.11 (0.07)	0	0	0.08 (0.06)
Other Fish	0	0.90 (0.90)	0	0.01 (0.01)	1.55 (1.55)
Calinetes sapidus	0	0	0	2.77 (2.77)	19.17 (12.40)
Palaemonetes pugio	0	0	0.03 (0.02)	0	0.75 (0.38)
Physia gyrina	0	0	0	0.01 (0.01)	0
Other Invertebrates	0	0	0	0	0.02 (0.02)

Table A2.8. Mean biomass of marsh vegetation in Broad Creek. Presented as dry weight (g 0.25 m^{-1}) and standard error of the mean (value within parenthesis). High marsh (a.) and low marsh (b.) biomass are presented in two separate tables.

a. High Marsh Species List	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Acorus calamus	169.98 (18.68)	30.03 (5.36)	15.27 (1.91)	148.26 (12.49)	22.23 (5.75)
Amaranthus cannabinus	0	0	0	0	1.74 (1.74)
Bidens laevis	0.51 (0.39)	5.34 (3.32)	0.22 (0.12)	0.05 (0.05)	56.85 (27.21)
Bidens sp.	0.33 (0.24)	0	0	0	1.33 (0.99)
Calystegia sepium	0.03 (0.03)	1.23 (0.82)	0.2	1.55 (0.91)	1.94 (1.25)
Cuscuta gronovii	0.08 (0.05)	1.38 (0.60)	0.09 (0.09)	0.01 (0.008)	0.13 (0.10)
DEAD	16.95 (3.81)	10.53 (2.13)	78.99 (9.98)	9.24 (5.52)	59.85 (7.00)
Dulichium arundinaceum	0	0	0	0	0
Galium tinctorium	0	3.05 (2.15)	2.12 1.38)	0.35 (0.31)	1.23 (0.86)
Impatiens capensis	9.32 (2.38)	2.81 (1.14)	2.15 (1.86)	3.78 (1.09)	1.37 (0.83)
Iris versicolor L.	0	5.04 (5.04)	0	0	0
Leersia oryzoides	2.29 (1.79)	6.97 (4.32)	5.46 (3.25)	4.46 (2.52)	2.97 (1.78)
Nuphar lutea	2.24 (2.24)	0	0	0	0.92 (0.66)
Peltandra virginica	13.04 (4.17)	3.83 (1.30)	0.55 (0.30)	23.32 (5.27)	6.58 (2.37)
Polygonum arifolium	9.21 (2.63)	17.60 (4.98)	0.69 (0.65)	5.87 (1.67)	54.61 (18.83)
Polygonum punctatum	0	0	4.27 (4.27)	0	0
Polygonum sagittatum	0.01 (0.01)	0.19 (0.13)	2.04 (1.42)	0.41 (0.41)	0.56 (0.33)
Schoenoplectus fluviatilis	12.31 (5.04)	4.98 (3.17)	5.40 (1.97)	0	8.13 (7.12)
S. tabernaemontani	0	0	0	0	0
Sparganium americanum	0	0	0	0	0
Typha latifolia	0	0	0	0	0
Zizania aquatica	0.36 (0.26)	0.63 (0.63)	0	0.02 (0.02)	15.13 (9.02)
Poaceae (unidentified species)	0	0	0	0.31 (0.31)	0
Sagittaria latifolia	0.64 (0.46)	0	0	0.56 (0.33)	0
Boehmeria cylindrica	0	0	0	0	0
Typha angustifolia	0	0	0	0	0
Mikania scandens	0	0	0	0	0
Aster sp.	0	0	0	0	0
Mentha arvensis	0	0	0.35 (0.35)	0	0

b. Low Marsh Species List	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Nuphar lutea	20.60 (4.46)	5.39 (1.51)	65.18 (8.00)	31.28 (3.82)	18.53 (4.17)	41.72 (8.03)	39.77 (7.36)
Zizania aquatica	2.01 (1.27)	1.44 (1.01)	0	0.19 (0.19)	0	0	0
Pontedaria cordata	0	0.61 (0.61)	0	0	0.26 (0.26)	0	0

Table A2.9. Mean biomass of marsh vegetation in Marshyhope Creek. Presented as dry weight (g 0.25 m^{-1}) and standard error of the mean (value within parenthesis). High marsh and low marsh biomass are separated into two separate tables.

a. High Marsh Species List	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Acorus calamus	136.92 (12.21)	24.18 (3.51)	15.6 (1.17)	115.03 (10.98)	29.09 (4.05)
Amaranthus cannabinus	0	0	0	0	0.59 (0.59)
Bidens laevis	0	0.005 (0.005)	0.17 (0.12)	0.36 (0.28)	0.56 (0.56)
Bidens sp.	0.02 (0.02)	0	0	0.05 (0.04)	0
Calystegia sepium	1.24 (0.58)	0.10 (0.08)	0.02 (0.01)	0.24 (0.17)	0
Cuscuta gronovii	0.13 (0.06)	3.45 (1.58)	0.02 (0.02)	0.02 (0.01)	0.05 (0.03)
DEAD	22.15 (4.19)	24.68 (4.32)	46.07 (6.95)	9.19 (2.80)	71.93 (9.46)
Dulichium arundinaceum	0	0	0	0	0.49 (0.49)
Galium tinctorium	0.21 (0.18)	0.76 (0.68)	1.98 (1.46)	0.07 (0.07)	0.05 (0.05)
Impatiens capensis	12.35 (2.77)	2.05 (0.64)	1.06 (0.54)	11.02 (2.37)	0.45 (0.25)
Iris versicolor L.	0	0	0.61 (0.61)	0	5.11 (5.11)
Leersia oryzoides	5.69 (3.70)	4.06 (2.24)	1.56 (0.50)	3.04 (1.07)	3.16 (1.56)
Nuphar lutea	0	0	0	0	0
Peltandra virginica	8.11 (3.39)	4.89 (1.49)	0.45 (0.31)	21.51 (6.06)	12.29 (5.52)
Polygonum arifolium	7.35 (3.16)	12.24 (5.23)	0.28 (0.20)	4.21 (1.15)	13.36 (6.60)
Polygonum punctatum	0	0.05 (0.05)	0.08 (0.08)	0	0.04 (0.04)
Polygonum sagittatum	0.002 (0.002)	0.08 (0.08)	0.28 (0.28)	0.08 (0.07)	2.93 (1.28)
Schoenoplectus fluviatilis	25.36 (8.92)	17.27 (6.49)	5.64 (2.32)	4.33 (2.24)	7.89 (3.26)
S. tabernaemontani	0	0	0.34 (0.34)	0	0.36 (0.20)
Sparganium americanum	0	0	0	0	0.72 (0.72)
Typha latifolia	1.27 (0.81)	3.15 (2.52)	5.97 (4.34)	0.76 (0.76)	3.07 (3.07)
Zizania aquatica	0.01 (0.01)	0.24 (0.24)	0	0.58 (0.58)	0
Poaceae (unidentified species)	0	0	0	0.38 (0.28)	0
Sagittaria latifolia	0.21 (0.14)	0.14 (0.10)	0.04 (0.04)	0.09 (0.07)	0
Boehmeria cylindrica	0	0.77 (0.77)	0	0	0
Typha angustifolia	0.14 (0.14)	0	0.88 (0.88)	0	0
Mikania scandens	0.33 (0.33)	0	0	0	0
Aster sp.	0	0	0.57 (0.55)	0	0
Mentha arvensis	0	0	0.11 (0.11)	0	0

b. Low Marsh Species List	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Nuphar lutea	16.88 (6.26)	4.76 (1.18)	22.15 (4.69)	33.41 (5.10)	16.62 (2.62)	62.48 (12.75)	24.27 (6.14)
Zizania aquatica	0.26 (0.13)	3.58 (1.57)	0.31 (0.17)	6.81 (5.53)	0.60 (0.55)	1.22 (0.65)	0.74 (0.53)
Pontedaria cordata	1.98 (1.98)	0.39 (0.27)	0	0	0	0	0

Table A2.10. Mean values of water quality and habitat measurements taken simultaneously with throw traps. Units of measurement are described after each descriptor. Stem density measure units are described in Appendix I. Plant species richness refers to low marsh richness only. Conductivity was not measured in 2000. Means for each variable are presented, along with their respective standard error of the means (value enclosed within parentheses).

a. Broad Creek	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Dissolved O_2 (ml L^{-1})	10.53 (1.16)	6.98 (0.67)	6.28 (0.50)	8.32 (0.51)	10.63 (0.34)	6.34 (0.65)	5.93 (0.27)
Temperature (°C)	25.30 (1.52)	18.72 (0.37)	26.08 (0.28)	26.19 (0.21)	19.23 (0.39)	24.14 (0.15)	24.98 (0.33)
Conductivity (μS cm^{-1})	.	.	123.01 (1.41)	131.73 (2.20)	142.63 (1.60)	155.76 (6.49)	204.01 (7.97)
Salinity (‰)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
Stem Density	3.88 (0.20)	3.89 (0.18)	4.06 (0.21)	3.83 (0.15)	3.22 (0.19)	3.39 (0.27)	3.00 (0.24)
Plant Species Richness	2.19 (0.33)	1.39 (0.16)	0.94 (0.06)	1.06 (0.06)	1.05 (0.57)	1.0 (0.0)	1.0 (0.0)

b. Marshyhope Creek	Aug 2000	Oct 2000	May 2001	Aug 2001	Oct 2001	May 2002	Aug 2002
Dissolved O_2 (ml L^{-1})	7.92 (0.53)	5.42 (0.62)	7.24 (0.25)	5.91 (0.34)	8.78 (0.44)	7.20 (0.50)	5.70 (0.41)
Temperature (°C)	25.54 (0.34)	18.78 (0.33)	24.64 (0.29)	24.71 (0.27)	16.72 (0.42)	21.39 (0.23)	23.82 (0.32)
Conductivity (μS cm^{-1})	.	.	126.25 (2.42)	153.54 (5.39)	320.73 (49.32)	532.76 (104.45)	834.80 (193.296)
Salinity (‰)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.1 (0.0)	0.16 (0.02)	0.27 (0.04)	0.41 (0.10)
Stem Density	3.81 (0.25)	3.72 (0.14)	3.12 (0.15)	3.67 (0.24)	3.42 (0.14)	3.67 (0.21)	2.83 (0.19)
Plant Species Richness	2.44 (0.56)	1.33 (0.11)	1.25 (1.17)	1.17 (0.09)	1.05 (0.12)	1.39 (0.12)	0.94 (0.13)

Table A2.11. Means of carbon and nitrogen elemental analysis for Broad Creek taxa. Units for isotopic ratios are parts per thousand. These units are defined in Chapter 3. If a species was analyzed in both May and October 2001, then a "total" mean is provided also. The first number in each cell is the mean value, followed by the standard error of the mean inside the parentheses.

Taxon	Date Code	δ^{13}C	δ^{15}N	%C	%N	C/N
Acorus calamus	May 2001	-27.49 (0.16)	13.23 (0.31)	40.59 (0.65)	2.41 (0.11)	16.98 (0.89)
Acorus calamus	October 2001	-27.23 (0.46)	13.44 (0.49)	39.09 (0.10)	2.18 (0.12)	18.14 (1.02)
Acorus calamus	Total	-27.36 (0.23)	13.33 (0.27)	39.84 (0.42)	2.29 (0.09)	17.56 (0.66)
Impatiens capensis	May 2001	-29.63 (0.10)	12.30 (0.76)	38.30 (1.22)	2.28 (0.34)	17.92 (2.48)
Impatiens capensis	October 2001	-29.51 (0.46)	11.52 (0.67)	37.04 (0.32)	2.05 (0.14)	18.31 (1.12)
Impatiens capensis	Total	-29.57 (0.22)	11.91 (0.49)	37.67 (0.63)	2.16 (0.18)	18.12 (1.26)
Leerzia oryzoides	October 2001	-27.21 (0.15)	12.90 (0.49)	40.23 (0.94)	1.341 (0.10)	30.53 (2.36)
Nuphar lutea	October 2001	-25.95 (0.19)	7.77 (0.55)	24.63 (1.92)	2.27 (0.13)	10.90 (0.87)
Peltandra virginica	May 2001	-26.46 (0.29)	10.92 (1.18)	37.34 (0.77)	3.96 (0.17)	9.47 (0.40)
Polygonum arifolium	May 2001	-28.80 (0.09)	11.82 (0.16)	39.52 (0.28)	2.59 (0.11)	15.31 (0.58)
Schoenoplectus fluviatilis	May 2001	-26.58 (0.09)	11.41 (0.28)	41.42 (0.36)	1.48 (0.11)	28.49 (2.12)
Schoenoplectus fluviatilis	October 2001	-27.40 (0.43)	11.68 (0.15)	41.28 (0.03)	1.12 (0.04)	37.00 (1.29)
Schoenoplectus fluviatilis	Total	-26.94 (0.24)	11.53 (0.17)	41.36 (0.20)	1.32 (0.09)	32.14 (2.11)
Anchoa mitchilli	October 2001	-24.57 (0.59)	17.43 (0.19)	46.39 (0.58)	13.23 (0.13)	3.51 (0.02)
Coenagrionidae	October 2001	-26.30(0.17)	12.68 (0.19)	44.45 (0.51)	11.76 (0.43)	3.78 (0.09)
Corbicula fluminea	October 2001	-28.86 (0.28)	11.45 (0.40)	47.93 (0.32)	9.37 (0.33)	5.13 (0.17)
Corixidae	May 2001	-26.56 (0.21)	11.36 (0.15)	46.08 (0.27)	11.51 (0.08)	4.00 (0.01)
Corixidae	October 2001	-25.99 (0.29)	11.63 (0.26)	47.55 (0.99)	10.12 (0.39)	4.75 (0.28)
Corixidae	Total	-26.28 (0.19)	11.50 (0.15)	46.81 (0.53)	10.82 (0.28)	4.38 (0.17)
Etheostoma olmstedi	May 2001	-26.27 (0.01)	15.98 (0.22)	44.31 (0.91)	12.58 (0.41)	3.52 (0.04)
Etheostoma olmstedi	October 2001	-25.04 (0.23)	15.17 (0.33)	45.62 (0.54)	13.90 (0.03)	3.28 (0.03)
Etheostoma olmstedi	Total	-25.65 (0.29)	15.58 (0.25)	44.97 (0.56)	13.24 (0.35)	3.40 (0.06)
Fundulus diaphanus (S)	October 2001	-25.69 (0.15)	16.48 (0.35)	46.26 (0.43)	13.03 (0.16)	3.55 (0.05)
Fundulus diaphanus (L)	May 2001	-24.99 (0.17)	16.17 (0.20)	44.26 (0.26)	13.80 (0.03)	3.21 (0.01)
Fundulus diaphanus (L)	October 2001	-25.05 (0.17)	16.76 (0.25)	44.25 (0.63)	12.53 (0.14)	3.53 (0.04)
Fundulus diaphanus (L)	Total	-25.02 (0.12)	16.49 (0.18)	44.26 (0.35)	13.10 (0.21)	3.39 (0.06)
Fundulus heteroclitus	May 2001	-25.16 (0.23)	16.58 (0.22)	43.70 (0.71)	13.33 (0.30)	3.28 (0.02)
Fundulus heteroclitus	October 2001	-25.34 (0.14)	16.97 (0.28)	44.43 (2.41)	11.94 (0.69)	3.73 (0.10)
Fundulus heteroclitus	Total	-25.27 (0.12)	16.81 (0.19)	44.14 (1.42)	12.50 (0.47)	3.55 (0.09)
Gammarus sp.	May 2001	-26.35 (0.25)	11.26 (0.12)	36.14 (0.91)	8.19 (0.26)	4.42 (0.07)
Gammarus sp.	October 2001	-25.88 (0.69)	10.24 (0.23)	34.64 (0.69)	7.91 (0.17)	4.44 (0.06)
Gammarus sp.	Total	-26.14 (0.33)	10.75 (0.20)	35.46 (0.61)	8.05 (0.15)	4.43 (0.04)
Lepomis macrochirus	October 2001	-25.60 (0.62)	15.35 (1.39)	41.77 (1.64)	12.88 (0.47)	3.24 (0.02)
Notropis hudsonius	May 2001	-26.66 (0.16)	15.42 (0.20)	45.27 (0.62)	13.33 (0.15)	3.40 (0.01)
Notropis hudsonius	October 2001	-25.72 (0.16)	15.65 (0.57)	45.64 (0.88)	13.52 (0.28)	3.38 (0.11)
Notropis hudsonius	Total	-26.26 (0.22)	15.52 (0.25)	45.43 (0.47)	13.41 (0.14)	3.39 (0.04)
High Marsh Soil	Total	-28.30 (0.13)	9.90 (0.26)	18.52 (2.96)	1.39 (0.22)	13.22 (0.15)
Low Marsh Soil	Total	-26.47 (0.17)	5.78 (0.20)	7.48 (0.64)	0.60 (0.02)	12.34 (0.75)

Table A2.12. Means of carbon and nitrogen elemental analysis for Marshyhope Creek taxa. Units for isotopic ratios are parts per thousand. These units are defined in Chapter 3. If a species was analyzed in both May and October 2001, then a "total" mean is provided also. The first number in each cell is the mean value, followed by the standard error of the mean inside the parentheses.

Taxon	Date Code	$\delta^{13}C$	$\delta^{15}N$	%C	%N	C/N
Acorus calamus	May 2001	-27.07 (0.19)	10.88 (0.49)	40.97 (0.48)	2.02 (0.07)	20.35 (0.55)
Acorus calamus	October 2001	-26.85 (0.19)	10.68 (0.25)	38.26 (0.28)	2.23 (0.04)	17.20 (0.44)
Acorus calamus	Total	-26.96 (0.13)	10.78 (0.26)	39.62 (0.52)	2.12 (0.05)	18.77 (0.62)
Impatiens capensis	May 2001	-29.41 (0.44)	9.02 (1.23)	37.84 (1.08)	2.67 (0.38)	15.86 (2.54)
Impatiens capensis	October 2001	-29.51 (0.54)	10.69 (0.54)	37.99 (1.20)	2.23 (0.35)	19.91 (4.99)
Impatiens capensis	Total	-29.45 (0.33)	9.78 (0.73)	37.91 (0.76)	2.47 (0.26)	17.70 (2.59)
Leerzia oryzoides	October 2001	-28.07 (0.13)	10.51 (0.53)	40.06 (0.24)	1.66 (0.19)	24.87 (2.98)
Nuphar lutea	October 2001	-27.29 (0.82)	8.52 (1.57)	27.59 (3.25)	2.19 (0.36)	13.85 (2.96)
Peltandra virginica	May 2001	-26.33 (0.57)	6.38 (1.01)	38.01 (1.06)	2.81 (0.33)	13.83 (1.44)
Polygonum arifolium	May 2001	-29.58 (0.43)	11.31 (0.99)	38.19 (0.82)	3.07 (0.22)	12.57 (1.07)
Schoenoplectus fluviatilis	May 2001	-27.88 (0.55)	10.02 (0.23)	40.21 (0.74)	1.92 (0.17)	21.94 (2.16)
Schoenoplectus fluviatilis	October 2001	-27.04 (0.27)	9.89 (0.71)	41.24 (1.14)	1.26 (0.23)	36.68 (7.44)
Schoenoplectus fluviatilis	Total	-27.55 (0.36)	9.96 (0.29)	40.62 (0.62)	1.65 (0.17)	27.84 (3.84)
Anchoa mitchilli	October 2001	-23.67 (0.98)	17.19 (0.21)	44.08 (2.02)	12.96 (0.60)	3.40 (0.02)
Coenagrionidae	October 2001	-27.18 (0.18)	13.49 (0.07)	45.70 (3.27)	11.79 (1.05)	3.88 (0.07)
Corixidae	May 2001	-26.35 (0.24)	11.11 (0.26)	45.55 (0.37)	11.49 (0.05)	3.96 (0.04)
Corixidae	October 2001	-25.24 (0.13)	10.15 (0.13)	48.96 (0.71)	10.06 (0.24)	4.88 (0.16)
Corixidae	Total	-25.74 (0.21)	10.59 (0.20)	47.41 (0.67)	10.71 (0.26)	4.47 (0.17)
Etheostoma olmstedi	May 2001	-25.18 (0.14)	15.14 (0.03)	45.86 (0.36)	13.36 (0.11)	3.43 (0.05)
Etheostoma olmstedi	October 2001	-25.47 (0.17)	15.53 (0.11)	45.07 (0.62)	13.54 (0.07)	3.33 (0.07)
Etheostoma olmstedi	Total	-25.28 (0.12)	15.27 (0.09)	45.60 (0.32)	13.42 (0.08)	3.40 (0.04)
Fundulus diaphanus (S)	October 2001	-26.47 (0.27)	14.84 (0.46)	53.45 (7.69)	14.76 (1.89)	3.60 (0.04)
Fundulus diaphanus (L)	May 2001	-24.95 (0.30)	15.60 (0.16)	44.83 (0.24)	13.91 (0.07)	3.22 (0.01)
Fundulus diaphanus (L)	October 2001	-25.95 (0.14)	15.25 (0.11)	42.46 (1.05)	11.48 (0.20)	3.70 (0.05)
Fundulus diaphanus (L)	Total	-25.35 (0.22)	15.46 (0.11)	43.88 (0.52)	12.94 (0.33)	3.41 (0.07)
Fundulus heteroclitus	May 2001	-24.62 (0.33)	15.31 (0.39)	44.68 (0.18)	13.75 (0.09)	3.25 (0.01)
Fundulus heteroclitus	October 2001	-26.47 (0.94)	14.69 (0.91)	43.65 (0.38)	12.45 (0.15)	3.51 (0.07)
Fundulus heteroclitus	Total	-25.39 (0.49)	15.05 (0.43)	44.25 (0.24)	13.21 (0.21)	3.36 (0.05)
Gammarus sp.	May 2001	-27.08 (0.42)	10.96 (0.26)	35.85 (1.01)	8.18 (0.25)	4.38 (0.04)
Gammarus sp.	October 2001	-26.34 (0.41)	8.94 (1.01)	33.68 (1.53)	6.95 (1.15)	5.11 (0.78)
Gammarus sp.	Total	-26.80 (0.31)	10.20 (0.52)	35.04 (0.88)	7.72 (0.47)	4.65 (0.29)
Morone americana	May 2001	-22.78 (0.04)	17.28 (0.12)	43.51 (0.21)	13.94 (0.15)	3.12 (0.02)
Notropis hudsonius	May 2001	-26.23 (0.21)	15.62 (0.19)	46.36 (0.54)	13.67 (0.06)	3.39 (0.03)
Notropis hudsonius	October 2001	-26.43 (0.39)	14.91 (0.14)	41.31 (2.50)	12.85 (0.71)	3.21 (0.03)
Notropis hudsonius	Total	-26.33 (0.21)	15.26 (0.17)	43.84 (1.52)	13.26 (0.36)	3.30 (0.04)
Palaemonetes pugio	October 2001	-23.68 (0.32)	16.07 (0.32)	43.60 (0.63)	12.60 (0.30)	3.46 (0.05)
High Marsh Soil	Total	-27.88 (0.28)	7.81 (0.14)	21.06 (3.80)	1.61 (0.30)	13.13 (0.22)
Low Marsh Soil	Total	-26.21 (0.46)	5.43 (0.14)	8.86 (1.57)	0.70 (0.10)	12.34 (0.53)

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APPENDIX III

PROGRAM SYNTAX FOR STATISTICAL ANALYSES

This appendix presents descriptions of the executable routines, syntax or menu commands that were used in three statistical programs used in this dissertation, SAS, SPSS and PC-ORD. For SAS programs, an example of an analytical run file of the ANOVA procedure used to test for differences between the creeks based on throw trap data is presented. The same basic model statement was used for all creek, date and creek*date comparisons for all variables of interest, although the throw trap data analysis required the most complex program. The procedure is presented as Figure A3.1

SPSS was used to generate summary statistics for comparisons between the creeks across all dates for each variable for graphical presentation and summary description in Appendix II. SPSS provides excellent output files that are easily transcribed into spreadsheet format. SPSS provides a syntax output for all analyses that identifies the specific command structure that occurs during menu-driven operations. The following syntax describes the routines that were used to calculate the means and related summary statistics. The bracketed term [variable] indicates where the variable under analysis is identified:

```
MEANS
TABLES=[variable]  BY creek  BY date
/CELLS MEAN COUNT STDDEV  STDERR  .
```

This routine was used to calculate means for every variable measured. SPSS was also

used to determine the correlation matrices presented in Chapter 2:

```
CORRELATIONS
/VARIABLES=[list of all variables]
/PRINT=TWOTAIL NOSIG
/MISSING=PAIRWISE .
```

PC-ORD was used for the multivariate procedures, specifically, for the Non-

Metric Multidimensional Scaling. This program does not provide an output file

identifying executable routines or permit mew to write my own code. I have provided the

menu tree of commands that were used to perform the analysis, plus all parameters and

options that were selected:

```
Ordination>NMS
        Distance Measure: Sorensen (Bray-Curtis)
        Autopilot Mode, Slow and Thorough
                Max # of iterations: 400
                Instability criterion: 0.00001
                Start # of axes: 6
                # of real runs: 40
                # of randomized runs: 50
```

Figure A3.1 Example SAS syntax used to compare differences between Broad Creek and Marshyhope Creek across all dates. Only the throw trap analysis included covariates; the flume study, while structured the same way, did not have corresponding water quality and habitat variables. All covariance matrix options that were compared are included. The covariance matrix structure with the lowest BIC score was used for the final run for each variable.

```
*egno [analysis].sas;

options ps=33;

data throw;
input date$ creek$ site$ trap$ /*these 4 variables identify each row of
data */ depth do temp1 cond sal temp2 stemdens vegrich vegbio /* these
9 variables are the measured covariates */ [List of all community level
(tot dens, tot biomass, species richness, etc.) and individual species
variables (FUDIDENS, FUDIBIO, etc.];
```

*natural log transformations of density and biomass data. A constant (1) was added to every cell in order to account for zero abundance;

```
logbio=log(bio+1);
.
.
.
.
logofishdens=log(ofishdens+1);

lines;

[data set was included in the file here];

run;

proc sort data=throw;
by date creek site trap;
```

*the next section calculates means of each variable by creek and date and creates a new data matrix of the means;

```
proc means data=throw noprint;
by date creek site;
var [variable list]
output out=meanthrow mean=/autoname;
quit;


proc print data=meanthrow;
quit;
```

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*the following section presents the model procedure including covariates for throw trap data. For analysis of other dependent variables associated with other collection methods (flume data, soil data, vegetation, etc.), there were no covariates included in the model statement;

```
proc mixed data=meanthrow covtest;
class date creek site;
model logfishabund_mean= creek
                                    date
                                    creek*date
                                    depth_mean
                                    logvegbio_mean
                                    temp1_mean
                                    do_mean
                                    sal_mean

/ddfm=kr outp=resids;
```

*Random statement identifying site within creek as the random factor;

```
        random site(creek);
```

*Random statement suggesting unequal variances between creeks;

```
        random site(creek);
        repeated / group=creek;
```

*Random statement suggesting unequal variances across dates;

```
        random site(creek);
        repeated / group=date;
```

*Comparison of different covariance matrix structures in the absence of unequal variances in either date or creek. The model with lowest BIC was kept in the final run;

```
        repeated date / subject=site(creek) type=cs r rcorr;
              *this statement is identical to random site(creek) above;


        repeated date / subject=site(creek) type=csh r rcorr;


        repeated date / subject=site(creek) type=AR(1) r rcorr;


        repeated date / subject=site(creek) type=ARH(1) r rcorr;


        repeated date / subject=site(creek) type=toeph r rcorr;
```

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*this section specifies the output structure of model results;

```
lsmeans creek date creek*date/ adjust=tukey diff=all cl;
ods output lsmeans=lsmean1;
ods listing exclude diffs; ods output diffs=diff1;
ods output tests3=stat1;
quit;
```

*This section provides a request to print out the residuals plus associated analyses to evaluate any biases in the previous model;

```
proc plot data=resids;
plot resid*pred
     resid*creek
     resid*date /vref=0;
quit;
data resids;
set resids;
aresid=ABS(resid);
run;
proc corr spearman data=resids;
var aresid pred;
quit;
proc univariate data=resids plot normal;
var resid;
quit;
proc print data=lsmean1;
quit;
proc print data=diff1;
quit;
proc print data=stat1;
quit;
```

* The final section requests that the means and associated statistics analyzed in the model statement be exported to Excel compatible files;

```
PROC EXPORT DATA= WORK.LSMEAN1
          OUTFILE= "C:\Egno\SAS
Output\ThrowTrap\Throw_community_fishabund means.xls"
          DBMS=EXCEL5 REPLACE;
RUN;
quit;
PROC EXPORT DATA= WORK.STAT1
          OUTFILE= "C:\Egno\SAS
Output\ThrowTrap\Throw_community_fishabund stats.xls"
          DBMS=EXCEL5 REPLACE;
RUN;
quit;
```

APPENDIX IV

DESCRIPTIONS OF COMPARTMENTS FOR NETWORK ANALYSIS:

BIOMASS AND PROCESS ESTIMATES

Ecological Network Analysis (ENA) relies on the construction of ecological networks of interactions, answering two primary questions: "who eats whom and by how much?" The process relies on the identification of important species compartments (or taxonomical functional groups), and how these functional groups are connected to each other (Ulanowicz 2004).

To identify how much input each compartment receives, energy budgets of each compartment need to be created. These budgets are simply an equation determining the partitioning of consumption, and in its simplest form is:

$$C = P + R + E$$

where C is consumption, P is production, R is respiration, and E is egestion. Estimations of these basic parameters are used to scale all relationships between each compartment. The difficulty in actually measuring all process rates of every compartment is obvious. But if you have reliable estimates of biomass for the compartments, it is possible to calculate the energy budgets based on relationships between these biomasses and metabolic rates (Almunia et al. 1999; Ulanowicz et al. 1999). Estimates of metabolic processes that yield process to biomass ratios including ratios like consumption :

biomass, production : biomass and respiration : biomass, help determine the energetic demands of the compartment (Christian and Luczkovich 1999; Hendriks 1999; Jorgensen et al. 1991; Longhurst 1983). This appendix discusses how biomasses and carbon demands were estimated for each compartment.

Compartment Descriptions

There were 46 unique compartments defined across all 10 trophic networks. Every effort was made to ensure that the data being used was as relevant to the tributaries of the Nanticoke River as possible, both spatially and temporally. The parameter estimation for 34 compartments relied on direct biomass estimates from the field studies of this project. These compartments consist of all the fish, macrophyte and soil compartments, and most of the invertebrates. The carbon budgets of seven compartments relied on the data provided by the Chesapeake Bay Program's Data Hub water quality and plankton community databases (Chesapeake Bay Program 2000). These compartments are: POC, DOC, picoplankton, phytoplankton, microzooplankton, mesozooplankton and macrobenthos. The biomasses and energetics of the remaining five compartments (i.e., benthic algae, the three bacterial compartments and meiofauna) are based on the best possible information available from other tidal freshwater marshes or assume similarity of function between tidal fresh and salt marshes.

The following descriptions provide a detailed explanation of the estimates, calculations and assumptions that went into the construction of each compartment. A brief description of the compartment and its constituents will be followed by a summary

of how biomass was estimated. Each section will then address the compartmental

energetics, focusing on the calculations of production, respiration and consumption rates.

Lastly, each description identifies the components of the compartment's diet. All flows

and processes are in terms of g carbon m^{-2} y^{-1} and biomasses are reported as g carbon m^{-2}.

1. Benthic algae: There has been little comprehensive research examining the ecology of

benthic algae in tidal freshwater marshes. Cyanophytes, bacillariophytes and

chlorophytes most likely dominate the epibenthic algal communities of the tidal

freshwater marshes (Odum et al. 1984). Whigham et al. (1980) examined benthic algal

communities in tidal freshwater marshes in New Jersey on the Delaware River in 1977.

Their survey study indicated that 65 of the 84 non-diatom species identified were

Chlorophytes, although numerical abundance was more evenly divided among

Cyanophytes, Bacillariophytes and Chlorophytes (Whigham et al. 1980).

Whigham et al. (1980) also measured algal standing crop (number of cells cm^{-2})

in mid-summer 1977 at sites near the discharge point of a wastewater treatment facility

(Whigham et al. 1980). For the purposes of this study, I used only the data from their

upstream control sites (#'s 7 and 8), since none of my sampling stations or marshes was

in the immediate vicinity of similar wastewater discharge. Only one other study

comprehensively examined algal abundance on marsh surfaces. In a tidal freshwater

marsh along the Pamunkey River, Virginia, chlorophyll-a content in the soils was used as

a measure of algal abundance (Neubauer et al. 2000; Anderson et al. 1998). They looked

at chlorophyll-a at different times of the growing season over two years, providing an

estimate of the seasonal algal abundance patterns that corresponded to my sampling dates.

Neubauer et al. (2000) presented their estimates of algal biomass as ug Ch-a cm^{-2}, which was converted to g carbon assuming that carbon content is approximately 50 times that of chlorophyll (Strickland 1965). The Whigham et al. (1980) estimates were converted from numerical counts to biomass assuming that there are 1.37E-07 kcal individual cell^{-1} and that there are approximately 9.9 kcal g carbon^{-1} (Schwinghamer et al. 1986). Means for both estimates were calculated for each season (May, August and October). Since I had no field estimates of any differences between the benthic algal communities of the two creeks, I used the same seasonal biomasses for all the networks for both Marshyhope Creek and Broad Creek.

Productivity was estimated based on annual P:B ratios for benthic organisms and the seasonal patterns of algal growth observed in the tidal freshwater portions of Potomac River. Assuming an average algal cell size of 10 μm, I estimated an average annual GPP:B ratio of 61 for the benthic algae (Schwinghamer et al. 1986). Since biomass was assumed to peak late spring through summer, GPP:B in May and August networks was assumed to be 1.5 times greater than the annual rate, while October GPP:B's were set equal to the annual rate (Lippson et al. 1979).

Respiration rates were estimated to account for 45 percent of gross primary production and were back calculated from the estimates of net primary production (Neubauer et al. 2000).

The algae extrude dissolved organic carbon into the water. This represents a significant transfer of net primary productivity directly to a detrital compartment of the system. This extrudate has been observed to range from 5 – 50 percent of net photosynthate (Baird and Ulanowicz 1989), although convention suggests that 25 percent is a probable proportion that follows this pathway (Almunia et al. 1999; Jorgensen et al. 1991).

2. Picoplankton. The Chesapeake Bay Program (CBP) has compiled a database of environmental and biological resources that includes information from across the Chesapeake Bay and its tidal tributaries in Maryland and Virginia (Chesapeake Bay Program 2000). The easily accessible data hub links the user to databases that provide raw numbers from dozens of sampling stations on variables ranging from water temperature to beach seine surveys of near shore fish communities (Chesapeake Bay Program 2005c). The parameters of the four planktonic compartments, POC, DOC and the benthic macrofauna compartment were based on the data acquired from the Chesapeake Bay Program databases.

The Virginia Chesapeake Bay Program Phytoplankton Monitoring Survey began monitoring plankton species abundance in 1985 at 17 stations. The survey added

collections for autotrophic picoplankton (green cells two μm or less in size) in 1989 with monthly collections occurring from 1990 through 2002. Maryland did not have a comparable picoplankton survey during this time span, although their phytoplankton survey counted green colored microflagellates (Chesapeake Bay Program 2004a). Several of the sites where Virginia collections occurred are considered tidal fresh, and data from these sites were used to estimate picoplankton abundance in the Nanticoke River. The CBP data is readily available at their website (Chesapeake Bay Program 2005b)

Sites TF5.5, TF3.3 and TF4.2 of the Virginia Chesapeake Bay Program Phytoplankton Monitoring Survey were all located within the tidal fresh zones of the James River, Pamunkey River and Rappahannock River, respectively, and were the only stations whose data I used. I selected the CBP sample data only from dates that corresponded to my own sampling. If data representing two or more dates from a given site were within two weeks of my field research trips, both dates were averaged and included as one estimate. The CBP picoplankton data counted numbers of cells liter^{-1}. These numbers were first converted to cells m^{-2} by calculating the mean water volume of a square meter of the Nanticoke marshes. Mean water depth of the throw traps was assumed to be equal to mean water depth of the marshes. In addition, since Secchi depth measurements approach one meter in the Nanticoke, the entire water depth of the marsh was considered to be in the euphotic zone (Chesapeake Bay Program 2005c). Each picoplankton abundance estimate was scaled to fill the mean volume m^{-2} of each marsh on each date.

Density estimates were converted to biomass assuming that mean organism size was <1um and that the energetic content of each cell was 5.24E-13 kcal (Schwinghamer et al. 1986). Assuming 1 kg of dry biomass is equal to 5258 kcal (Peters 1983), a picoplankton cell is 9.97E-14 g dry weight. This value was multiplied by the picoplankton abundance and then, assuming carbon accounts for 40% of dry weight, scaled to grams carbon m^{-2} (Jorgensen et al. 1991).

Production rates were estimated similarly to the benthic algae compartment. In this case, mean annual GPP:B was set at 249 (Schwinghamer et al. 1986), and seasonal effects were estimated from Lippson et al. (1979). Respiration was again assumed to account for 45% of gross primary productivity (Neubauer et al. 2000). Picoplankton extrude net photosynthate (~25 percent) to the DOC compartment, as described in benthic algae.

3. Phytoplankton: This compartment contained all autotrophic plankton >1 μm. In tidal freshwater regions, the phytoplankton community is comprised of mostly Chlorophytes (e.g., *Ulothrix* spp. and *Pediatstrum* spp.), Cyanophtes (e.g., *Merismopedia* spp.) and Bacillariophytes (e.g., *Centrales*, *Leptocylindricus* spp., and *Cyclotella* spp.) (Lippson et al. 1979) (Chesapeake Bay Program 2005b). As with the picoplankton, only sites located in tidal freshwater regions of Chesapeake tributaries were considered when determining which species were present. The station codes of these sites were: ET5.1, TF1.5, TF2.3, TF4.2 and TF5.5. These site designations correspond to tidal freshwater regions of the Choptank River, Patuxent River, Potomac River, Pamunkey River and James River, respectively.

Measures of chlorophyll-a, however, were deemed to be a more effective measure of phytoplankton abundance, which CBP surveys measured in terms of μg L^{-1} (there were difficulties in calculating body sizes for the large number of species identified in the surveys) (Chesapeake Bay Program 2005c). Data from only the sampling station on the Nanticoke River near Sharptown, Maryland, were considered. Seasonal means were calculated in the same way as described for benthic algae, based on the means of the CBP data that corresponded with the sample dates in this study. Carbon content of the phytoplankton was assumed to be 50 times that of chlorophyll-a (Strickland 1965). This measure of biomass per unit volume was scaled to biomass per square meter based on mean water depth measured during the throw trap sampling. Lastly, the autotrophic picoplankton biomass from each corresponding date was subtracted from these estimates to arrive at the biomass for the larger phytoplankton.

Productivity was assumed to be similar to that of the benthic algae, with an annual GPP:B of 61. GPP:B in May networks was assumed to be 1.5 times greater than the annual rate, August networks were assumed to be only 0.7 times as great and October GPP:B's were set equal to the annual rate (Lippson et al. 1979). Respiration rates were estimated to account for 45 percent of gross primary production and were back calculated from the estimates of net primary production (Neubauer et al. 2000). As with benthic algae and picoplankton, this compartment is also directly linked to DOC representing the fate of about 25 percent of net photosynthate (Neubauer et al. 2000; Mann and Wetzel 1996).

<u>4 and 5, Low Marsh Roots and High Marsh Roots</u>: Belowground biomass is not nearly as well studied a component of wetland vegetation as is aboveground biomass. Yet there have been studies that examined the relationship between the two in tidal freshwater marshes (Whigham and Simpson 1978; Whigham et al. 1978). Whigham et al. (1978) calculated a series of linear relationships between peak aboveground biomass and a plant species corresponding belowground biomass (Whigham and Simpson 1978). Using the maximum biomass observed within each year (either 2001 or 2002), I used these equations to estimate each belowground biomass for each species in each year, and then combined these biomasses based on the location the plant occurred to estimate both low marsh and high marsh biomass. Finally, I determined a mean across both years. *Nuphar lutea* rhizomes comprised almost all the low marsh biomass, while the remaining species were typically found only in the high marsh. Relationships between above- and belowground macrophyte biomass are complicated, with likely high levels of translocation in either direction based on the time of the year. It was assumed that belowground biomass remained constant throughout the span of the study in each creek with no seasonal variation (Neubauer et al. 2000).

There is some evidence that some carbon is fixed from the dissolved inorganic carbon pools in the soils (Hwang and Morris 1994), but for the purposes of these networks, belowground activity, either production or respiration, refers to that portion of whole plant activity that likely occurs belowground. Also, using the convention of the gas

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flux study of tidal fresh marshes, belowground biomass was assumed to remain constant across the growing season (Neubauer et al. 2000)

Productivity rates were determined assuming that in rhizomatous perennials, which accounted for the vast majority of belowground biomass, belowground net annual productivity is between 25 and 50 percent of the biomass (Whigham, unpublished). I assumed that P:B relationship for marsh roots was 0.375. Respiration was scaled according to estimations of seasonal patterns observed by Anderson et al. (1998) in plant community production and respiration, with P:R increasing over the growing season yet overall P and R declining as senescence begins in summer (Neubauer et al. 2000).

Macrophytes (#'s 6 through 15): The macrophyte species compartments represent the dominant species that were observed in the marshes from 2001 through 2002. Nine compartments represent the dominant plant species, *Nuphar lutea* (6), *Zizania aquatica* (7), *Acorus calamus* (8), *Polygonum arifolium* (9), *Leerzia oryzoides* (10), *Peltandra virginica* (11), *Impatiens capensis* (12), *Bidens* spp. (13) and *Schoenoplectus fluviatis* (14), and one composite compartment for the remaining plants, Other Macrophytes, (15). Other Macrophytes contains species such as *Calystegia sepium, Gallium tinctorum, Polygonum sagittatum, Typha* spp. and *Sagittaria latifolia*. The biomass of this composite compartment was generally greater later in the growing season and contains many annual species that replace *Acorus* in the high marsh as the early season dominant fades through the summer.

The relationship between biomass and productivity has typically been inferred from standing crop measurements of aboveground vegetation. This relationship is complicated by the seasonal sequence of dominant species expressed in terms of standing biomass, where massive early season growth of perennials is gradually replaced by annual species (Whigham and Simpson 1992). Most censuses rely on a series of measurements taken across the growing season to estimate total plant community production (Whigham and Simpson 1992; Doumlele 1981). Biomass production estimated in this manner has observed community biomass to range from about 600 g m^{-2} in *Nuphar*-dominated marshes to over 1800 g m^{-2} in *Phragmites*-dominated marshes (Whigham et al. 1978). It is likely that these estimates under-report actual biomass production because they cannot account for senescence of plant leaves that occurred before measurement, leaching of organic carbon from plant tissue and herbivory. Carbon gas flux studies, however, in marshes of the Pamunkey River have provided the most detailed picture of macrophyte community development. Anderson et al. (1998) were able to estimate monthly production and respiration of a *Peltandra*-dominated marsh system. They estimated that gross macrophyte photosynthesis in these marshes was 996 g carbon year^{-1}, with up to 46 percent of this consumed during macrophyte respiration (Neubauer et al. 2000). Net photosynthesis ranged between 536 and 725 g carbon m^{-2} y^{-1}. Summing my estimates of aboveground vegetation across all three sample dates in each year falls within the range that Neubauer et al. estimated. Therefore, I used the standing crop measurements as surrogates for net primary production during each season.

NPP:B was assumed to be 1 for each species, where accumulated biomass represents the measure of productivity. The remainder of GPP was apportioned to leaching losses (estimated to be <10% of the difference), herbivory (<10 percent of the difference and the balance to plant respiration (Neubauer et al. 2000).

These marshes undergo a complete turnover of aboveground biomass each year. Estimates of decomposition rates suggest that within 120 days, less than 20 percent of original biomass remains (Whigham et al. 1980). I also compared my estimates of plant community biomass in October 2001 to "dead macrophytes" collected in May 2002. I assumed that the dead macrophytes provided an estimate of previous year production that survived until the following growing season. Only six to ten percent of the October crop persisted until the following spring.

Given that aboveground losses approach 100 percent each year, I determined that the net macrophyte production during the spring and summer networks (the four from May and August) should carry over into the next season. Attempting to account for the all of May production internally in the network would produce huge excesses of carbon material that had to go somewhere. Yet these marshes are presumed to be net importers of organic material during the early growing season, but they begin to export organic carbon as the plants begin to senesce (Odum 1988). Therefore, net macrophyte production in May networks was exported as "stored biomass" and imported into August as "macrophyte detritus." Similarly, August net production was carried over to October networks as a detrital input. The October networks, however, were set to process both the

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import of August generated macrophyte detritus, plus most of the net macrophyte production. Particulate organic carbon content in the waters of the Nanticoke River is substantially greater in October than during spring or summer and suggests one possible fate for the macrophyte production (Chesapeake Bay Program 2005c; Findlay et al. 1990).

Lastly, all biomasses were halved assuming that half of the innundated marsh surface was high marsh and half was low marsh. Plant fidelity to marsh type approached 100 percent in this study with only a few instances of *Nuphar* appearing in the high marsh and *Polygonum punctatum* found in the low marsh. Only *Zizania aquatica* was collected with similar abundance between high and low marshes, but its contribution to overall community biomass was still very small.

16 and 17. <u>Free Bacteria and POC Bacteria</u>: Bacteria constitute a very important, but often unappreciated, component of ecosystem function. There is very little research that has explicitly identified and examined bacterial roles in tidal freshwater marshes. All compartment parameters for the free living bacteria have been inferred from salt marshes under the presumption that function and abundance are fairly similar (Austin and Findlay 1989).

Biomass was estimated from studies of seston in a tidal marsh on the Delaware River (Huang et al. 2003). Mean bacterial biomass was estimated based on their observations for free living bacteria and bacteria attached to particulate organic carbon

(POC). Most bacteria Huang et al. observed was free living, but there was a small yet significant biomass of bacteria directly associated with suspended POC. These means were then scaled by the seasonal differences that had been incorporated in other networks of the Chesapeake Bay (Baird and Ulanowicz 1989). The resultant biomasses reflected both studies where microbial biomass peaked in summer (embodied in the August networks) and were lowest in the October networks as biological activity decreases.

P:B and R:B ratios were derived from Baird and Ulanowicz (1989) assuming that bacterial processes are similar across tidal estuarine systems. Rates reflected the biomass patterns where P:B and R:B were increased from May to their peak in August and declined to their lowest levels by October.

Free bacteria was assumed to receive trophic inputs from only dissolved organic carbon (DOC), while POC bacteria were trophically linked only to the POC upon which they are attached (Baird and Ulanowicz 1989).

18. <u>Sediment Bacteria</u>: Most research regarding microbial processes in tidal freshwater marshes focuses on bacterial abundance and function in marsh sediments (Findlay et al. 1990; Austin and Findlay 1989). Bacterial biomass and activity appear fairly robust in these systems, registering few if any functional or compositional changes even with species replacements in the surrounding macrophytes and nitrogen enrichment (Otto et al. 1999). Multiple measures of microbial biomass have been reported for tidal freshwater

marshes of Tivoli Bay in the Hudson River. These biomasses were used to calculate a mean sediment bacterial biomass for the 10 networks.

These means were then scaled by the seasonal differences that appeared in networks of the mesohaline region of the Chesapeake Bay (Baird and Ulanowicz 1989). Again, it was assumed that there were no functional differences between bacterial elements in mesohaline and freshwater benthic environments.

This assumption also extended to the energetics of the microbes. P:B and R:B ratios were again derived from Baird and Ulanowicz (1989), and the rates reflected the unimodal seasonal pattern of increasing activity from May, peaking in August and declining by October.

Similarly to the other bacterial compartments, sediment bacterial trophic inputs were limited to those originating on their host detrital pool. For all functional purposes, it was assumed that the high marsh hosted more microbial biomass and activity due to the lower frequency of tidal flushing and higher rates of particulate organic deposition (Odum et al. 1984)

19. Microzooplankton: Microzooplankton biomass estimates were based on data obtained from the Baywide CBP Plankton Database (Chesapeake Bay Program 2005b). The survey provides counts of microzooplankton liter^{-1}. The surveys identified all heterotrophic planktonic organisms less than 202 μm as microzooplankton. Surveys in

Maryland put a lower size constraint of 44 μm on this category of organisms

(Chesapeake Bay Program 2000). The members of this compartment include ciliates,

rotifers, copepod nauplii and meroplankton.

Data was taken from nine different sampling stations in tidal freshwater zones of

the Choptank River, Patuxent River, Potomac River, Pamunkey River and James River.

Two criteria were used to sort the data into suitable groups to estimate mean

microzooplankton abundance. First, I considered only plankton data that was collected

within two weeks of the date of my sampling efforts on the Nanticoke River and

compiled sets of up to seven estimates of microzooplankton abundance for each date.

Then I classified the CBP plankton samples based on their corresponding estimates of

salinity from the CBP Water Quality surveys (Chesapeake Bay Program 2005c). From

October 2001 through the conclusion of my field sampling, salinity rose appreciably as

the effects of a regional drought began to affect the Nanticoke River biota. Since salinity

is a major factor that influences zooplankton abundance, its effect needed to be

incorporated into these trophic networks (Lenz 2000). Therefore, I used only the data

from zooplankton surveys that had salinity measures similar to those in Broad Creek and

Marshyhope Creek for each date. All Broad Creek microzooplankton estimates were

based on the sampling station data with salinities less than 0.5. May 2001 and August

2001 Marshyhope networks baseline estimates were identical to their Broad Creek

counterparts. The microzooplankton of the October 2001, May 2002 and August 2002

Marshyhope networks differed as CBP sample stations with higher salinity were included

while those with lower salinities were omitted.

These means were then converted from numbers liter^{-1} to numbers m^{-2} using the same process as described in picoplankton (2). Numerical density was converted to biomass by assuming that the average individual mass of a microzoplankter is approximately 5E-07 g wet weight (Schwinghamer et al. 1986), and that dry mass is approximately 20 percent of wet mass, and carbon content is 50 percent of dry mass (Jorgensen et al. 1991).

Production and respiration in the networks were based on the work of Schwinghamer et al. (1986) that used allometric relationships to estimate annual P:B in different size classes of organisms. P:B was estimated based on the following relationship Schwinghamer et al. described:

$$P:B = 0.073M^{-0.337}$$

Where P:B is expressed as an annual rate and M is body mass in kilocalorie equivalents. The annual P:B rate was estimated to be 25. This was seasonally adjusted assume that process rates would be halved for every 10° C change in temperature (Ernest et al. 2003; Withers 1992). Mean environmental temperature was calculated for each network and used to scale the P:B ratio accordingly. Respiration was determined using the equation Schwinghamer et al. (1986) derived from the data presented in other summaries of biomass, production and respiration rates in animals (Banse and Mosher 1980; Banse 1979):

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$$\text{Log}_{10}R = 0.367 + 0.993\log_{10}P$$

where both R and P are in terms of kcal m^{-2} y^{-1}. Absolute values for P and R were converted from g carbon to kcal and vice versa assuming that there are 9.9 kcal g carbon^{-1} (Cummins and Wuycheck 1971).

Microzooplankton were trophically linked to picoplankton, phytoplankton, free bacteria, POC bacteria and POC (Lenz 2000; Baird and Ulanowicz 1989). Specific flow rates were allowed to float based on availability of supply (Ulanowicz 2004).

20. <u>Mesozooplankton</u>: This compartment contained all heterotrophic planktonic organisms greater than 220 μm in size. Representative members include Calanoids (*Acartia tonsa* and *Eurytemora affinis*), Cladocerans (*Bosmina* spp. and *Alona* spp.), Cyclopoids (*Halicyclops* sp. and *Eucyclops agilis*) and Harpacticoids (*Canuella elongata*).

The data used in this compartment was also obtained from the CBP plankton database (Chesapeake Bay Program 2005b). Estimates of biomass and energetic processes were determined the same way that microzooplankton estimates were constructed, and the reader is referred to the previous section for specifics. Only mean body masses were calculated differently. These estimates were based on published

density biomass relationships for various species (e.g. NOAA-GLERL 2004; USACE 1999).

Mesozooplankton were trophically linked to phytoplankton, microzooplankton and POC. No link is established with POC bacteria since the biomass of the bacteria is very low compared to that of POC. Also, because the fate of the bacteria is tied to the POC, the pathway between bacteria and the larger zooplankton is intact, just mediated by passage through POC.

21. <u>Meiofauna</u>: The meiofauna of tidal freshwater marshes consists of organisms that are less than 0.5 mm and greater than 63 μm. These organisms are an important food resource for many species of juvenile fish and invertebrates, representing a major pathway from the marsh benthos to higher-level consumers (Yozzo and Odum 1993). Dominant taxonomic groups include Nematoda, Ostracoda, Tardigrada, Oligochaeta, *Manyunkia* spp. (a polychaete) and harpacticoid and cyclopoid copepods (Yozzo and Smith 1995). No surveys of benthic organisms in the Chesapeake Bay's tidal tributaries account for these small organisms. CBP benthic surveys in Maryland, for example, use a 0.5 mm sieve when processing field samples (Chesapeake Bay Program 2004b). For organisms smaller than those in the CBP Benthic Database, estimates of biomass from Tivoli Bay, Hudson River, New York, were used.

Yozzo and Smith (1995) compared differences in abundance of total meiofauna and the major taxa listed above in four microhabitats of the Tivoli Bay marshes, pools

and hummocks of the high and low marsh for an entire year. Since there is little evidence of hummock formation in the low marshes along the Nanticoke River, estimates of biomass from this microhabitat were not considered. The remaining three means were used to generate a grand mean for meiofaunal abundance. These numerical abundances were scaled up from numbers $(10 \text{ cm})^{-2}$ to numbers m^{-2}, and then converted to biomass assuming that an average individual body mass was 0.000001 g wet weight, which was the median size of meiofaunal organisms defined by Schwinhamer et al (1986).

Production and respiration rates were calculated in the same way that the microzooplankton and mesozooplankton were, relying on allometric relationships to determine P:B, and then using P:R relationships to estimate R:B (Wilson and Parkes 1998; Schwinghamer et al. 1986; Banse 1979).

Meiofauna were assumed to consume only benthic algae and POC in the low and high marsh sediments (Montagna et al. 1995).

22. <u>Benthic Macrofauna</u>: This compartment contains all larger benthic organisms, excluding the taxa placed into separate compartments. Taxa included within this compartment include Chironomid larvae (*Chironomus* spp. and *Xenochironomus* spp.), *Cyathura polita* and oligochaete worms (*Limnodrilus* spp.). Data was obtained from the Chesapeake Bay Program Baywide Benthic Database (Chesapeake Bay Program 2004b). Several filters were placed on the data before biomass estimates were calculated to prevent both double counting taxa in different compartments and to reduce the biomass

inflation that certain large benthic organisms would add to mean benthic abundance. First, all taxa that were placed in other compartments were removed, typically *Gammarus* spp. and *Corbicula fluminea*. Secondly, *Rangia cuneata*, the brackish water clam, was also removed. While I have observed these bivalves in the Nanticoke River, I have not come across them at my research sites. In the Nanticoke River, they appear to prefer sandy substrates in areas with marginally oligohaline water, over a mile down river from my most down stream marsh sites (personal observation). There may be, however, some overlap between this compartment and meiofauna, specifically in regard to oligochaetes as Yozzo and Smith (1995) did not define an upper-size limit on what they considered to be meiofauna. Given the size of the samples they collected (3.5 cm diameter by 4 cm deep) compared to those collected by the CBP affiliates (22.5 cm^2), I assumed that all organisms placed in this compartment would have been excluded from those collected by Yozzo and Smith (1995).

Biomass estimates were arrived at in a similar manner to those other compartments that relied on CBP data. Only CBP sample stations that were in tidal freshwater regions were considered that were located in the Upper Chesapeake Bay, James River, Mattawoman Creek, Northeast River, Pamunkey River, Patuxent River, Potomac River and Rappahannock River (Chesapeake Bay Program 2004b). Only CBP data from dates within two weeks of my field collections were considered for each network. Additionally, salinity effects were considered in the same way they were for the zooplankton compartments, by adding or removing abundance estimates based on similarity to salinities I estimated for each network. Biomass estimates for October 2001,

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May 2002 and August 2002 networks for Marshyhope Creek were affected by this assumption. CBP estimates were in units of g ash free weight $(22.5 \text{ cm})^{-2}$. These values were scaled up to g ash free weight m^{-2} and converted to g carbon assuming that the ratio of ash free weight / dry weight was 0.77 (Cummins and Wuycheck 1971).

Production and respiration rates were estimated using the same method as in the zooplankton and meiofauna compartments. Allometric relationships were used to determine P:B, and then I used P:R relationships to estimate R:B (Wilson and Parkes 1998; Schwinghamer et al. 1986; Banse 1979).

Macrobenthos diet was assumed to be limited to consumption of benthic algae, meiofauna, Sediment POC and suspended POC (Lippson and Lippson 1997).

23. *Corbicula fluminea*: The Asian clam is considered to be an invasive species in the Chesapeake Bay region. It is a source of some environmental concern regarding its potential biofouling abilities in the Chesapeake Bay. First identified in the United States in 1938 in Washington state and reaching Maryland by the 1980s (USGS-NAS 2005), the species was positively identified in the Nanticoke River by 1991 (Counts 1991). Due to its widespread presence and apparent integration into ecosystems around the Bay, any actions to control its spread have been recognized as an unrealistic objective (Chesapeake Bay Program 2002).

Biomass estimates are based on the field collections of this study. The species was only collected in the throw trap, so no transformations were made to its biomass. The species was only observed in the mucky sediments of the low marsh, so its biomass was halved, reflecting the assumption that half the inundated marsh surface was low marsh.

Productivity was estimated using an allometric relationship relating body size to production in field populations of animals, similarly to those of the other invertebrate compartments (Banse and Mosher 1980). Mean individual mass of the clams in each network were used for the estimates of body mass in the equation, assuming that a smaller mean mass indicates the population contains more juveniles and hence greater productive capacity than a population dominated larger individuals. Respiration rates were determined using the relationship described by Schwinghamer et al. (1986).

The *Corbicula* compartment was linked to more compartments than any other living taxon. While there is evidence that the species does preferenctially feed on phytoplankton (Foe and Knight 1985), it was assumed that *Corbicula* also consumes other planktonic organisms (Voshell 2002). Furthermore, since the clams live at the sediment surface, benthic algae and low marsh sediment POC were also connected to this compartment.

24. Corixidae: The family Corixidae is comprised of the hemipteran aquatic insects commonly known as waterboatmen. These insects were surprisingly abundant at all locations throughout most of the field research, with over 15,000 collected in one square

meter on one occasion. They were frequently found in the stomach contents of many fish species that utilized the marsh.

Biomass estimates were based on the direct measures of abundance in the throw trap data measured as g wet weight m^{-2}. This biomass was converted to g carbon m^{-2} assuming that 20 percent of wet weight is dry weight (Jorgensen et al. 1991), and that 46 – 47 percent of dry mass is carbon (estimate based on mass spec analysis of body tissue from Chapter 5).

P:B ratio was estimated for each network using the relationships described by Banse and Mosher (1980):

$$\log_{10} P:B = -0.24 - 0.38\log_{10}M$$

where M is body mass expressed in terms of kilocalories. Masses were converted assuming 0.792 kcal (g wet weight)$^{-1}$ (Cummins and Wuycheck 1971). R:B was estimated using the relationship described in detail in the microzooplankton compartment (Schwinghamer et al. 1986).

Corixidae feed in a manner very differently than other aquatic true bugs. Their beaks are distinctly modified for scavenging, and they scour the sediment surface looking for food (McCafferty 1988). They are classified as collector-gatherers, and while some species evidence some specialization (Voshell 2002), most species consume any small

organisms and organic detritus that they come across. Corixidae feed on the following compartments: Benthic algae, micro- and mesozooplankton, meiofauna, POC and low marsh sediment POC.

25. *Gammarus* spp.: This compartment contains the amphipods of the genus *Gammarus*. Individuals that were keyed out to the species level were all *Gammarus fasciatus*, although there is evidence that the congener, *Gammarus dairberi,* is also present (Chesapeake Bay Program 2005a), even though this species is presumed to have a stronger affinity for brackish water than its congener (USGS-NAS 2004). Not as abundant as Corixidae in the Nanticoke marshes, these amphipods do provide a pathway from benthic production to higher-level consumer organisms. The species was commonly collected throughout the field collections, but was entirely absent by August 2002, presumably due to the increase in salinity as the drought effects intensified.

Biological parameters were calculated in the same manner as those for Corixidae, and the reader is referred to the previous compartment for additional details. The only scaling factor that differed was carbon - dry mass ratio. For the amphipods, elemental analysis determined that approximately 35 percent of dry mass is carbon.

Functionally, amphipods are considered to be omnivores. The most common food sources are organic particles and benthic algae, but will also consume small organisms they come across (Voshell 2002; Waterman 1960). This compartment receives inputs from benthic algae, meiofauna and POC.

26. <u>Odonate Larvae</u>: The odonate larvae collected in this study consisted of members of two families, green-eyed skimmers (Corduliidae) and narrow-winged damsel flies (Coenagrionidae) (Hilsenhoff 2001; Pennak 1978). Biomass and numerical abundance were fairly low in all networks, but since these animals function as predators in aquatic systems they were included in the networks.

Biological parameters were calculated in the same manner as those for Corixidae, and the reader is referred to that compartment for additional details about calculations and assumptions. The only scaling factor that differed was the carbon - dry mass ratio. For the odonates, elemental analysis determined that approximately 45 percent of dry mass is carbon.

Odonate larvae are classified as engulfer-predators. While large specimens of dragonfly larvae will consume fish, odonates more commonly feed on zooplankton and aquatic insects with prey size increasing as odonate body size increases (Voshell 2002; McCafferty 1988). The typical size of the odonate larvae collected in this study was quite small for both Corduliidae and Coenagrionidae and this limited the trophic interactions of this compartment based on size of prey organisms. The compartment receives inputs from Mesozooplankton, macrobenthos and other insects.

27. <u>Other aquatic invertebrates</u>: This compartment contains all other aquatic insects that were not contained in any of the preceeding macroinvertebrate compartments that were

collected in the throw trap collections. Taxa such as Dipteran larvae, *Lethocercus* sp., and Ephmeropteran larvae, which were collected in low abundance and erratically, make up the membership of this compartment. They were included in the networks because of this consistent presence and because they are all identified as prey items for higher-order consumer organisms.

Biological parameters were calculated in the same manner as those for Corixidae, and the reader is referred to that compartment for additional details about calculations and assumptions. The only scaling factor that differed was the carbon - dry mass ratio. For these invertebrates, elemental analysis determined that approximately 44 percent of dry mass is carbon.

Since the compartment represents a compilation of many species, the trophic behavior is not as specified as it was for other compartments. Benthic algae, phytoplankton, microzooplankton, mesozooplankton, meiofauna, macrobenthos, POC and POC in both sediment types were linked to this compartment, suggesting an omnivorous feeding behavior of these combined organisms (Voshell 2002; Lippson and Lippson 1997).

28. *Palaemonetes pugio*: The grass shrimp were erratically present, but when collected they often had relatively large biomass. In 2001, they were not present in May in either creek, but they then appeared in small numbers by August in Marshyhope Creek and later in October in even larger densities. They were not captured in Broad creek in either

August or October 2001. In 2002, the shrimp were again absent during May. But by

August 2002, the shrimp were finally present in Broad Creek and reached their largest

biomass in Marshyhope Creek. This species was collected in both throw traps and flume

traps, assuming that they were a potentially important prey item of any larger fish that

enter the marshes (Murdy et al. 1997).

Biological parameters were calculated in the same manner as those for

Corixidae, and the reader is referred to that compartment for additional details about

calculations and assumptions. The only scaling factor that differed was the carbon - dry

mass ratio. For the grass shrimp, elemental analysis determined that approximately 43.6

percent of dry mass is carbon.

The specimens collected were typically smaller than reported mean body size.

Therefore, size of prey items again limited the trophic connections to this compartment.

The species was treated as an opportunistic grazer on epibenthic sources and was linked

to benthic algae, meiofauna and POC (Gregg and Fleeger 1999; Kneib 1985; Welsh

1975).

29. *Calinectes sapidus*: The blue crab was not a commonly captured species, and did not

appear at any sampling sites until May 2002. In other studies of tidal freshwater marshes,

this species was frequently captured and its presence should not been seen as an anomaly

(Rozas and Odum 1987; McIvor and Odum 1986). The arrival of the crab coincided with

the increase of salinity through 2002. While not captured at every sight, juvenile crab

carcasses were observed at all sites in Marshyhope Creek, but never in Broad Creek. The captured individuals were all males and mostly juveniles (mean carapace width 32 mm).

Biological parameters were calculated in the same manner as those for Corixidae, and the reader is referred to that compartment for additional details about calculations and assumptions. The only scaling factor that differed was the carbon - dry mass ratio. For the grass shrimp, elemental analysis determined that approximately 45 percent of dry mass is carbon.

Adult blue crabs are omnivores, feeding on bivalves, crustaceans, fish, annelids, plants and detritus including dead fish and plants (Williams 1984). Studies of juvenile crabs suggest that they are opportunists feeding on zooplankton in open bays, but utilizing marsh-derived carbon sources (Fantle et al. 1999). Preference for prey in the sediments declines as the crabs increase in size (Mantelatto and Christofoletti 2001). In these networks, *Callinectes* feeds upon Benthic algae, macrobenthos, Corbicula fluminea, other aquatic invertebrates, *Palaemonetes pugio* and POC.

Fish compartments: The fish compartments represent the most resolved component of the trophic networks. I defined 12 fish compartments, one for every species that occurred with any appreciable frequency. Certain species were collected so infrequently that I discounted their importance as significant actors in the transitional zone of the tidal marshes (*Alosa pseudoharengus*, *Micropterus salmoides*, *Menidia beryllina*, *Ameiurius nebulosus* and *Cyprinella analostana*). This section will describe the methodologies used

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to estimate the parameters for all fish compartments. Individual species will be described afterward, commenting on salinity effects on animal abundance, species-specific parameters and dietary information.

The throw trap and flume trap data provided the estimates for mean biomass for the networks. The throw trap data was used preferentially over the flume since it provided a direct measure of biomass per unit area. Earlier analyses suggested that the proportions of animals collected were not significantly different between traps, so whenever possible only throw trap data was used to compile biomass estimates (see Chapter 2). Some species, however, were captured infrequently and did not appear uniformly in both trap types on every sampling date. If the throw trap did not capture a given species but the flume did, a proportional relationship was created to estimate biomass per unit area from the flume data. The biomass of the target species was converted to a proportion of total flume biomass for a given creek. This proportion was multiplied by the corresponding mean total fish biomass collected in the throw trap. Since proportional abundance was similar between trapping techniques, this technique provides an estimate of the biomass of the species not captured by the throw trap yet whose total biomass is constrained by the limit of the throw trap biomass.

Biomass was converted from the field measurements of g wet weight m^{-2} to g carbon m^{-2}. Scaling values were determined through elemental analysis of carbon in dried tissues of all the fish species and will be provided as each species is discussed. For all

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species, dry mass was assumed to constitute 20 percent of the wet mass (Jorgensen et al. 1991).

Once the biomass was established, it was used to scale the consumption, production and respiration rates of the fish. The initial calculations focused on consumption to biomass ratios (C:B). The software package EcoPath with EcoSim 5 offers a series of subroutines dubbed EcoEmpire that will estimate energetic parameters of various components of aquatic ecosystems (Pauly et al. 2000). One calculation EcoEmpire provides is a C:B ratio for fish based on aspects of fish morphology, environmental factors and generic feeding behavior (Pauly et al. 1990). The relationship is formalized in the following equation (Palomares and Pauly 1998):

$$C:B = 3.06 \ (W_\infty^{-0.2018})(T^{0.6121})(A^{0.5156})(3.53^h)$$

where W_∞ is the weight of the species as it approached maximum length, T is the habitat water temperature, A is the aspect ratio of the caudal fin and h is a dummy variable expressing food type that scales demands based on how digestible the food items are. Asymptotic body masses were estimated using body mass:length relationships calculated for each species collected in this study. Maximum body lengths were determined from multiple sources (Froese and Pauly 2005; Murdy et al. 1997; Rohde et al. 1994). Mean water temperature measured in the throw traps was used as an estimate of habitat temperature. The aspect ratio is a dimensionless ratio calculated for the caudal fin as the ratio $h^2 \ s^{-1}$, where h^2 is the height squared and s the surface of that fin. The larger the

aspect ratio, the more active the species is, with respective increases in energetic demands (Palomares and Pauly 1998). Aspect ratios were obtained for all species from FishBase (Froese and Pauly 2005).

Consumption was apportioned to productivity, respiration and egestion according to estimates of the proportional demand of each process as follows (Brett and Groves 1979):

$$100C = 27E + 44R + 29P$$

where C, E, R and P refer to consumption, egestion, respiration and production, respectively. Since the estimate of consumption already included the effects of environmental conditions and life history characteristics, the estimates of P:B and R:B will vary accordingly.

All fish compartments were assumed to be net exporters of carbon from the marsh. No large piscivorous fish were ever collected in either the flume trap or throw trap. Predation on the small fish most likely occurred at low tide when the refuge the marshes offered was not available (Rozas and Odum 1987). There is virtually no SAV in the subtidal margins of these marshes, leaving the small fish very vulnerable, which is the probable pathway of carbon flow from small fish to larger pelagic and benthic predators of the open river (Rozas and Odum 1987a). I also have no realistic estimate of predatory behavior by waterbirds. Species such as *Ardea herodias* (great blue heron), *Casmerodius*

albus (great egret) and *Ceryle alcyon* (belted kingfisher) were observed occasionally in the marshes. The same holds for herpetofauna and mammals, although I never saw any of these animals active in the marshes. Given this lack of information, therefore, I have estimated approximately 10 percent of production leaves the system through losses to higher order consumers. This is identified in the networks as an export from the system.

30. *Anguilla rostrata*: This fish species was less frequently captured than other species, but was present in the seven of the 10 sample periods. The american eel is a catadromous fish, and sexually immature eels live in brackish and fresh waters of the Chesapeake region for approximately the first five years of their lives before returning to the Atlantic Ocean to breed (Murdy et al. 1997). All eels collected in this study were very small juveniles, with the largest specimen captured measuring only 160 mm TL.

The energetics of the american eel were calculated differently than the other fish compartments. The eel body form has no caudal fin in order to calculate an aspect ratio, a measurement I relied on to calculate C:B (Palomares and Pauly 1998). I used an allometric relationship for generic fish to estimate P:B (Banse and Mosher 1980). C:B and R:B were estimated according to the proportional allocation defined by Brett and Groves (1979).

Adult eels feed on insects, mollusks, worms, crustaceans and small fish (Murdy et al. 1997). All the eels I collected were very small, and their size limited their trophic linkages in this network. The juveniles likely feed on small invertebrates, including insect

nymphs and larvae, cladocerans, and oligochaetes (Odum et al. 1984). The compartment

feeds on mesozoplankton, meifauna, benthic macrofauna and other aquatic invertebrates.

31. *Anchoa mitchilli*: The bay anchovy is a planktivorous fish that is extremely abundant

throughout the Chesapeake Bay. It is tolerant of a wide range of salinity (1 – 33 ‰), but

higher population densities are associated with an estuarine environment (Lippson et al.

1979). I collected bay anchovies in both creeks from October 2001 through August 2002.

This time span corresponds with the increase in salinity and water conductivity as

freshwater input declined due to a prolonged drought.

Biomass was converted to g carbon assuming carbon:dry mass is 0.45. Maximum

individual length is 10 cm, which translates to a maximum wet mass of 3.39 g (Murdy et

al. 1997). Aspect ratio for the bay anchovy is 2.88 (Froese and Pauly 2005).

The bay anchovy feeds almost exclusively on zooplankton, but when planktonic

abundance is low, it is reported that the species will engage in benthic feeding behavior

(Murdy et al. 1997). Studies of feeding behavior determined that the anchovies consume

icthyoplankton, microzooplankton and copepods (Wang and Houde 1994; Sheridan

1978). Since the CBP surveys of zooplankton incorporate ichthyoplankton into the

microzooplankton and mesozooplankton categories, the bay anchovy was linked to only

three compartments: microzooplankton, mesozooplankton and a minimal connection to

meiofauna.

32. _Notropis hudsonius_: The spottail shiner was frequently collected in both creeks, although it was absent from Broad Creek in August 2001 and from Marshyhope Creek in August 2002. It is usually found in waters with salinity below 5 ‰, although it has been observed in habitats with higher salinity (Murdy et al. 1997).

Elemental analysis indicated that carbon:dry mass ratio was 0.44. Maximum individual length is 15 cm, equivalent to a maximum body mass of 20.04 g wet weight (Rohde et al. 1994). Aspect ratio for is 1.75.

The spottail shiner feeds on a broad range of small organisms. They will consume small mollusks, cladocerans, copepods, ostracods, and benthic insect larvae (Odum et al. 1984). Inspection of gut contents indicated the shiners were also consuming particulate detritus and gammarid amphipods. The compartment is trophically linked to mesozooplankton, meiofauna, macrobenthos, _Corbicula fluminea_, _Gammarus_ spp. and suspended POC.

33. _Fundulus diaphanus_ < 35 mm TL: The banded killifish was the most abundant fish captured in the tidal freshwater marshes of the Nanticoke River. Individuals ranged in total length from 12 mm to 90 mm and appearing to use the marshes throughout their entire life cycle. Some research has suggested that these fish prefer subtidal habitats (Weisberg 1986), but every collection method I used in the high marsh (including baited minnow traps in interior high marshes) captured the banded killifish. It is commonly

found in mixed schools with *Fundulus heteroclitus,* as was frequently the case in this study (Murdy et al. 1997).

The smaller banded killifish had higher mean carbon content than the larger *F. diaphanus* specimens. Carbon content : dry mass was 0.48. I used a maximum length 35 mm as specified by compartmental definitions. Aspect ratio is 0.82 (Froese and Pauly 2005). While the calculation estimating C:B calls for an asymptotic maximum body mass, younger organisms of a given species have greater energetic requirements than larger individuals, since there is presumably more consumption devoted to somatic growth. The smaller maximum length produces a higher C:B, and consequently, higher P:B and R:B.

These fish consume insects, worms, small crustaceans and mollusks (Murdy et al. 1997; Weisberg 1986; Baker-Dittus 1978). There were, however, sharp differences in diet between *F. diaphanus* < 35 mm and those that were larger. The stomachs of killifish < 35 mm never contained any Corixidae or *Gammarus* spp., while the larger specimens did. Because of this apparent shift in trophic activity based on individual size, I divided the species into two compartments. This compartment of smaller *F. diaphanus* was limited to feeding on smaller benthic prey items: meiofauna, benthic macrofauna, *Corbicula*, other aquatic invertebrates and POC .

34. *Fundulus diaphanus > 35mm*: This compartment contains the larger banded killifish that frequently consumed Corixidae and *Gammarus* spp., suggesting that the larger banded killifish occupy a different trophic role in the marshes than their smaller siblings.

Carbon accounts for 43.5 percent of dry mass, a smaller ratio than for the smaller fish. The banded killifish can grow to lengths of 11 cm with a maximum estimated wet body mass of 11.43 g. Aspect ratio is 0.82 (Froese and Pauly 2005).

The stomach contents of larger killifish included substantial numbers of Corixidae and *Gammarus* spp. As the fish grow larger, they switch to larger prey items. Compartment linkages were added to the two macroinvertebrate compartments and eliminated from meiofauna, assuming that prey preference shifts to larger organisms (Weisberg 1986; Baker-Dittus 1978).

35. *Fundulus heteroclitus*: The mummichog was often captured with *F. diaphanus*. Very few small mummichogs were collected over the study, and median total length was usually over 50 mm, 15 – 20 mm longer than its congener, *F. diaphanus*. *F. heteroclitus* tolerates a much wider range of salinity than the banded killifish and is a frequent resident of salt marshes (Yozzo and Smith 1998; Halpin 1997).

Carbon:dry mass ratio was similar to F. diaphanus > 35 mm at 0.44. *F. heteroclitus* can reach a maximum total length of 120 mm, yielding a maximum

individual wet mass of 28.79 g. The caudal fin aspect ratio is slightly higher than *F.*

diaphanus at 0.9 (Froese and Pauly 2005).

There is a great deal of overlap between the diets of *F. diaphanus* and *F.*

hetoeroclitus. These fish consume small benthic crustaceans, small mollusks, annelid

worms, insects and algae (Odum et al. 1984; Baker-Dittus 1978). Stomach contents

typically contained Corixidae, *Gammarus* spp., Corbicula and detrital material. *F.*

heteroclitus does not assimilate particulate detritus or algae particularly well (especially

detritus), but algae is nonetheless presumed to be a dietary component (D'Avanzo and

Valiela 1990). The compartment was linked to benthic algae, macrobenthos, *Corbicula*,

Corixidae, *Gammarus* spp. and other aquatic invertebrates.

36. <u>*Gambusia holbrooki*</u>: The mosquitofish was another commonly collected species, but

it was entirely absent from all Marshyhope collections in October 2001. This fish

typically is found near the water surface occupying a somewhat different functional role

from the very abundant killfishes, with less feeding activity focusing on the benthos

(Brown-Peterson and Peterson 1990).

Carbon accounts for 44 percent of dry mass in the mosquitofish. Maximum length

is variable based on sex, with females growing significantly larger than males, but most

individuals collected were females. I used a maximum size of 6.5 cm (Murdy et al. 1997).

Aspect ratio is 0.75 (Froese and Pauly 2005).

Gambusia is regarded as an insectivorous fish, consuming primarily insects and insect larvae. There is evidence that dietary habits shift in brackish waters to more benthic organisms (Odum et al. 1984), but examination of stomach contents revealed no dietary shifts as salinity rose in the late 2002 networks. Particulate detritus was commonly found in the stomachs. This compartment was linked to four others, benthic macrofauna (i.e., the insect larvae), Corixidae, other aquatic invertebrates and POC.

37. *Gobiosoma bosc*: Adult naked gobies are typically found in oligohaline habitats, but young fish migrate upstream into less saline waters (Odum et al. 1984; Lippson and Moran 1974). The fish were present in only two networks, May 2002 and August 2002 in Marshyhope Creek. Their arrival coincided with the relatively large increase in salinity in Marshyhope Creek.

The carbon:dry mass used for *Gobiosoma* was 0.43. Maximum fish size is six cm and maximum body mass was calculated to be 3.41 g (Murdy et al. 1997). Aspect ratio is 0.605 (Froese and Pauly 2005).

Naked gobies are benthic feeders consuming organisms like annelid worms, gammarid amphipods and other small crustaceans (Odum et al. 1984). The compartment diet consists of meiofauna, benthic macrofauna and *Gammarus* spp.

38. *Morone americana*: The white perch is found throughout the entire Chesapeake Bay, but most often in waters with salinities below 18 ‰. The fish in the May networks on

both creeks were mostly YOY, with only a few fish over 50 mm TL. Later in the year, the white perch population consisted of larger individuals, typically 100 mm or larger.

Elemental analysis indicated the carbon:dry mass is 0.435. Maximum individual length was assumed to be 400 mm, and maximum body mass was calculated as 989 g (Murdy et al. 1997). The aspect ratio of the caudal fin is 0.8 (Froese and Pauly 2005).

Stomach contents of the white perch contained Corixidae, *Gammarus* spp. insect body parts and detritus, consistent with published accounts of juvenile dietary preferences (Murdy et al. 1997; Odum et al. 1984). The compartment was linked to benthic macrofauna, *Corbicula*, Corixidae, *Gammarus* spp. Odonate larvae, and other insects.

39. *Etheostoma olmstedi*: The tessellated darter was included in eight of the 10 networks, absent only from August 2001 and October 2002. It is most commonly associated with freshwater habitats, but has been found in habitats with salinity reaching 13 ‰ (Murdy et al. 1997).

The carbon:dry mass ratio determined by elemental analysis was 0.455. Maximum individual length is 11.7 cm, and maximum body mass was estimated to be 13.26 g. The aspect ratio is 0.92.

Etheostoma consumes small crustaceans, insects, snails and algae (Odum et al. 1984). In these networks, it was linked to benthic algae, meiofauna, macrofauna, other aquatic invertebrates and POC.

40. *Lepomis macrochirus*: The bluegill was rarely captured in Marshyhope Creek, but was fairly common in Broad Creek, appearing in all networks except May 2001. In Marshyhope Creek, the fish was only collected during August 2001 and appears only in that Marshyhope network. The species can tolerate a wide range of salinities compared to its congeners, but it was never found at any station with salinity measurements greater than 0.1 ‰, so its absence from Marshyhope Creek is somewhat puzzling, especially before August 2002.

The carbon : dry mass ratio is 43.5 percent. Maximum length is 31 cm and I estimated maximum body mass to be 560 g (Murdy et al. 1997). Aspect ratio is 1.39 (Froese and Pauly 2005).

This fish is considered an opportunistic feeder, consuming insects, small crustaceans, molluscs, and plant material (Odum et al. 1984). Stomach contents did not show any specimens consuming plant material or algae, so this fish was linked only to compartments containing small invertebrates: macrobenthos, Corbicula, Corixidae, odonate larvae and other aquatic invertebrates.

41. _Trinectes maculatus_: The hogchoker is another species that was not frequently caught. Its spotty temporal distribution is more likely due to life history traits than the rise in salinity from late 2001 onward. Spawning occurs from May through September, peaking in June, and larval and juvenile hogchokers move upstream into low salinity nursery grounds (Lippson and Moran 1974). All individuals collected were juveniles, with median sizes ranging from 12 - 50 mm TL.

Carbon:dry mass ratio was 0.435. Maximum length used for C:B calculations was 20 cm, which translates to a maximum body mass of 62.51 g. Aspect ratio was 0.79.

Juvenile hogchokers are benthic feeders, consuming worms, very small crustaceans, detritus and algae (Murdy et al. 1997; Odum et al. 1984). The compartment is linked to benthic algae, meiofauna, benthic macrofauna, other aquatic invertebrates and POC.

42. Macrophyte Detritus: In most aquatic networks, detrital compartments consist of dissolved organic and particulate organic components, both suspended in the water column and in the sediments (Almunia et al. 1999; Baird and Ulanowicz 1989). The fate of primary production of phytoplankton and benthic algae intuitively makes sense when linked to water-column POC or sediment POC – dead cells becoming small, utilizable organic particles. In networks of wetland systems, however, detritus has been divided between labile and refractory detritus, partitioning detritus based on decomposition rates (Ulanowicz et al. 1999).

Aboveground plant material in tidal freshwater marshes persists for several months and gradually is incorporated into DOC, suspended POC and sediment POC (Whigham et al. 1980). Every collection of aboveground biomass I made included significant biomass from dead plant material. Furthermore, there can be direct transfers from living macrophytes to DOC that are functionally different than flow from dead plant material to detrital pools (Mann and Wetzel 1996). The manner in which detritus is treated can greatly affect the results network analysis, emphasizing the importance of these non-living pools of carbon (Allesina et al. 2005). Therefore, all macrophyte net primary production that ended up in other detrital pools after senescence was mediated through the macrophyte detritus compartment in order to emphasize this difference.

Biomass estimates for this compartment were based on the standing crop of plant material identified as "dead." No effort was made to sort the dead material according to species, so the compartment is an agglomeration of all dead macrophyte biomass.

August and October networks receive inputs into this compartment that represents stored biomass that was produced in the previous time period. In October, current production is also processed through the macrophyte detritus compartment. This characterization of biomass fate reflects the nearly complete turnover of aboveground biomass by the onset of the next growing season and its near total passage into the various POC and DOC detrital compartments. Macrophyte detritus does not export any

material from the system – all material that passes through this compartment ends up in one of the other four detrital compartments.

43. <u>Particulate Organic Carbon (POC)</u>: This compartment contains all the particulate organic carbon that is suspended in the water column. Biomass estimates for this detrital pool were based on measures of particulate carbon in water samples taken from the Nanticoke River near Sharptown, Maryland, by Maryland DNR, part of a baywide monitoring program sponsored by the Chesapeake Bay Program (Chesapeake Bay Program 2005c). I only used data that were collected at approximately the same time as I was collecting field samples, allowing a two-week window on either side of my sample dates for data inclusion. The CBP data provided estimates of particulate carbon from two separate samples taken at the collection site, one from the top of the water column and one at the bottom. The mean of these to values was used as the baseline estimate of particulate carbon (mg L^{-1}). Baseline estimates were converted to g carbon m^{-2} scaling the final value based on mean water depth estimated during throw trap collections.

The detrital compartments were used to balance the networks based on the demand deficiencies that were present after MATLOD estimated compartmental demands. The convention used for the treatment of macrophyte production (i.e., exporting production from one network to the next) provided the necessary inputs for the August and October networks, but May networks had a deficiency that needed to be addressed. Deficiency ranged from 150 to 171 g carbon m^{-2}. Annual sediment accretion rates are fairly high especially in tidal freshwater marshes, to nearly 11 mm y^{-1} (Orson et

al. 1992), although measurement of net inputs appears to be very sensitive to the manner in which fluxes are measured (Murray and Spencer 1997). Anderson et al. (1998) empirically observed that their measures of microalgal and macrophyte production could not account for all the carbon that tidal freshwater marshes process and suggested that deposition of sediment probably accounts for this difference. In subsequent sediment accretion studies, they estimated annual sediment input rate to tidal freshwater marshes along the Pamunkey River, Virgina, to be 517 ± 353 g carbon $m^{-2} y^{-1}$ (Neubauer et al. 2002).

The carbon deficit in May was addressed by adding an exogenous input to POC, assuming that it is the spring/summer season that receives a net input of material to the marsh surface, most likely deposited as POC to the marsh sediments (Pasternack and Brush 2001). While there is still sediment deposition occurring through late summer, it was assumed that net POC input was at its greatest in May. By late August, as Pasternack and Brush (2001) observed, the deposition rates decline significantly. POC was exported from the systems in October networks, a reflection of the greater amounts of POC in the water column in the fall (Chesapeake Bay Program 2005c).

44. <u>Dissolved Organic Carbon (DOC)</u>: This compartment contains all the dissolved organic carbon that is in the water column. The estimates of biomass were based on data collected by Maryland DNR for the Chesapeake Bay Program, presented in the CBP Water Quality Database (Chesapeake Bay Program 2005c). As with other compartments, I only considered data that was temporally related to my networks. Estimates of DOC are

provided for multiple water layers in the data set. I combined these estimates into one mean value for each date that served as the baseline estimate of DOC for both creek systems. Baseline estimates were converted to g carbon m^{-2}, scaling the final value based on mean water depth estimated during throw trap collections.

The fate of DOC was either consumption by free bacteria or export from the system. Macrophytes, benthic algae and phytoplankton either leach out or extrude DOC into the water column. Net primary production should yield a positive net flow into the DOC compartment. DOC concentration is typically higher in water on the ebb tide, suggesting net export of DOC (Roman and Daiber 1989). Some evidence suggests that there is little difference through the growing season in DOC flux from the marshes (Odum and Smith 1985). The export of carbon as DOC was usually around 40 g carbon m^{-2} y^{-1} in each network, although there was more variability in Broad Creek than Marshyhope Creek.

45 and 46. <u>High and Low Marsh Sediments</u>: Carbon content of the soils was based on direct measures of organic content. Estimates of percent organic matter were converted to biomass by constructing a linear regression equation relating soil bulk density to organic matter content. Recent studies in sediment dynamics of tidal freshwater marshes provided data from a variety of marshes, and only sites with characteristics similar to the Nanticoke marshes were used in the regression model (Zelenke-Merrill 1999). Biomasses were converted to g carbon based on data from the elemental analysis of the Broad Creek

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and Marshyope Creek sediments. Only the top 10 cm of soil were considered to be active in the network, and biomass was scaled accordingly (Ulanowicz et al. 1999).

Soil POC was the primary resource for microbial activity and most carbon losses (bacterial respiration) and exports (sequestration of carbon in soil) were mediated in part by the soils. Distinctions were drawn between these two detrital pools. Flushing effects are more pronounced in the low marsh, and I assumed that most transfers from POC (i.e., net input) would fall in the high marsh where water flow velocities would be sufficiently low enough for particulate material to precipitate out. Most marshes lacked a well-defined berm, where POC deposition rates are typically the highest (Pasternack and Brush 2001). Also, while organic content was greater in the high marsh, the estimated bulk density of these soils was lower, suggesting greater soil porosity and the likelihood that water infiltration rates would be greater there than in the low marsh. Macrophyte production was also significantly greater in the high marsh, further suggesting that there was more organic material flux in the high marsh than the low marsh.

BIBLIOGRAPHY

Able, K. W. and Hagan, S. M. 2000. Effects of common reed (*Phragmites australis*) invasion on marsh surface macrofauna: response of fishes and decapod crustaceans. *Estuaries*. 23(5): 633-646.

Able, K. W., Hagan, S. M., and Brown, S. A. 2003. Mechanisms of marsh habitat alteration due to *Phragmites*: response of young-of-the-year mummichog (*Fundulus heteroclitus*) to treatment for *Phragmites* removal. *Estuaries*. 26(2B): 484-494.

Able, K. W., Nemerson, D. M., Bush, R., and Light, P. 2001. Spatial variation in Delaware Bay (U.S.A.) marsh creek fish assemblages. *Estuaries*. 24(3): 441-452.

Allesina, S. and Bondavalli, C. 2003. Steady state of ecosystem flow networks: A comparison between balancing procedures. *Ecological Modelling*. 165(2-3): 221-229.

Allesina, S., Bondavalli, C., and Scharler, U. M. 2005. The consequences of the aggregation of detritus pools in ecological networks. *Ecological Modelling*. 189(1-2): 221-232.

Almunia, J., Basterretxeaa, G., Arísteguia, J., and Ulanowicz, R. E. 1999. Benthic-pelagic switching in a coastal subtropical lagoon. *Estuarine, Coastal and Shelf Science*. 49(3): 363-384.

Anderson, I. C., Neubauer, S. C., Neikirk, B. B., and Wetzel, R. L. 1998. *Exchanges of Carbon and Nitrogen between Tidal Freshwater Wetlands and Adjacent Tributaries*. Virginia Coastal Resources Management Program, Virginia Department of Environmental Quality.

Angradi, T. R., Hagan, S. M., and Able, K. W. 2001. Vegetation type and the intertidal macroinvertebrate fauna of a brackish marsh: *Phragmites* vs. *Spartina*. *Wetlands*. 21(1): 75-92.

Ator, S. W., Denver, J. M., and Brayton, M. J. 2004. *Hydrologic and Geochemical Controls on Pesticide and Nutrient Transport to Two Streams on the Delmarva Peninsula*. U.S. Geological Survey, Reston, VA. Scientific Investigations Report 2004-5051.

Austin, H. K. and Findlay, S. E. G. 1989. Benthic bacterial biomass and production in the Hudson River Estuary. *Microbial Ecology*. 18(2): 105-116.

Bachman, L. J., Lindsey, B. D., Brakebill, J., and Powars, D. S. 1998. *Ground-Water Discharge and Base-Flow Nitrate Loads of Nontidal Streams, and Their Relation to a Hydrogeomorphic Classification of the Chesapeake Bay Watershed, Middle*

Atlantic Coast. U.S. Geological Survey, Baltimore, MD. U.S. Geological Survey Water-Resources Investigations Report 98-4059.

Baird, D., McGlade, J. M., and Ulanowicz, R. E. 1991. The comparative ecology of six marine ecosystems. *Philosophical Transactions of the Royal Society of London: Biological Sciences*. 333(1266): 15-29.

Baird, D. and Ulanowicz, R. E. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs*. 59(4): 329-364.

Baird, D. and Ulanowicz, R. E. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Marine Ecology Progress Series*. 99(3): 221-237.

Baker-Dittus, A. M. 1978. Foraging patterns of three sympatric killifish. *Copeia*. 1978(3): 383-389.

Baldwin, A. H., Egnotovich, M. S., and Clarke, E. 2001. Hydrologic change and vegetation of tidal freshwater marshes: Field, greenhouse, and seed-bank experiments. *Wetlands*. 21(4): 519-531.

Baldwin, A. H. and Pendleton, F. N. 2003. Interactive effects of animal disturbance and elevation on vegetation of a tidal freshwater marsh. *Estuaries*. 26(4A): 905-915.

Banse, K. 1979. On weight dependence of net growth efficiency and specific respiration rates among field populatons of invertebrates. *Oecologia*. 38: 111-126.

Banse, K. and Mosher, S. 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs*. 50(3): 355-379.

Batzer, D. P., Dietz-Brantley, S. E., Taylor, B. E., and DeBiase, A. E. 2005. Evaluating regional differences in macroinvertebrate communities from forested depressional wetlands across eastern and central North America. *Journal of the North American Benthological Society*. 24(2): 403-414.

Bedford, B. L., Walbridge, M. R., and Aldous, A. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. *Ecology*. 80(7): 2151-2169.

Bender, E. A., Case, T. J., and Gilpin, M. E. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology*. 65(1): 1-13.

Bertness, M. D., Ewanchuk, P. J., and Silliman, B. R. 2002. Anthropogenic modification of New England salt marsh landscapes. *Proceedings of the National Academy of Sciences*. 99(3): 1395-1398.

Boesch, D. F. and Turner, R. E. 1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries*. 7: 460-468.

Boesch, D. F. 1996. Science and management in four U.S. coastal ecosystems dominated by land-ocean interactions. *Journal of Coastal Conservation*. 2: 103-114.

Boon, P. I. and Bunn, S. E. 1994. Variations in the stable isotope composition of aquatic plants and their implications for food web analysis. *Aquatic Botany*. 48(2): 99-108.

Bowden, W. B. 1986. Nitrification, nitrate reduction, and nitrogen immobilization in a tidal freshwater marsh sediment. *Ecology*. 67(1): 88-99.

Bowden, W. B. 1987. The biogeochemistry of nitrogen in freshwater wetlands. *Biogeochemistry*. 4(3): 313-348.

Bowden, W. B., Vörösmarty, C. J., Morris, J. T., Peterson, B. J., Hobbie, J. E., and Steudler, P. A. M. I. B. 1991. Transport and processing of nitrogen in a tidal freshwater wetland. *Water Resources Research*. 27(3): 389-408.

Boyer, K. E. and Zedler, J. B. 1998. Effects of nitrogen additions on the vertical structure of a constructed cordgrass marsh. *Ecological Applications*. 8(3): 692-705.

Brakebill, J. W. and Preston, S. D. 2003. A hydrologic network supporting spatially referenced regression modeling in the Chesapeake Bay watershed. *Environmental Monitoring and Assessment*. 81(1-3): 73-84.

Brakebill, J. W. and Preston, S. D. 2004. Digital data used to relate nutrient inputs to water quality in the Chesapeake Bay watershed, version 3.0. http://md.water.usgs.gov/publications/ofr-2004-1433/sparv3.htm. Accessed on 5/15/2005.

Brett, J. R. and Groves, T. D. D. 1979. Physiological Energetics. p.280-352. In, Hoar, W. S., Randall, D. J., and Brett, J. R., (eds.), *Fish Physiology, Volume VIII*. Academic Press, Inc., New York.

Brown-Peterson, N. and Peterson, M. S. 1990. Comparative life history of female mosquitofish, *Gambusia affinis*, in tidal freshwater and oligohaline habitats. *Environmental Biology of Fishes*. 27(1): 33-41.

Bulger, A. J., Hayden, B. P., Monaco, M. E., Nelson, D. M., and McCormick-Ray, M. G. 1993. Biologically-based estuarine salinity zones derived from a multivariate analysis. *Estuaries*. 16(2): 311-322.

Campbell, K. L. and Edwards, D. R. 2001. Phosphorus and water quality impacts. p.91-109. In, Ritter, W. F. and Shirmohammadi, A., (eds.), *Agricultural Non-Point Source Pollution: Watershed Management and Hydrology*. Lewis Publishers, Boca Raton, FL.

Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N., and Smith, V. H. 1998. Nonpoint pollution of surface waters with phosphorus and

nitrogen. *Ecological Applications*. 8(3): 559-568.

Carpenter, S. R., Kitchell, J. F., and Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. *Bioscience*. 35(10): 634-639.

Chesapeake Bay Foundation. 1996. *Nanticoke River Watershed: Natural and Cultural Resources Atlas*. Chesapeake Bay Foundation, Anapolis, Maryland.

Chesapeake Bay Foundation. 2005. *2005 State of the Bay*. Chesapeake Bay Foundation, Annapolis, Maryland.

Chesapeake Bay Program. 2000. *The 2000 User's Guide to Chesapeake Bay Program Biological and Living Resource Monitoring Data* . Chesapeake Bay Program, Annapolis, MD.

Chesapeake Bay Program. 2001. *Bay Program Partners*. http://www.chesapeakebay.net/baypartners.htm. Accessed on 7/21/2003.

Chesapeake Bay Program. 2002. *Invasive Species in the Chesapeake Bay Watershed: A Workshop to Develop Regional Invasive Species Management Strategies*. Chesapeake Bay Program, http://www.chesapeakebay.net/search/pubs.htm. Accessed on 10/18/2004.

Chesapeake Bay Program. 2003a. *Watershed Profiles: The Nanticoke Watershed*. http://www.chesapeakebay.net/wspv31/(0n150q45dd52kf45e3dsug45)/WspAbout .aspx?basno=421&topic=5. Accessed on 12/14/2004.

Chesapeake Bay Program. 2003b. *The Chesapeake Bay Program: 20 Years of Progress -- Remaining Challenges*. Chesapeake Bay Program, Annapolis, Maryland.

Chesapeake Bay Program. 2004a. *Virginia Chesapeake Bay Program Phytoplankton Monitoring Survey Data Dictionary*. ftp://ftp.chesapeakebay.net/Pub/Living_Resources/plank/phyto/VAPHDOC.pdf. Accessed on 10/28/2005.

Chesapeake Bay Program. 2004b. *Maryland Chesapeake Bay Program Benthic Monitoring Survey Data Dictionary*. ftp://ftp.chesapeakebay.net/Pub/Living_Resources/benth/mdbedoc.pdf. Accessed on 5/15/1910.

Chesapeake Bay Program. 2004c. *The State of the Chesapeake Bay and its Watershed*. Chesapeake Bay Program, Annapolis, MD.

Chesapeake Bay Program. 2004d. *Mainstem Bay Summer Dissolved Oxygen Concentrations*. http://www.chesapeakebay.net/status.cfm?SID=117&subjectarea=INDICATORS. Accessed on 2/10/2005.

Chesapeake Bay Program. 2005a. *Baywide Benthic Database*.
http://www.chesapeakebay.net/data/data_desc.cfm?DB=CBP_BENDB. Accessed on 9/22/2005.

Chesapeake Bay Program. 2005b. *Baywide CBP Plankton Database*.
http://chesapeakebay.net/data/data_desc.cfm?DB+CBP_PLANKDB. Accessed on 9/14/2005.

Chesapeake Bay Program. 2005c. *CBP Water Quality Database (1984-present)*.
http://www.chesapeakebay.net/modsc.htm. Accessed on 8/22/2005.

Chesapeake Bay Program. 2005d. *CBP Watershed Model Scenario Output Database*,
Phase 4.3. http://www.chesapeakebay.net/data/index.htm. Accessed on 8/30/2005.

Chesapeake Bay Program. 2006. *Chesapeake Bay 2005 Health and Restoration
Assessment, Part One: Ecosystem Health*. Chesapeake Bay Program, Annapolis, Maryland. CBP/TRS 279/06.

Chick, J. H., Jordan, F., Smith, J. P., and McIvor, C. C. 1992. A comparison of four
enclosure traps and methods used to sample fishes in aquatic macrophytes. *Journal of Freshwater Ecology*. 7(4): 353-361.

Chick, J. H. and McIvor, C. C. 1994. Patterns in the abundance and composition of fishes
among beds of different macrophytes: Viewing a littoral zone as a landscape. *Canadian Journal of Fisheries and Aquatic Sciences*. 51(12): 2873-2882.

Chick, J. H. and McIvor, C. C. 1997. Habitat selection by three littoral zone fishes:
Effects of predation pressure, plant density and macrophyte type. *Ecology of Freshwater Fish*. 6(1): 27-35.

Christian, R. R. and Luczkovich, J. J. 1999. Organizing and understanding a winter's
seagrass foodweb network through effective trophic levels. *Ecological Modelling*. 117(1): 99-124.

Cifuentes, L. A., Sharp, J. H., and Fogel, M. L. 1988. Stable carbon and nitrogen isotope
biogeochemistry in the Delaware estuary. *Limnology and Oceanography*. 33(5): 1102-1115.

Clarke, K. R. 1993. Non-parametric analyses of changes in community structure.
Australian Journal of Ecology. 18: 117-143.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem.
Marine Ecology Progress Series. 210: 223-253.

Collins, E. R., Barker, J. C., Carr, L. E., Brodie, H. L., and Martin, J. H. 1999. *Poultry
Wast Management Handbook*. Natural Resource, Agriculture, and Engineering Service, Ithaca, New York.

Cooper, S. R. 1995. Chesapeake Bay watershed historical land use: Impact on water quality and diatom communities. *Ecological Applications*. 5(3): 703-723.

Counts, C. L. 1991. *Corbicula* (Bivalvia: Corbiculidae). *Tryonia: Miscellaneous Publications of the Department of Malacology, The Academy of Natural Sciences of Philadelphia*. No. 21.

Cowardin, L. M., Carter, V., Golet, F. C., and LaRoe, E. T. *Classification of Wetlands and Deepawater Habitats of the United States*. U.S. Fish and Wildlife Service Publications, Washington, D.C. FWS/OBS-79/31.

Crain, C. M., Silliman, B. R., Bertness, S. L., and Bertness, M. D. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology*. 85(9): 2539-2549.

Crow, G. E. and Hellquist, C. B. 2000a. *Aquatic and Wetland Plants of Northeastern North America, Volume One, Pteridophytes, Gymniosperms and Angiosperms: Dicotyledons*. The University of Wisconsin Press, Madison, Wisconsin.

Crow, G. E. and Hellquist, C. B. 2000b. *Aquatic and Wetland Plants of Northeastern North America, Volume Two, Angiosperms: Monocotyledons*. The University of Wisconsin Press, Madison, Wisconsin.

Cummins, K. W. and Wuycheck, J. C. 1971. Caloric equvalents for investigation in ecological energetics. *International Association of Theoretical and Applied Limnology*. (18): 1-143.

D'Avanzo, C. and Valiela, I. 1990. Use of detrital foods and assimilation of nitrogen by coastal detritivores. *Estuaries*. 13(1): 20-24.

Dahl, T. 2000. *Status and Trends of Wetlands in the Conterminous United States, 1986-1997*. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C.

Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., and Tu, K. P. 2002. Stable Isotopes in Plant Ecology. *Annual Review of Ecology and Systematics*. 33(507-559):

Dawson, T. E. and Brooks, P. D. 2001. Fundamentals of stable isotope chemistry and measurement. p.1-18. In, Unkovich, M., Pate, J., McNeill, A., and Gibbs, D. J., (eds.), *Stable Isotope Techniques in the Study of Biological Processes and Functioning of Ecosystems*. Kluwer Academic Press, Netherlands.

Delmarva Poultry Industry, Inc. 2005. *Delmarva and U.S. Poultry Facts*. http://www.dpichicken.org/index.cfm?content=facts. Accessed on 8/18/2005.

Deaton, L. E. and Greenberg, M. J. 1986. There is no horohalinicum. *Estuaries*. 9(1): 20-30.

Denver, J. M., Ator, S. W., Debrewer, L. M., Ferrari, M. J., Barbaro, J. R., Hancock, T. C., Brayton, M. J., and Nardi, M. R. 2004. *Water Quality in the Delmarva Peninsula Delaware, Maryland and Virginia, 1999-2001*. U.S. Geological Survey, Reston, VA. U.S. Geological Survey Circular 1228.

Doumlele, D. G. 1981. Primary production and seasonal aspects of emergent plants in a tidal freshwater marsh. *Estuaries*. 4(2): 139-142.

Driscoll, C. T., Whitall, D., Aber, J., Boyer, E., Castro, M., Cronan, C., Goodale, C. L., Groffman, P., Hopkinson, C., Lambert, K., Lawrence, G., and Ollinger, S. 2003. Nitrogen pollution in the northeastern United States: Sources, effects, and management options. *Bioscience*. 53(4): 357-374.

Ehleringer, J. R. and Rundel, P. W. 1989. Stable isotopes: history, units and instrumentation. p.1-16. In, Rundel, P. W., Ehleringer, J. R., and Nagy, K. A., (eds.), *Stable Isotopes in Ecological Research*. Springer-Verlag, New York.

Ernest, S. K., Enquist, B. J., Brown, J. H., Charnov, E. L., Gillooly, J. F., Savage, V. M., White, E. P., Smith, F. A., Hadly, E. A., Haskell, J. P., Lyons, S. K., Maurer, B. A., Niklas, K. J., and Tiffney, B. 2003. Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecology Letters*. 6(11): 990-995.

Ernst, H. R. 2003. *Chesapeake Bay Blues: Science, Politics and the Struggle to Save the Bay*. Rowman and Littlefield Publishers, Inc., Lanham, Maryland, USA.

Erskine, P. D., Bergstrom, D. M., Schmidt, S., Stewart, G. R., Tweedie, C. E., and Shaw, J. D. 1998. Subantarctic Macquarie Island - a model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. *Oecologia*. 117(1-2): 187-193.

Fabiano, M., Vassallo, P., Vezzulli, L., Salvo, V. S., and Marques, J. C. 2004. Temporal and spatial change of exergy and ascendency in different benthic marine ecosystems. *Energy - The International Journal*. 29(11): 1697-1712.

Fantle, M. S., Dittel, A. I., Schwalm, S. M., Epifanio, C. E., and Fogel, M. L. 1999. A food web analysis of the juvenile blue crab, *Callinectes sapidus,* using stable isotopes in whole animals and individual amino acids. *Oecologia*. 120(3): 416-426.

Field, R. T. and Philipp, K. R. Jun 2000. Vegetation changes in the freshwater tidal marsh of the Delaware Estuary. *Wetlands Ecology and Management*. 8(2-3): 79-88.

Findlay, S., Howe, K., and Austin, H. K. 1990. Comparison of detritus dynamics in two

tidal freshwater wetlands. *Ecology*. 71(1): 288-295.

Findlay, S., Schoeberl, K., and Wagner, B. 1989. Abundance, composition, and dynamics of the invertebrate fauna of a tidal freshwater wetland. *Journal of the North American Benthological Society*. 8(2): 140-148.

Flemer, D. A., Heinle, D. R., Keefe, C. W., and Hamilton, D. H. 1978. Standing crops of marsh vegetation of two tributaries of Chesapeake Bay. *Estuaries*. 1(3): 157-163.

Flynn, K. M., McKee, K. L., and Mendelssohn, I. A. 1995. Recovery of freshwater marsh vegetation after a saltwater intrusion event. *Oecologia*. 103(1): 63-72.

Foe, C. and Knight, A. 1985. the effect of phytoplankton and suspended sediment on the growth of *Corbicula fluminea* (Bivalvia). *Hydrobiologia*. 127: 105-115.

Ford, M. A. and Grace, J. B. 1998. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *Journal of Ecology*. 86(6): 974-982.

Froese, R. and Pauly, D. 2005. *FishBase*. http://www.fishbase.org.

Galloway, J. N., Aber, J. D., Erisman, J. W., Seitzinger, S. P., Howarth, R. W., Cowling, E. B., and Cosby, B. J. 2003. The nitrogen cascade. *BioScience*. 53(4): 341-356.

Gotceitas, V. and Colgan, P. 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia*. 80(2): 158-166.

Gotceitas, V. and Colgan, P. 1990. The effects of prey availability and predation risk on habitat selection by juvenile bluegill sunfish. *Copeia*. (2): 407-417.

Grace, J. B. 2001. The roles of community biomass and species pools in the regulation of plant diversity. *Oikos*. 92(2): 193-207.

Gratton, C. and Denno, R. F. 2003. Inter-year carryover effects of a nutrient pulse on Spartina plants, herbivores, and natural enemies. *Ecology*. 84(10): 2692-2707.

Green, E. K. and Galatowitsch, S. M. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. *Journal of Applied Ecology*. 39(1): 134-144.

Gregg, C. S. and Fleeger, J. W. 1999. Grass shrimp *Palaemonetes pugio* predation on sediment- and stem-dwelling meiofauna: field and laboratory experiments. *Marine Ecology Progress Series*. 175: 77-86.

Hagy, J. D., Boynton, W. R., Keefe, C. W., and Wood, K. V. 2004. Hypoxia in Chesapeake Bay, 1950-2001: Long-term change in relation to nutrient loading and river flow. *Estuaries*. 27(4): 634-658.

Hair, J. F., Anderson, R. E., and Tatham, R. L. 1992. *Multivariate Data Analysis with Readings*. MacMillan, New York.

Halpin, P. M. 1997. Habitat use patterns of the mummichog, *Fundulus heteroclitus*, in New England. 1. Intramarsh variation. *Estuaries*. 20(3): 618-625.

Hamilton, P. A., Denver, J. M., Phillips, P. J., and Shedlock, R. J. 1993. *Water-Quality Assessment of the Delmarva Peninsula, Delaware, Maryland and Virginia -- Effects of Agricultural Activities on, and Distribution of, Nitrate and other Inorganic Constituents in the Surficial Aquifer*. U.S. Geological Survey, Towson, MD. U.S. Geological Survey Open File Report 93-40.

Hannon, B. 1973. The structure of ecosystems. *Journal of Theoretical Biology*. 41: 535-546.

Hanson, S. R., Osgood, D. T., and Yozzo, D. J. 2002. Nekton use of a *Phragmites australis* marsh on the Hudson River, New York, USA. *Wetlands*. 22(2): 326-337.

Harrison, S. S. C., Bradley, D. C., and Harris, I. T. 2005. Uncoupling strong predator prey interactions in streams: the role of marginal macrophytes. *Oikos*. 108(3): 433-448.

Hastings, R. W. and Good, R. E. 1977. Population analysis of the fishes of a freshwater tidal tributary of the lower Delaware River. *Bulletin of the New Jersey Academy of Science*. 22(2): 13-20.

Hauxwell, J., Cebrian, J., and Valiela, I. 2003. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series*. 247: 59-73.

Heinle, D. R. and Flemmer, D. A. 1976. Flows of material between poorly flooded tidal marshes of an estuary. *Marine Biology*. 35: 359-373.

Hendriks, A. J. 1999. Allometric scaling of rate, age and density parameters in ecological models. *Oikos*. 86(2): 293-310.

Heymans, J. J., Ulanowicz, R. E., and Bondavalli, C. 2002. Network analysis of the South Florida Everglades graminoid marshes and comparison with nearby cypress ecosystems. *Ecological Modelling*. 149(1-2): 5-23.

Hilsenhoff, W. L. 2001. Diversity and classification of insects and collembola. p.661-732. In, Thorp, J. H. and Covich, A. P., (eds.), *Ecology and Classification of North American Freshwater Invertebrates* . Academic Press, San Diego.

Hirata, H. and Ulanowicz, R. E. 1984. Information theoretical analysis of ecological networks. *International Journal of Systems Science*. 15(2): 261-270.

Hochberg, Y. 1988. A sharper Bonferroni procedure for multiple tests of significance.

Biometrika. 75(4): 800-802.

Horton, T. 2003. *Turning the Tide: Saving the Chesapeake Bay*. Island Press, Washington, D.C.

Howard, R. J. and Mendelssohn, I. A. 1999. Salinity as a constraint on growth of oligohaline marsh macrophytes. I. Species variation in stress tolerance. *American Journal of Botany*. 86(6): 785-794.

Howard, R. J. and Mendelssohn, I. A. 2000. Structure and composition of oligohaline marsh plant communities exposed to salinity pulses. *Aquatic Botany*. 68(2): 143-164.

Howes, B. L., Howarth, R. W., Teal, J. M., and Valiela, I. 1981. Oxidation-reduction potentials in a salt marsh: Spatial patterns and interactions with primary production. *Limnology and Oceanography*. 26(2): 350-360.

Huang, S. C., Kreeger, D. A., and Newell, R. I. E. 2003. Tidal and seasonal variations in the quantity and composition of seston in a North American, mid-Atlantic saltmarsh. *Estuarine, Coastal and Shelf Science*. 56(3-4): 547-560.

Hughes, J. E., Deegan, L. A., Wyda, J. C., Weaver, M. J., and Wright, A. 2002. The effects of eelgrass habitat loss on estuarine fish communities of southern New England. *Estuaries* . 25(2): 235-249.

Hwang, Y. H. and Morris, J. T. 1994. Whole plant gas exchange responses of *Spartina alterniflora* (Poaceae) to a range of constant and transient salinities. *American Journal of Botany*. 81: 659-665.

Jessup, B. K., Markowitz, A., and Stribling, J. B. 1999. *Family-Level Key to the Invertebrates of Maryland and Surrounding Areas*. Maryland Department of Natural Resources, Chesapeake Bay and Watershed Program, Resource Assessment Service, Monitoring and Non-Tidal Assessment Division, Annapolis, Maryland. CBWP-MANTA-EA-99-2.

Johnson, K. H., Vogt, K. A., Clark, H. J., Schmitz, O. J., and Vogt, D. J. 1996. Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology & Evolution*. 11(9): 372-377.

Jordan, F. 2002. Field and laboratory evaluation of habitat use by rainwater killifish (*Lucania parva*) in the St. Johns River Estuary, Florida. *Estuaries*. 25(2): 288-295.

Jordan, F., Babbitt, K. J., and McIvor, C. C. 1998. Seasonal variation in habitat use by marsh fishes. *Ecology of Freshwater Fish*. 7(4): 159-166.

Jordan, F., Coyne, S., and Trexler, J. C. 1997. Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m^2 throw trap.

Transactions of the American Fisheries Society. 126(6): 1012-1020.

Jørgensen, S. E., Nielsen, S. N., and Jørgensen, L. A. 1991. *Handbook of Ecological Parameters and Ecotoxicology*. Pergamon Press, Oxford.

Kadlec, R. H. and Knight, R. L. 1996. *Treatment Wetlands*. CRC Press, Boca Raton, Florida.

Karr, J. D., Showers, W. J., Gilliam, J. W., and Andres, A. S. 2001. Tracing nitrate transport and environmental impact from intensive swine farming using delta nitrogen-15. *Journal of Environmental Quality*. 30(4): 1163-1175.

Karr, J. D., Showers, W. J., and Hinson, T. H. 2002. Nitrate source identification using δ^{15}N in a ground water plume near an intensive swine operation. *Ground Water Monitoring and Remediation*. 22(2): 68-75.

Kearney, M. S., Grace, R. E., and Stevenson, J. C. 1988. Marsh loss in Nanticoke Estuary, Chesapeake Bay. *Geographical Review*. 78(2): 205-220.

Kemp, W. M., Sampou, P. A., Garber, J., Tuttle, J., and Boynton, W. R. 1992. Seasonal depletion of oxygen from bottom waters of Chesapeake Bay: Roles of benthic and planktonic respiration and physical exchange processes. *Marine Ecology Progress Series*. 85(1-2): 137-152.

Kemp, W. M., Twilley, R. R., Stevenson, J. C., Boynton, W. R., and Means, J. C. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. *Marine Technology Society Journal*. 17(2): 78-89.

Keough, J. R., Hagley, C. A., Ruzycki, E., and Sierszen, M. 1998. δ^{13}C composition of primary producers and role of detritus in a freshwater coastal ecosystem. *Limnology and Oceanography*. 43(4): 734-740.

Keough, J. R., Sierszen, M. E., and Hagley, C. A. 1996. Analysis of a Lake Superior coastal food web with stable isotope techniques. *Limnology and Oceanography*. 41(1): 136-146.

Kerry, J., Boorse, D., and Buchsbaum, R. 2004. Effect of nutrient enrichment and salinity on salt marsh invertebrates in the Plum Island estuary. *Biological Bulletin*. 207(2): 174.

Kiddon, J. A., Paul, J. F., Buffum, H. W., Strobel, C. S., Hale, S. S., Cobb, D., and Brown, B. S. 2003. Ecological condition of US Mid-Atlantic estuaries, 1997-1998. *Marine Pollution Bulletin*. 46(10): 1224-1244.

Killgore, K. J., Morgan II, R. P., and Rybicki, N. B. 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac River. *North

American Journal of Fisheries Management. 9(1): 101-111.

Klopatek, J. 1978. Nutrient dynamcis of freshwater riverine marshes and the role of emergent macrophytes. p.195-216. In, Good, R. E., Whigham, D. F., and Simpson, R. L., (eds.), *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York.

Kneib, R. T. 1985. Predation and disturbance by grass shrimp *Palaemonetes pugio* Holthuis, in soft-substratum benthic invertebrate assemblages. *Journal of Experimental Marine Biology and Ecology*. 93(1-2): 91-102.

Kneib, R. T. 1987. Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology*. 68(2): 379-386.

Kneib, R. T. 1997. Early life stages of resident nekton in intertidal marshes. *Estuaries*. 20(1): 214-230.

Kreitler, C. W. and Browning, L. A. 1983. Nitrogen-isotope analysis of groundwater nitrate in carbonate aquifers: Natural sources versus human pollution. *Journal of Hydrology*. 61(1-3): 285-301.

Kreitler, C. W., Ragone, S. E., and Katz, B. G. 1978. ^{15}N/^{14}N ratios of ground-water nitrate, Long Island, New York. *Ground Water*. 16(6): 404-409.

Kushlan, J. A. 1981. Sampling characteristics of enclosure fish traps. *Transactions of the American Fisheries Society*. 110(4): 557-562.

Latham, P. J., Pearlstine, L. G., and Kitchens, W. M. 1994. Species association changes across a gradient of freshwater, oligohaline, and mesohaline tidal marshes along the lower Savannah River. *Wetlands*. 14(3): 174-183.

Lavrentyev, P. J., Gardner, W. S., and Johnson, J. R. 1997. Cascading trophic effects on aquatic nitrification: Experimental evidence and potential implications. *Aquatic Microbial Ecology*. 13(2): 161-175.

Lazzari, M. A. 2002. Epibenthic fishes and decapod crustaceans in northern estuaries: A comparison of vegetated and unvegetated habitats in Maine. *Estuaries*. 25(6A): 1210-1218.

Leck, M. A. and Simpson, R. L. 1994. Tidal freshwater wetland zonation: Seed and seedling dynamics. *Aquatic Botany*. 47(1): 61-75.

Leck, M. A. and Simpson, R. L. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *American Journal of Botany*. 82(12): 1547-1557.

Lenz, J. 2000. Introduction. p.1-30. In, Harris, R. P., Wiebe, P. H., Lenz, J., Skjoldal, H. R., and Huntley, M., (eds.), *ICES Zooplankton Methodology Manual*. Academic Press, San Diego, California.

Ley, J. A., Montague, C. L., and McIvor, C. C. 1994. Food habits of mangrove fishes: A comparison along estuarine gradients in northeastern Florida Bay. *Bulletin of Marine Science*. 54(3): 881-889.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology*. 23(4): 399-417.

Lippson, A. J., Haire, M. S., Holland, A. F., Jacobs, F., Jensen, J., Moran-Johnson, R. L., Polgar, T. T., and Richkus, W. A. 1979. *Environmental Atlas of the Potomac Estuary*. Martin Marietta Corporation, Environmental Center and Martin Marietta Laboratories, Baltimore, MD.

Lippson, A. J. and Lippson, R. L. 1997. *Life in the Chesapeake Bay: An Illustrated Guide to the Fishes, Invertebrates, Plants, Birds and Other Animals of Bays and Inlets from Cape Cod to Cape Hatteras*. Johns Hopkins University Press, Baltimore MD.

Lippson, A. J. and Moran, R. L. 1974. *Manual for Identification of Early Developmental Stages of Fishes of the Potomac River Estuary*. Environmental Technology Center, Martin Marietta Corporation, Baltimore, MD.

Livingston, R. J. 1984. Trophic response of fishes to habitat variability in coastal seagrass systems. *Ecology*. 65(4): 1258-1275.

Longhurst, A. 1983. Benthic-pelagic coupling and export of organic carbon from a tropical Atlantic continental shelf - Sierra Leone. *Estuarine, Coastal and Shelf Science*. 17: 261-285.

Lowrance, R., Altier, L. S., Newbold, J. D., Schnabel, R. R., Groffman, P. M., Denver, J. M., Correll, D. L., Gilliam, J. W., Robinson, J. L., Brinsfield, R. B., Staver, K. W., Lucas, W., and Todd, A. H. 1997. Water quality functions of riparian forest buffers in Chesapeake Bay watersheds. *Environmental Management*. 21(5): 687-712.

Mann, C. J. and Wetzel, R. G. 1996. Loading and utilization of dissolved organic carbon from emergent macrophytes. *Aquatic Botany*. 53(1-2): 61-72.

Mantelatto, F. L. M. and Christofoletti, R. A. 2001. Natural feeding activity of the crab *Callinectes ornatus* (Portunidae) in Ubatuba Bay (Sao Paulo, Brazil): Influence of season, sex, size and molt stage. *Marine Biology*. 138(3): 585-594.

Marshall, H. G. and Burchardt, L. 2004. Phytoplankton composition within the tidal freshwater-oligohaline regions of the Rappahannock and Pamunkey Rivers in Virginia. *Castanea*. 69(4): 272-283.

Maryland DNR. 2002. *Drought Impacts on Maryland and Chesapeake Bay*. http://www.dnr.state.md.us/bay/monitoring/river/drought/bay_salinity_2002.html. Accessed on 11/6/2005.

Maryland DNR. 2004. *Nutrient Limitation: Results for the Lower Eastern Shore Basin*. http://www.dnr.state.md.us/bay/monitoring/limit/les_results.html. Accessed on 3/12/2006.

Mathieson, S., Cattrijsse, A., Costa, M. J., Drake, P., Elliott, M., Gardner, J., and Marchand, J. 2000. Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. *Marine Ecology Progress Series*. 204: 225-242.

McCafferty, W. P. 1988. *Aquatic Entomology, 2nd Edition*. Jones and Bartlett Publishers, Boston.

McClelland, J. W. and Valiela, I. 1998a. Linking nitrogen in estuarine producers to land-derived sources. *Limnology and Oceanography*. 43(4): 577-585.

McClelland, J. W. and Valiela, I. 1998b. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. *Marine Ecology Progress Series*. 168: 259-271.

McClelland, J. W., Valiela, I., and Michener, R. H. 1997. Nitrogen-stable isotope signatures in estuarine food webs: A record of increasing urbanization in coastal watersheds. *Limnology and Oceanography*. 42(5): 930-937.

McCune, B. and Grace, J. B. 2002. *Analysis of Ecological Communities*. MJM Software Design, Glenden Beach, Oregon.

McCune, B. and Medford, M. J. 1999. PC-ORD. MJM Software Design, Glenden Beach, Oregon.

McElfish Jr., J. M. 1998. *Almanac of Enforceable State Laws to Control Nonpoint Source Water Pollution*. Environmental Law Institute, Washington D.C.

McFarland, E. R. 1995. *Relation of Land Use to Nitrogen Concetrations in Ground Water in the Patuxent River Basin, Maryland.* U.S. Geological Survey Earth Science Information Center, Open file Reports, Box 25286, MS 517, Denver, CO 80225 (USA). 94-4170.

McGarigal, K., Cushman, S., and Stafford, S. 2000. *Multivariate Statistics for Wildlife and Ecology Research*. Springer-Verlag, New York.

McIvor, C. C. 1987. *Marsh Fish Community Structure: Roles of Geomorphology and Salinity*. Doctoral Dissertation. University of Virginia, Charlottesville, Virginia.

McIvor, C. C. and Odum, W. E. 1985. Use of flumes for sampling fishes and macrocrustaceans on marsh surface. *Estuaries*. 8(2B): 75A.

McIvor, C. C. and Odum, W. E. 1986. The flume net: A quantitative method for sampling fishes and macrocrustaceans on tidal marsh surfaces. *Estuaries*. 9(3): 219-224.

McIvor, C. C. and Odum, W. E. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology*. 69(5): 1341-1351.

McKee, K. L. and Mendelssohn, I. A. 1989. Response of a freshwater marsh plant community to increased salinity and increased water level. *Aquatic Botany*. 34(4): 301-316.

Merritt, R. W., Benbow, M. E., and Hudson, P. L. 2002. Wetland macroinvertebrates of Prentiss Bay, Lake Huron, Michigan: Diversity and functional group composition. *Great Lakes Entomologist*. 35(2): 149-160.

Meyer, D. L., Johnson, J. M., and Gill, J. W. 2001. Comparison of nekton use of *Phragmites australis* and *Spartina alterniflora* marshes in the Chesapeake Bay, USA. *Marine Ecology Progress Series*. 209: 71-84.

Meyerson, L. A., Chambers, R. M., and Vogt, K. A. 1999. The effects of *Phragmites* removal on nutrient pools in a freshwater tidal marsh ecosystem. *Biological Invasions*. 1(2-3): 129-136.

Meyerson, L. A., Saltonstall, K., Windham, L., Kiviat, E., and Findlay, S. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management*. 8(2-3): 89-103.

Mitsch, W. J. and Gosselink, J. G. 2000. *Wetlands*. 3rd. John Wiley, New York.

Monaco, M. E. and Ulanowicz, R. E. 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. *Marine Ecology Progress Series*. 161: 239-254.

Montagna, P. A., Blanchard, G. F., and Dinet, A. 1995. Effect of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. *Journal of Experimental Marine Biology and Ecology*. 185(2): 149-165.

Montague, C. L. and Ley, J. A. 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in northeastern Florida Bay. *Estuaries*. 16(4): 703-717.

Murdy, E. O., Birdsong, R. S., and Musick, J. A. 1997. *Fishes of Chesapeake Bay*. Smithsonian Institution Press, Washington, D.C.

Murray, A. L. and Spencer, T. 1997. On the wisdom of calculating annual material budgets in tidal wetlands. *Marine Ecology Progress Series*. 150(1-3): 207-216.

National Drought Mitigation Center. 2002. *U.S. Drought Monitor*. http://www.drought.unl.edu/dm/archive.html. Accessed on 11/6/2005.

Nelson, D. W. and Sommers, L. E. 1996. Total carbon, organic carbon, and organic matter. p.961-1010. In, Sparks, D. L., Page, A. L., Helmke, P. A., Loeppert, R. H.,

Soltanpour, P. N., Tabatabai, M. A., Johnston, C. T., and Sumner, M. E., (*Methods of Soil Analysis, Part 3: Chemical Methods*. Soil Science Society of America, Inc., Madison, WI.

Neubauer, S. C., Anderson, I. C., Constantine, J. A., and Kuehl, S. A. 2002. Sediment deposition and accretion in a mid-Atlantic (U.S.A.) tidal freshwater marsh. *Estuarine, Coastal and Shelf Science*. 54: 713-727.

Neubauer, S. C., Miller, W. D., and Anderson, I. C. 2000. Carbon cycling in a tidal freshwater marsh ecosystem: a carbon gas flux study. *Marine Ecology Progress Series*. 199: 13-30.

Nixon, S. W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia*. 41: 199-219.

NOAA-GLERL. 2004. EEGLE: *Episodic events -- great lakes experiment*. http://www.glerl.noaa.gov/eegle. Accessed on 9/15/2005.

O'Neil, T. A., Steidl, R. J., Edge, W. D., and Csuti, B. 1995. Using wildlife communities to improve vegetation classification for conserving biodiversity. *Conservation Biology*. 9(6): 1482-1491.

Odum, E. P. 1985. Trends expected in stressed ecosystems. *Bioscience*. 35(7): 419-422.

Odum, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics*. 19: 147-176.

Odum, W. E., Smith III, T. J., Hoover, J. K., and McIvor, C. C. 1984. *The Ecology of Tidal Freshwater Marshes of the United States East Coast: A Community Profile*. U.S. Fish and Wildlife Service, Office of Biological Services, Washington D.C. FWS/OBS-81/24.

Odum, W. E. and Smith, D. 1985. DOC flux from tidal freshwater and salt marshes as estimated with replicate flumes. *Estuaries*. 8(2B): 74A.

Orson, R. A., Simpson, R. L., and Good, R. E. 1992. The paleoecological development of a late Holocene, tidal freshwater marsh of the upper Delaware River Estuary. *Estuaries*. 15(2): 130-146.

Osgood, D. T., Yozzo, D. J., Chambers, R. M., Jacobson, D., Hoffman, T., and Wenk, J. 2003. Tidal hydrology and habitat utilization by resident nekton in *Phragmites* and non-*Phragmites* marshes. *Estuaries*. 26(2B): 522-533.

Otto, S., Groffman, P. M., Findlay, S. E. G., and Arreola, A. E. 1999. Invasive plant species and microbial processes in a tidal freshwater marsh. *Journal of Environmental Quality*. 28(4): 1252-1257.

Page, H. M. 1997. Importance of vascular plant and algal production to macro-

invertebrate consumers in a southern California salt marsh. *Estuarine, Coastal and Shelf Science*. 45(6): 823-834.

Palomares, M. L. D. and Pauly, D. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine & Freshwater Research*. 49(5): 447-453.

Pasternack, G. B. and Brush, G. S. 2001. Seasonal variations in sedimentation and organic content in five plant associations on a Chesapeake Bay tidal freshwater delta. *Estuarine, Coastal and Shelf Science*. 53(1): 93-106.

Patrício, J., Ulanowicz, R. E., Pardal, M. A., and Marques, J. C. 2004. Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication. *Estuarine, Coastal and Shelf Science*. 60(1): 23-35.

Pauly, D., Christensen, V., and Sambilay Jr., V. 1990. Some features of fish food consumption estimates used by ecosystem modelers. *ICES COUNCIL MEETING 1990 (COLLECTED PAPERS)*. 9 pp.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science*. 57(3): 697-706.

Pennak, R. W. 1978. *Fresh Water Invertebrates of the United States*. John Wiley & Sons, New York.

Perry, J. E. and Hershner, C. H. 1999. Temporal changes in the vegetation pattern in a tidal freshwater marsh. *Wetlands*. 19(1): 90-99.

Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge UK.

Peterson, B. J. and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*. 18: 293-320.

Peterson, J. E. and Baldwin, A. H. 2004a. Seedling emergence from seed banks of tidal freshwater wetlands: Response to inundation and sedimentation. *Aquatic Botany*. 78(3): 243-254.

Peterson, J. E. and Baldwin, A. H. 2004b. Variation in wetland seed banks across a tidal freshwater landscape. *American Journal of Botany*. 91(8): 1251-1259.

Peterson, M. S., Gustafson, D. E. and Moore, F. R.1987. Orientation behavior of *Lepomis macrochirus* Rafinesque to salinity fluctuations *Journal of Fisheries Biology*. 30: 451-458.

Peterson, M. S. and Meador, M. R. 1994. Effects of salinity on freshwater fishes in coastal plain drainages in the southeastern U.S. *Reviews in Fisheries Science*.

2(2): 95-121.

Peterson, M. S. and Ross, S. T. 1991. Dynamics of littoral fishes and decapods along a coastal river-estuarine gradient. *Estuarine, Coastal and Shelf Science*. 33(5): 467-483.

Phillips, S. W., Focazio, M. J., and Bachman, L. J. 1999. *Discharge, Nitrate Load, and Residence Time of Ground Water in the Chesapeake Bay Watershed*. U.S. Geological Survey, Reston, VA. USGS Fact Sheet FS-150-99.

Posey, M. H., Alphin, T. D., Meyer, D. L., and Johnson, J. M. 2003. Benthic communities of common reed *Phragmites australis* and marsh cordgrass *Spartina alterniflora* marshes in Chesapeake Bay. *Marine Ecology Progress Series*. 261: 51-61.

Preston, S. D. and Brakebill, J. W. 1999. *Application of Spatially Referenced Regression Modeling for the Evaluation of Total Nitrogen Loading in the Chesapeake Bay Watershed*. U.S. Geologic Survey, WRIR-99-4054.

Quinn, G. P. and Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, U.K.

Rader, R. B. and Richardson, C. J. 1994. Response of macroinvertebrates and small fish to nutrient enrichment in the northern Everglades. *Wetlands*. 14(2): 134-146.

Rapport, D. J and Whitford, W. G. 1999. How ecosystems respond to stress. *Bioscience*. 49(3):193-203.

Rohde, F. C., Arndt, R. G., Lindquist, D. G., and Parnell, J. F. 1994. *Freshwater Fishes of the Carolinas, Virginia, Maryland and Delaware*. The University of North Carolina Press, Chapel Hill.

Roman, C. T. and Daiber, F. C. 1989. Organic carbon flux through a Delaware Bay salt marsh: Tidal exchange, particle size distribution, and storms. *Marine Ecology Progress Series*. 54(1-2): 149-156.

Rozas, L. P. and Hackney, C. T. 1983. The importance of oligohaline estuarine wetland habitats to fisheries resources. *Wetlands*. 3: 77-89.

Rozas, L. P., McIvor, C. C., and Odum, W. E. 1988. Intertidal rivulets and creekbanks: Corridors between tidal creeks and marshes. *Marine Ecology Progress Series*. 47(3): 303-307.

Rozas, L. P. and Odum, W. E. 1987a. Fish and macrocrustacean use of submerged plant beds in tidal freshwater marsh creeks. *Marine Ecology Progress Series*. 38(2): 101-108.

Rozas, L. P. and Odum, W. E. 1987b. The role of submerged aquatic vegetation in influencing the abundance of nekton on contiguous tidal fresh-water marshes. *Journal of Experimental Marine Biology and Ecology*. 114(2-3): 289-300.

Rozas, L. P. and Odum, W. E. 1988. Occupation of submerged aquatic vegetation by fishes: Testing the roles of food and refuge. *Oecologia*. 77(1): 101-106.

Rozas, L. P. and Odum, W. E. 1987. Use of tidal freshwater marshes by fishes and macrofaunal crustaceans along a stream-order gradient. *Estuaries*. 10(1): 36-43.

Sanville, W. D., Eilers, H. P., Boss, T. R., and Pfleeger, T. G. 1986. Environmental gradients in Northwest freshwater wetlands. *Environmental Management.* 10(1): 125-134.

SAS Institute, I. 2003. *SAS/STAT Software, Version 8.2*. SAS Insititute, Inc., Cary, North Carolina.

Savino, J. F., Marschall, E. A., and Stein, R. A. 1992. Bluegill growth as modified by plant density: An exploration of underlying mechanisms. *Oecologia*. 89(2): 153-160.

Savino, J. F. and Stein, R. A. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society*. 111(3): 255-266.

Savino, J. F. and Stein, R. A. 1989. Behavior of fish predators and their prey: Habitat choice between open water and dense vegetation. *Environmental Biology of Fishes*. 24(4): 287-293.

Schindler, D. E., Carpenter, S. R., Cole, J. J., Kitchell, J. F., and Pace, M. L. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science*. 277(5323): 248-251.

Schroeder, G. L. 1982. Stable isotope ratios as naturally occurring tracers in the aquaculture food web. *Aquaculture*. 30(1-4): 203-210.

Schwinghamer, P., Hargrave, B., and Hawkins, C. M. 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Marine Ecology Progress Series*. 31: 131-142.

Serafy, J. E., Harrell, R. M., and Hurley, L. M. 1994. Mechanical removal of *Hydrilla* in the Potomac River, Maryland: Local impacts on vegetation and associated fishes. *Journal of Freshwater Ecology*. 9(2): 135-143.

Shenk, G. W. and Linker, L. C. 2000. *Simulating the Chesapeake Bay Watershed with Time-Varying Land Use and Management Actions*. Chesapeake Bay Program, Annapolis, Maryland.

Sheridan, P. 1997. Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, U.S.A. *Estuarine, Coastal and Shelf Science*. 44(4): 455-469.

Sheridan, P. F. 1978. Food habits of the bay anchovy, *Anchoa mitchilli*, in Apalachicola Bay, Florida. *Northeast Gulf Science*. 2(2): 126-132.

Silliman, B. R. and Bertness, M. D. 2004. Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. *Conservation Biology*. 18(5): 1424-1434.

Simpson, R. L., Good, R. E., Leck, M. A., and Whigham, D. F. 1983. The ecology of freshwater tidal wetlands. *Bioscience*. 33(4): 255-259.

Simpson, R. L., Whigham, D. F., and Walker, R. 1978. Seasonal patterns of nutrient movement in a freshwater tidal marsh. p.243-257. In, Good, R. E., Whigham, D. F., and Simpson, R. L., (eds.), *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York.

Slack, W. T., O'Connell, M. T., Peterson, T. L., Ewing III, J. A., and Ross, S. T. 1997. Ichthyofaunal and habitat associations of disjunct populations of southern redbelly dace. *Phoxinus erythrogaster* (Teleostei: Cyprinidae) in Mississippi. *American Midland Naturalist*. 137(2): 251-265.

Smil, V. 2002. Nitrogen and food production: Proteins for human diets. *Ambio*. 31(2): 126-131.

Smith, R. A., Schwarz, G. E., and Alexander, R. B. 1997. Regional interpretation of water-quality monitoring data. *Water Resources Research*. 33(12): 2781-2798.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Biologiske Skrifter*. 4: 1-35.

Speiran, G. K., Hamilton, P. A., and Woodside, M. D. 1997. *Natural Processes for Managing Nitrate in Ground Water Discharged to Chesapeake Bay and other Surface Waters: More than Forest Buffers*. U.S. Geological Survey, Reston, VA. FS-178-97.

SPSS, Inc. 1999. *SPSS 10*. SPSS, Inc., Chicago, Illinois.

Staver, K. W. and Brinsfield, R. B. 2001. Agriculture and water quality on the Maryland Eastern Shore: Where do we go from here? *BioScience*. 51(10):859-868.

Strickland, J. D. H. 1965. Measuring the production of marine phytoplankton. *Federal Research Board of Canada*. 122: 1-172.

Stroup, C. F., Brindley, A., and Kazyak, P. F. 1991. *Characterization of the Current Biological Communities within the Nanticoke River in the Vicinity of the Vienna*

SES. Power Plant and Environmental Review Division, Maryland Department of Natural Resources, Tidewater Administration, Annapolis, MD. PPSE-8-18.

Subrahmanyam, C. B. and Coultas, C. L. 1980. Studies on the animal communities in two north Florida salt marshes. Part 3. Seasonal fluctuations of fish and macroinvertebrates. *Bulletin of Marine Science*. 30(4): 790-818.

Svengsouk, L. J. and Mitsch, W. J. 2001. Dynamics of mixtures of *Typha latifolia* and *Schoenoplectus tabernaemontani* in nutrient-enrichment wetland experiments. *American Midland Naturalist*. 145(2): 309-324.

Szyrmer, J. Ulanowicz, R. E. 1987. Total flows in ecosystems. *Ecological Modelling*. 35(1-2): 123-136.

Thayer, G. W. and Chester, A. J. 1989. Distribution and abundance of fishes among basin and channel habitats in Florida Bay. *Bulletin of Marine Science*. 44(1): 200-219.

The Nature Conservancy. 1998. *Draft Nanticoke River Bioreserve Strategic Plan*. Unpublished report.

Tilman, D. 1986. Resources, competition and the dynamics of plant communities. p.51-75. In, Crawley, M. J., (ed.), *Plant Ecology*. Blackwell Publishing, Oxford, UK.

Tilman, D., Lehman, C. L., and Thomson, K. T. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences*. 94(5): 1857-1861.

Tiner, R. W. 2005. Assessing cumulative loss of wetland functions in the Nanticoke River Watershed using enhanced National Wetlands Inventory data. *Wetlands*. 25(2): 405-419.

Tiner, R. W. 1993. *Field Guide to Coastal Wetland Plants of the Southeastern United States*. University of Massachusetts Press, Amherst, MA.

Tsou, T. S. and Matheson, R. E. 2002. Seasonal changes in the nekton community of the Suwannee River Estuary and the potential impacts of freshwater withdrawal. *Estuaries*. 25(6B): 1372-1381.

Turner, A. M. and Trexler, J. C. 1997. Sampling aquatic invertebrates from marshes: Evaluating the options. *Journal of the North American Benthological Society*. 16(3): 694-709.

Ulanowicz, R. E. 1980. An hypothesis on the development of natural communities. *Journal of Theoretical Biology*. 85: 223-245.

Ulanowicz, R. E. 1983. Identifying the structure of cycling in ecosystems. *Mathematical Biosciences*. 65(2): 219-237.

Ulanowicz, R. E. 1986. A phenomenological perspective of ecological development. p. 73-81. In, Poston, T. M. and Purdy, R., (eds.), *Aquatic Toxicology and Environmental Fate: Ninth Volume*. American Society for Testing and Materials, Philadelphia, Pennsylvania.

Ulanowicz, R. E. 1995. Ecosystem trophic foundations: Lindeman exonerata. p. 549-560. In, Patten, B. C. and Jorgensen, S. E., (eds.), *Complex Ecology: The Part-Whole Relation in Ecosystems*. Prentice-Hall, Englewood Cliffs, NJ.

Ulanowicz, R. E. 1996. Trophic flow networks as indicators of ecosystem stress. p.358-368. In, Polis, G. A. and Winemiller, K. O., (eds.), *Food Webs: Integration of Patterns & Dynamics* . Chapman and Hall, New York.

Ulanowicz, R. E. 1997. *Ecology, the Ascendent Perspective*. Columbia University Press, New York.

Ulanowicz, R. E. 2002. *NETWRK 4.2b: A Package of Computer Algorithms to Analyze Ecological Flow Networks*. http://cbl.umces.edu/~ulan/ntwk/network.html.

Ulanowicz, R. E. 2004. Quantitative methods for ecological network analysis. *Computational Biology and Chemistry*. 28(5-6): 321-339.

Ulanowicz, R. E., Bondavalli, C., and Egnotovich, M. S. 1997. *Network Analysis of Trophic Dynamics in South Florida Ecosystems: the Cypress Wetland Ecosystem*. USGS/BRD, Coral Gables.

Ulanowicz, R. E., Bondavalli, C., Heymans, J. J., and Egnotovich, M. S. 1999. *Network Analysis of Trophic Dynamics in South Florida Ecosystems: the Mangrove Ecosystem*. USGS/BRD, Coral Gables, FL.

Ulanowicz, R. E., Heymans, J. J., and Egnotovich, M. S. 2000. *Network Analysis of Trophic Dynamics in South Florida Ecosystems s: the Gramminoid Ecosystem*. USGS/BRD, Coral Gables, FL.

Ulanowicz, R. E. and Norden, J. S. 1990. Symmetrical overhead in flow networks. *International Journal of Systems Science*. 21(2): 429-437.

USACE. 1999. Appendix H. *Zooplankton Data, Lower Snake River Water Quality and Post Draw-Down Temperature and Biological Productivity Modeling Study*. http://www.nww.usace.army.mil/lsr/REPORTS/water_quality/appendix_h.htm. Accessed on 9/16/2005.

USGS-NAS. 2004. *Species Fact Sheet: Gammarus daiberi*. http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=25. Accessed on 11/1/2005.

USGS-NAS. 2005. *Species Fact Sheet: Corbicula fluminea*. http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=92. Accessed on

11/17/2005.

Valiela, I. and Bowen, J. L. 2002. Nitrogen sources to watersheds and estuaries: role of land cover mosaics and losses within watersheds. *Environmental Pollution*. 118(2): 239-248.

Valiela, I., Foreman, K., LaMontagne, M., Hersh, D., Costa, J., Peckol, P., DeMeo-Andreson, B., D'Avanzo, C., Babione, M., and et al. 1991. Couplings of watersheds and coastal waters: Sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. *Estuaries*. 15(4): 443-457.

van der Valk, A. G. 1981. Succession in wetlands: A Gleasonian approach. *Ecology*. 62(3): 688-696.

Vander Zanden, M. J. and Rasmussen, J. B. 2001. Variation in delta ^{15}N and delta ^{13}C trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography*. 46(8): 2061-2066.

Vanni, M. J., Layne, C. D., and Arnott, S. E. 1997. "Top-down" trophic interactions in lakes: Effects of fish on nutrient dynamics. *Ecology*. 78: 1-20.

Verhoeven, J. T. A., Koerselman, W., and Meuleman, A. F. M. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: Relations with atmospheric inputs and management regimes. *Trends in Ecology & Evolution*. 11(12): 494-497.

Vitousek, P., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H., and Tilman, D. G. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications*. 7(3): 737-750.

Voshell, J. R. 2002. *A Guide to Common Freshwater Invertebrates of North America*. The McDonald & Woodward Publishing Company, Blacksburg, VA.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., and Parmenter, R. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*. 30: 257-300.

Wagner, C. M. and Austin. H. M. 1999. Correspondence between environmental gradients and summer littoral fish assemblages in low salinity reaches of the Chesapeake Bay, USA. *Marine Ecology Progress Series* . 177: 197-212.

Wainright, S. C., Weinstein, M. P., Able, K. W., and Currin, C. A. 2000. Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. *Marine Ecology Progress Series*. 200: 77-91.

Wang, J. C. S. and Kernehan, R. J. 1979. *Fishes of the Delaware Estuaries: A Guide to*

the Early Life Histories. Ecological Analysts, Inc., Towson, Maryland.

Wang, S. B. and Houde, E. D. 1994. Energy storage and dynamics in bay anchovy
  Anchoa mitchilli. *Marine Biology*. 121(2): 219-227.

Waterman, T. 1960. *The Physiology of Crustacea, Volume I Metabolism and Growth*.
  Academic Press, New York.

Weinstein, M. P. and Balletto, J. H. 1999. Does the common reed, *Phragmites australis*,
  affect essential fish habitat? *Estuaries*. 22(3B): 793-802.

Weinstein, M. P., Litvin, S. Y., Bosley, K. L., Fuller, C. M., and Wainright, S. C. 2000.
  The role of tidal salt marsh as an energy source for marine transient and resident
  finfishes: a stable isotope approach. *Transactions of the American Fisheries
  Society*. 129(3): 797-810.

Weis, J. S. and Weis, P. 2000. Behavioral responses and interactions of estuarine animals
  with an invasive marsh plant: a laboratory analysis. *Biological Invasions*. 2(4):
  305-314.

Weis, J. S., Windham, L., Santiago-Bass, C., and Weis, P. 2002. Growth, survival, and
  metal content of marsh invertebrates fed diets of detritus from *Spartina
  alterniflora* Loisel. and *Phragmites australis* Cav. Trin. ex Steud. from metal-
  contaminated and clean sites. *Wetlands Ecology and Management*. 10(1): 71-84.

Weisberg, S. B. 1986. Competition and coexistence among four estuarine species of
  Fundulus. *American Zoologist*. 26(1): 249-257.

Welsh, B. L. 1975. The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh
  ecosystem. *Ecology*. 56(3): 513-530.

Whigham, D. F., McCormick, J., Good, R. E., and Simpson, R. L. 1978. Biomass and
  primary production in freshwater tidal wetlands of the middle Atlantic coast. p.3-
  20. In, Good, R. E., Whigham, D. F., and Simpson, R. L., (eds.), *Frehswater
  Wetlands: Ecological Processes and Management Potential*. Academic Press,
  New York.

Whigham, D. F. and Simpson, R. L. 1978. The relationship between aboveground and
  below ground biomass of freshwater tidal wetland macrophytes. *Aquatic Botany*.
  5: 355-364.

Whigham, D. F. and Simpson, R. L. 1982. Germination and dormancy studies of
  Pontederia cordata L. *Bulletin of the Torrey Botanical Society* . 109(4): 524-528.

Whigham, D. F. and Simpson, R. L. 1992. Annual variation in biomass and production of
  a tidal freshwater wetland and comparison with other wetland systems. *Virginia
  Journal of Science*. 43(1A): 8-14.

Whigham, D. F., Simpson, R. L., and Lee, K. 1980. *The Effect of Sewage Effluent on the Structure and Function of a Freshwater Tidal Marsh Ecosystem*. New Jersey Water Resource Research Institute, Rutgers University, B-60-NJ.

White, C. J. *Chesapeake Bay: A Field Guide*. Tidewater Publishers, Centreville, MD.

Whiteside, M. C. and Lindegaard, C. 1980. Complementary procedures for sampling small benthic invertebrates. *Oikos*. 35(3): 317-320.

Wigand, C., McKinney, R. A., Charpentier, M. A., Chintala, M. M., and Thursby, G. B. 2003. Relationships of nitrogen loadings, residential development, and physical characteristics with plant structure in New England salt marshes. *Estuaries*. 26(6): 1494-1504.

Williams, A. B. 1984. *Shrimps, Lobsters and Crabs of the Atlantic Coast, Maine to Florida*. Smithsonian Institution Press, Washington D.C.

Willis, J. M. and Hester, M. W. 2004. Interactive effects of salinity, flooding, and soil type on *Panicum hemitomon*. *Wetlands*. 24(1): 43-50.

Wilson, J. G. and Parkes, A. 1998. Network analysis of the energy flow through teh Dublin Bay ecosystem. *Biology and Environment Proceedings of the Royal Irish Academy*. 98B(3): 179-190.

Windham, L. and Meyerson, L. A. 2003. Effects of common reed (*Phragmites australis*) expansions on nitrogen dynamics of tidal marshes of the northeastern U.S. *Estuaries*. 26(2B): 452-464.

Wisheu, I. C. and Keddy, P. 1996. Three competing models for predicting the size of species pools: A test using eastern North American wetlands. *Oikos*. 76(2): 253-358.

Withers, P. C. 1992. *Comparative Animal Physiology*. Saunders College Publishing, Fort Worth, Texas.

Wolf, D. C., Gilmour, J. T., and Gale, P. M. 1988. *Estimating Potential Ground and Surface Water Pollution From Land Application of Poultry Litter, Part 2*. Arkansas Water Resources Research Center, Fayetteville, Arkansas. USGS Project G-1409-3.

Woo, I. and Zedler, J. B. 2002. Can nutrients alone shift a sedge meadow towards dominance by the   invasive *Typha* x *glauca*? *Wetlands*. 22(3): 509-521.

Yozzo, D. J. and Odum, W. E. 1993. Fish predation on epiphytic microcrustacea in Tivoli South Bay, a Hudson River tidal freshwater wetland. *Hydrobiologia*. 257(1): 37-46.

Yozzo, D. J. and Smith, D. E. 1995. Seasonality, abundance, and microhabitat

distribution of meiofauna from a Chickahominy River, Virginia tidal freshwater marsh. *Hydrobiologia*. 310(3): 197-206.

Yozzo, D. J. and Smith, D. E. 1998. Composition and abundance of resident marsh-surface nekton: comparison between tidal freshwater and salt marshes in Virginia, USA. *Hydrobiologia*. 362(1-3): 9-19.

Zelenke-Merrill, J. 1999. *Tidal Freshwater Marshes as Nutrient Sinks: Particulate Nutrient Burial and Denitrification*. Doctoral Dissertation. University of Maryland, College Park, Maryland.