ASCENDENCY AS AN ECOLOGICAL INDICATOR IN THE NITROGEN FLOW OF THE NEUSE RIVER ESTUARY, NORTH CAROLINA, USA

by

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(Under the Direction of John R. Schramski)

ABSTRACT

Ascendency, a holistic measure of a system's aggregate activity and flow distribution, is employed to evaluate sixteen seasonal models of nitrogen flow in the Neuse River Estuary. The results and methods are contrasted with ascendency's typical use with carbon food web models. Ascendency (A), developmental capacity (C), A/C ratio, total system throughput, average mutual information, overheads, and Finn's cycling index values for the Neuse are reported. The use of the A/C ratio, rather than ascendency alone, for ecosystem comparisons is supported as found in other recent studies. An indicator ratio (A_{g+d}) is presented as an alternative to ascendency for short-term analysis, distinguishing between increases in ascendency via growth (g) and development (d), and increases coupled with information loss. Focusing on ascendency as an ecological indicator, an attempt is made to use ascendency theory to inform ecological managers while employing the Neuse River Estuary's nitrogen flow to inform ascendency theory.

INDEX WORDS: Ascendency, Ecological Indicator, Environmental Management, Eutrophication, Goal Function, Modeling, Network Analysis, Nitrogen Cycling.

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DEDICATION

To Clayton C. Smith, the only person I have encountered who believed unconditionally that I could do no wrong. In this most egregious of errors, teaching me that sometimes trust precedes being trustworthy.

ACKNOWLEDGEMENTS

This thesis would not have been completed without the constant support and level-headed encouragement of my major professor, *Dr. John R. Schramski*. I walked into his office with doubts and walked out with a plan, and I have not looked back since. I would like to thank my committee members, *Dr. Bernard C. Patten* and *Dr. E. William Tollner* for reviewing my work and serving on my committee despite overwhelmingly busy schedules. I would also like to thank *Dr. David K. Gattie* for encouraging me to pursue a Master's Degree, granting me access to the Gattie Lending Library, and welcoming me to the engineering family. Special thanks to the staff at the University of Georgia's Department of Engineering, in particular *Sherry Wrona* who has made the impossible possible and saved me on countless occasions. I would like to thank *Rebecca Wiessner* and all my friends for their support and for putting up with my ecosystem ramblings. Finally, I thank my parents, *Ed and Lora Novak* whose financial contributions, counseling, and unwavering support made this possible.

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GLOSSARY OF MATHEMATICAL SYMBOLS

Symbol	Definition	First Use
FCI	Finn's Cycling Index	4
NEA	Network Environ Analysis	11
I/D	The I/D ratio (Indirect Effects / Direct Effects)	12
A/C	The A/C ratio (Ascendency / Developmental Capacity)	13
AMI	Average Mutual Information	18
TST	Total System Throughput	18
$T_{..}$	Flow from any arbitrary compartment to any other	19
$T_{.j}$	Flow from any arbitrary compartment to compartment *j*	19
$T_{i.}$	Flow from compartment *i* to any arbitrary compartment	19
T_{ij}	Flow from compartment *i* to compartment *j*	19
T_i	All flows leaving compartment *i*	19
T'_i	All flows entering compartment *i*	19
T_{ik}	Flow from compartment *i* to compartment *k*	19
E_i	Exports from compartment *i*	19
D_i	Imports to compartment *i*	19
D_j	Imports to compartment *j*	19
R_i	Dissipation from compartment *i*	19
A_{g+d}	Growth and Development Ratio	32
S_1	Number of observations of scenario #1	32
S_{total}	Total number of observations	32

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CHAPTER 1

INTRODUCTION

1.1 PREFACE

Many of the challenges faced by research scientists and global citizens are increasingly complex. Historically we have addressed mainly problems which can be resolved by a single individual, or which bend willingly to our modern technology. Simultaneously we circumvent more arduous challenges. Solving what we can, pushing the more resilient issues into the future, we fuel the evolution of the complex problem. A lifetime of study on the subjects of economic stability, educational development, resource management, or disease pathology no longer allows an individual to unilaterally resolve the problems at hand. Whether focusing on a stagnant economy or a diseased population, the major components of each system form an interconnected network. A number of these problems owe their complex nature to the sheer quantity, sensitivity, and dynamic nature of such a network. Once a network reaches a certain complexity, simple formulas and intuition must yield to a more comprehensive, network oriented, system-wide science. Systems approaches have found fruitful application to a multitude of problem-rich subject areas including economics, education, molecular biology, and ecology (Foster 2006, Rosi *et al.* 2006, Tang *et al.* 2009, Gattie *et al.* 2006).

1.2 PURPOSE OF STUDY

In this study we focus on ascendency as an ecological indicator, in an attempt to use ascendency theory to inform ecological managers while using the Neuse River Estuary's nitrogen flow to inform ascendency theory itself. It is this dynamic exchange between theory and application that hone the scientific tools upon which we rely. The objectives of this study include interpretation of short term changes in ascendency in the Neuse River Estuary's nitrogen flow, evaluation of ascendency's performance outside its typical model applications, and to investigate spatial comparisons in the Neuse River Estuary's nitrogen flow and their implications to ascendency theory.

Ascendency's usefulness to an ecological manager hinges on its ability to capture the qualitative status of an ecosystem. However, accurate interpretations of change in ascendency ultimately determine its functionality. While the author is not aware of any existing standards which delineate short-term from long-term changes in ascendency, we proceed with the assumption that any ascendency changes observed in our analysis of the Neuse River Estuary's four years of nitrogen data should be considered short-term. Although short-term dynamics do ultimately determine long-term trends, it is difficult if not impossible to obtain the perspective required to interpret short-term changes in that light. We will investigate alternative ascendency-based indicators to more accurately track ascendency in the short-term.

Since its formulation, ascendency has been employed as an ecological indicator and goal function. Its applications to varying ecosystems, and theoretically even non-living systems, are readily unapparent in the literature as it's primarily applied to aquatic, carbon, food-web models. In this study we analyze seventeen models of the Neuse River Estuary's nitrogen flow (Christian and Thomas 2003) as an example of an ascendency application outside its traditional bounds. In addition, generating the related indices allows investigation of changes in ascendency when models differ in currency or structure. Finally, we examine how the Neuse River Estuary is compared to other ecosystems (spatial comparisons). How these comparisons are drawn, and which indicators are included, play a defining role in what conclusions emerge. Our goal here is to take the traditional approach and propose rational alternatives if necessary.

1.3 NEUSE RIVER ESTUARY

The nitrogen flow data analyzed is from the Neuse River Estuary, in coastal North Carolina, USA, a 40-mile-long tidal estuary emptying into Pamlico Sound. As part of the Albemarle-Pamlico estuary system, the estuary provides a nursery for the majority of commercial fish and shellfish caught in North Carolina. The estuarine system, covering almost 370,000 acres and 21 miles of coastline, reaches inland via the Neuse River Basin. Containing 74 separate municipalities with an estimated population of 1.3 million people as of 2000, the basin is under significant anthropogenic stress. Housing a number of endangered vertebrates and invertebrates, the Neuse's future holds more than implications to human development in the balance (Office of Environmental Education, N.C. http://www.eenorthcarolina.org).

Nothing may be of more value to our understanding of the Neuse River Estuary and similar ecosystems than a simplified yet accurate representation of a particular facet of interest. Ecological indicators, such as ascendency, allow us to follow the trajectory of a particular aspect of an ecosystem. They offer the possibility of a simplified, focused view of an ecosystem characteristic. Although they do not encompass every detail of an ecosystem, well developed indicators reduce complexity and provide the possibility of quick yet insightful observations.

The potential benefits from an ascendency analysis of the Neuse River Estuary data are many. Understanding the current status of an ecosystem gives us a baseline for temporal comparisons. Its spatial proximity with major population centers imparts a heightened importance on assessments that include anthropogenic effects. Concepts of health and quality of this waterway are of deep importance due to its multifaceted contributions as a freshwater source, nursery for the fish and shellfish economies in the area, trade, transit, recreation, and inherent ecological value. In addition, ascendency's application to perturbation effects provides a host of applications for the Neuse, including pollution, bloom, and annual hurricane events.

1.4 NITROGEN CYCLING

In the ever-changing landscape of biochemistry certain elements, due to their limited availability, act as gatekeepers for life sustaining reactions. Concepts deeply related to ascendency's goals of quantifying growth and development depend on the presence of such limiting nutrients. Depending on the aquatic ecosystem of interest, iron, phosphorous, and nitrogen, are often the usual suspects. Boyer *et al.* (1994) evaluated nitrogen uptake during the same four year period as the model data analyzed herein. The study concludes that the Neuse River Estuary is nitrogen limited, and it is with this assumption we will proceed.

In the Neuse River Estuary nitrogen model, nitrogen is cycled through various chemical forms. A unit of currency flowing from one compartment to another could represent a trophic interaction such as grazing (PN-phyto → PN-hetero), or a chemical transformation like nitrification ($NH_4 \rightarrow NO_x$) (Figure 1.1). The importance of cycling, the return of a unit of currency to a compartment it has previously occupied, is heightened when the currency being cycled is a limiting nutrient. In the Neuse River Estuary nitrogen model the cycling, here demonstrated using Finn's Cycling Index (FCI), is particularly high (Figure 1.2). More recently, Kazanci *et al.* (2009) demonstrated the ability to calculate a cycling index using a stochastic process (particle tracking) rather than Finn's differential, continuous, approach.

Previous ascendency applications tend to favor biomass models, often following carbon transfers dominated by trophic interactions (Baird and Heymans 2000, Patricio and Ulanowicz 2004, Scharler and Baird 2005). When energy relevant questions surface, some conversion between biomass and energy is performed rather than beginning with an energetic model. Although energetic models may speak directly to thermodynamic questions, and one's inability to overstate carbons role in everything from the creation of biomass to climate change, here we explore ascendency's potential use in nitrogen modeling.

1.5 NEUSE RIVER ESTUARY MODEL

Nitrogen in the Neuse River Estuary has been abstracted, in a previous study (Christian and Thomas 2003) over sixteen seasons to form a model of compartments and flows. The model, shown in Figure 1.1, consists of compartments and concomitant flows between these compartments as well as input and output flows connecting the compartments with the external environment. The compartments represent the standing stocks of nitrogen in the estuary. The compartments differ from one another in the form, or association, of the nitrogen within. For example, particulate nitrogen associated with phytoplankton, particulate nitrogen associated with zooplankton, and nitrogen in the form of ammonia, are distinct compartments. Nitrogen's presence in a particular compartment is exclusive, and a particular quantity cannot coexist in multiple compartments. The compartments form an exhaustive description of the nitrogen in the estuary; all nitrogen in the estuary is contained in one of these compartments. Nitrogen stocks are temporally averaged per season and spatially averaged across the estuary. Nitrogen stocks are measured in mmol N/m^2. Nitrogen flows are quantified as mmol N/m^2 season, and are similarly averaged.

The flows of nitrogen throughout the Neuse River Estuary contain volumes of information. In the search for significance and to wade through the immense detail we look to network analysis. Its importance notwithstanding, the Neuse River Estuary is a single ecosystem after all and our goals here include not only using ascendency to better understand the ecosystem but using the ecosystem to better understand ascendency analysis. We hope to accomplish this through our three main objectives: interpretation of short term changes in ascendency in the Neuse River Estuary's nitrogen flow, evaluation of ascendency's performance outside its typical model applications, and to investigate (spatial) comparisons between the Neuse River Estuary and other ecosystems as well as their implications to ascendency theory.

1.7 FIGURES

Figure 1.1: Nitrogen flow in the Neuse River Estuary modeled as compartments and flows (Christian and Thomas 2003). Flows are notated using departure destination orientation. For example, f_{61} is the identifier given to the flow from X_6 to X_1. Flows interacting with the environment by crossing the system boundary are labeled y and z, outputs and inputs, respectively.

Figure 1.2: Finn's cycling index for the Neuse River Estuary (1985). Finn's cycling index is a dimensionless ratio enumerating the fraction of flows being cycled in a system. Values are means for the four years of Christian and Thomas' (2003) study.

Figure 1.1

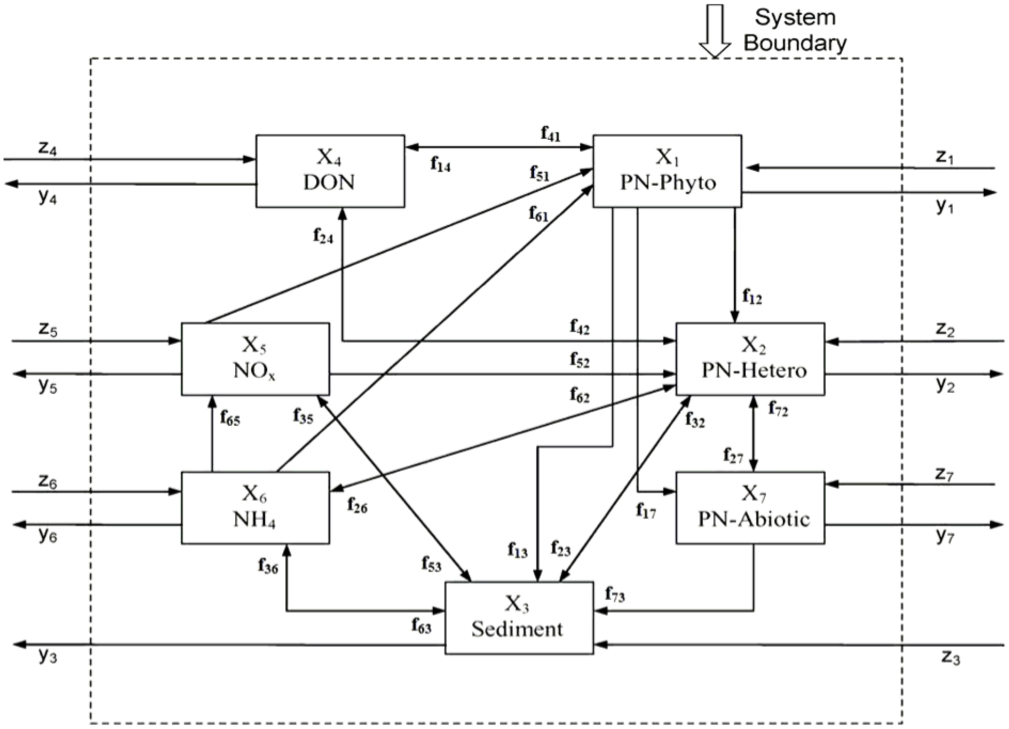
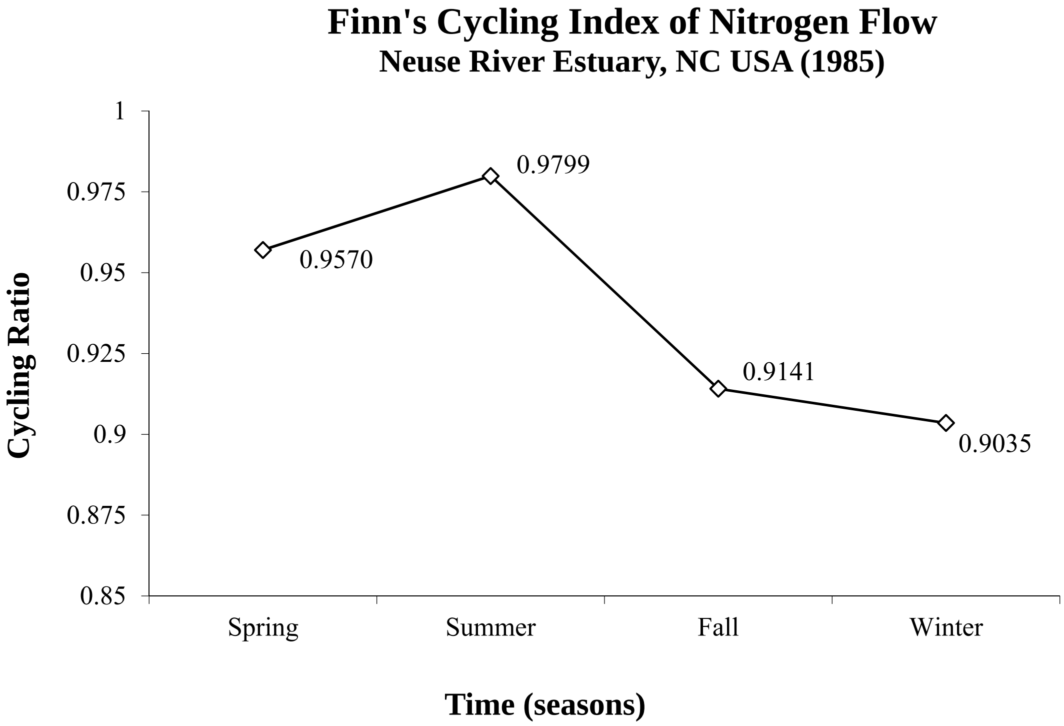

System Boundary
X_4 DON
X_1 PN-Phyto
X_5 NO$_x$
X_2 PN-Hetero
X_6 NH$_4$
X_7 PN-Abiotic
X_3 Sediment
z_1 y_1 z_2 y_2 z_3 y_3 z_4 y_4 z_5 y_5 z_6 y_6 z_7 y_7
f_{41} f_{14} f_{51} f_{61} f_{24} f_{12} f_{42} f_{52} f_{62} f_{65} f_{35} f_{32} f_{72} f_{27} f_{26} f_{17} f_{13} f_{23} f_{36} f_{53} f_{73} f_{63}

Figure 1.2


Finn's Cycling Index of Nitrogen Flow
Neuse River Estuary, NC USA (1985)
Cycling Ratio
1
0.975
0.95
0.925
0.9
0.875
0.85
0.9570
0.9799
0.9141
0.9035
Spring
Summer
Fall
Winter
Time (seasons)

CHAPTER 2

LITERATURE REVIEW

2.1 NETWORK ANALYSIS

The complexity regarding ecological questions of the day, combine the previously mentioned numerous and sensitive connections with the intractability of life in motion. To combat this lack of understanding, many network-based approaches have been developed for, or adapted to, such ecological investigations. Underpinning most of these approaches is Leontief's concept of Input Output Analysis which was developed to answer economic questions of his time (Leontief 1936). Input Output Analysis assigns a direction and magnitude to the before mentioned connections while illuminating the interdependent nature inherent in a system. Leontief's research, later adapted to a wide range of applications, modeled internal and external flows exposing the hidden dynamics within industry, economics, and pollution.

Network analysis is a specific application of Input Output Analysis and its first applications in ecology were to link ecosystem components with their system using energy flows (Hannon 1973). Building on this foundation, many network analyses have been developed to better understand ecosystems including environs (Patten 1978), exergy (Jørgensen 1983), emergy (Odum 1983), and ascendency (Ulanowicz 1986). Each approach brings their own assessment of ecosystem via analysis specific goal functions. Goal functions are measurable parameters, or calculated from measurable parameters, whose quantitative flux may indicate a qualitative change such as anthropogenic effects, natural cycles, growth and maturation, or other perturbation effects. More specifically goal functions refer to a “goal” that a modeled ecosystem asymptotically approaches while unimpeded by outside-the-system effects. While the ecosystem itself has analogous ecological indicators, attractors and orientors theorized to govern the direction of development, goal function terminology is reserved for the representative models. The reader is directed to *Eco Targets, Goal Functions and Orienters* (Müller and Leupelt 1998) for a complete treatment of the concept.

Patten's network environ analysis (NEA) empowers us to recognize imbedded features such as the combined magnitude of indirect interactions (Patten 1978). Such subtleties are often overlooked using the "outside looking in" traditional empirical approach. Environ theory partitions the environment of a subsystem of interest into distinct input and output environments (environs). The input environ represents what has occurred in the past within-system environment that enables a current output from a focal compartment. Conversely, the output environ represents within-system effects propagated from points of focal compartment inputs (Fath and Patten 1999). Distinct analyses within NEA include flow analysis based on Hannon's original formulation (Hannon 1973), storage analysis (Matis and Patten 1981), and utility analysis (Patten 1991). Emerging from these techniques, NEA researchers have developed multiple independent hypotheses regarding ecosystem traits. These hypotheses include network amplification or components of the network receiving more than they contribute (Patten *et al.* 1990), network homogenization (Patten *et al.* 1990) where network activity tends towards uniform flow distributions, network synergism (Patten 1991) creating inherently positive network relations, and the dominance of indirect effects (Higashi and Patten 1986). The dominance of indirect effects hypothesis states that a system receives greater influence from indirect effects than from direct ones. Furthermore, the ratio of indirect effects (I) to direct effects (D) has been suggested as an ecological goal function. Considered a measure of network complexity the system’s I/D ratio reflects the amount of network pathways and is expected to correlate to specific exergy (Jørgensen and Nielsen 1998), which we will investigate in the next section.

Another ecological analysis invokes the universal applicability of thermodynamics to answer ecological questions. Energy can be partitioned into components available and unavailable to do work, exergy and anergy respectively. Exergy, a measure of order, is an alternate concept to entropy, a measure of disorder (Jørgensen and Svirezhev 2004). Both facilitate open discussion of irreversible processes and their relation to the second law of thermodynamics. However some studies suggest, exergy having the same units as energy, not being a state variable unlike entropy, and being clearly defined for systems far from thermodynamic equilibrium, make exergy the preferred choice for ecosystem analysis (Jørgensen and Svirezhev 2004). Exergy has also been suggested as an ecological goal function (Jørgensen and Mejer 1983). An ecosystem is theorized to maximize exergy storage, the accumulation and retention of useable energy. Maximizing exergy in an ecosystem involves maximizing storage in biotic compartments which equivocates to maximizing biomass. “The associated accumulation of mass or energy is reflected in structure, function, gradients, order, organization, and information” (Fath *et al.* 2001).

One ecological analysis relates all energy and matter on earth back to solar radiation. Through the use of material specific conversions (transformities) one is theoretically able to determine the amount of solar radiation it takes to create a natural or synthetic product. H. T. Odum's embodied energy (emergy) concept investigates the quality of energy as it changes form. It suggests that we consider an object's energetic value not equivalent to how much energy we can squeeze out of it, but to its emergy, the amount of joules of solar energy (emjoules) required to generate its current form. Energy originating from the sun passes through system specific energy transformations increasing the emergy. Emergy analysis speaks directly to sustainability, resource management, and industrial production. However, its applications to ecosystem status and health (Brown and Ulgiati 2004) are our interest here. As a goal function it has been suggested that ecosystems maximize emergy and empower (the associated energy flow required in each transformation step resulting in heightened emergy).

Finally, in our limited review of the modern applications of Leontief's seminal work and the ensuing goal functions, lies our focal topic. We will investigate Ulanowicz's ascendency theory and its application as an environmental indicator and goal function to address the objectives of this study.

2.2 ASCENDENCY THEORY

Since the formulation of ascendency (Ulanowicz 1986, 1997), its application to a multitude of ecosystem-based questions is readily apparent in ecological publications. Early attempts illuminate its applicability to aquatic ecosystems, specifically carbon models of aquatic food webs (Ulanowicz 1980). As the theory gains acceptance ascendency is employed in numerous studies, however its primary application in aquatic systems and biomass (carbon) quantified food web models continues (Ulanowicz 1987, Baird and Ulanowicz 1989). To a lesser degree ascendency analysis and its use as an ecological indicator has been applied to varying model currencies (energy: Herendeen 1989) and models containing non-living, albeit still food web inclusive, compartments (Heymans and McLachlan 1996).

Ascendency has been employed to quantify the status of a particular ecosystem (Ray *et al.* 2000, Wolff *et al.* 2000, Halfon *et al.* 1996, Baird and Ulanowicz 1989). In 2000 Ray *et al.* used relative ascendency (A/C ratio), ascendency (A) divided by the developmental capacity (C), to quantify anthropogenic effects upon the Sundarban Mangrove in India and Bangladesh. This analysis has been used as an indicator of ecosystem health and integrity (Costanza 1992, Heymans and Baird 2000). The effects of perturbations and short-term changes upon ecosystems are a continuous source of both theoretical and applied ecosystem studies and pertain to our first objective. Ascendency has been used to measure the effects of such ecosystem perturbations (Almunia *et al.* 1999, Baird and Heymans 1996). In addition to critical aspect quantification in an ecosystem, sometimes it becomes beneficial to compare two ecosystems, and how these comparisons are drawn relates to our third objective. Ascendency as an index has been used to compare temporally distinct ecosystems (Baird *et al.* 1991), and spatially separate ones (Baird and Ulanowicz 1989).

Ascendency has been employed to investigate ecosystem status with regard to an aspect of interest, or in more general terms of health. It has been used to assess an ecosystem's integrity and stability, to quantify an ecosystem's response to a perturbation, and to compare temporally or spatially separated ecosystems. Ascendency's flexibility as an ecological indicator emerges from its ability to combine the degree of system complexity with the aggregate system activity.

2.4 NEUSE RIVER ESTUARY RESEARCH

Management of something as complex as an ecosystem seems somewhat of a herculean task. Everything from day to day decisions to long term planning requires temporally and scientifically current information. Understanding nitrogen flow in the Neuse River Estuary relates causal factors such as nitrogen import from terrestrial systems with residual effects like algal bloom events. Christian *et al.* (1991) investigated nutrient distribution patterns across the Neuse River Estuary and found relatively low flushing times. Analogous to cellular turnover, the flushing time is the quantity of time the flow requires to replace the current volume of water in the estuary. Whatever happens in the Neuse River Estuary stays in the Neuse River Estuary, at least for a prolonged time. In addition, they noted high levels of cycling in the estuary even during relatively high periods of turnover. Boyle *et al.* (1994) specifically looked at nitrogen uptake in the Neuse River Estuary during the same four year period as the aforementioned Christian and Thomas (2003) study. Boyle reported in excess of six fold increases in nitrate (NO_3^-) following a flood event during the winter/spring of 1987. During this same period, a bloom of the dinoflagellate *Heterocapsa triqueta* was observed in the estuary and resulted in heightened values of particulate nitrogen.

Christian and Thomas investigated the potential of network analysis to aid management practices in their 2003 study. Employing NETWRK 4 (precursor to NETWRK 4.2 used in this study), a software package developed by Ulanowicz and others, they utilize the system perspective to investigate the estuary's symptoms of eutrophication. Focusing on loading (import), uptake, and fate of nitrogen in the estuary they conclude that the time between loading and productivity is, “not likely to be consistent or even linear”. Gattie *et al.* (2006) analyzed two of the Christian and Thomas models (seasons) of nitrogen flow in the Neuse River Estuary using NEA. In both seasons, the study reported that over 40% of nitrogen flow was due to indirect connectivity. Consistent with the previously mentioned high cycling values, a picture of a large volume, high cycling, slow flushing, and self-sustaining estuary begins to emerge.

A series of studies investigate the potential of NEA to illuminate meaning in the nitrogen flow of the Neuse River Estuary (Borret *et al.* 2006, Gattie *et al.* 2006, Schramski *et al.* 2006, Schramski *et al.* 2007, Whipple *et al.* 2007). Focusing on comparative network environ analysis, temporal changes in indirect effects, and distributed control these studies, not unlike our own, recognize the significance of comparing a food web of trophic interactions to a biogeochemical network dominated by non-trophic flows. Emerging from this treatment of NEA are questions regarding how the model's nitrogen currency affects its results. Whipple *et al.* (2007) concludes, "The use of nitrogen as a currency, instead of biomass or carbon, may also influence CNEA (comparative network environ analysis) results." This parallels our investigation of ascendency's applicability to non-traditional currencies, included in the second objective of this study. In an earlier treatment of the subject Christian et al. (1996) generalizes on the subject. "We consider that networks constructed for the purposes of studying biogeochemical cycles are fundamentally different from those based on foodwebs and trophodynamics."

In addition to scholarly articles, two North Carolina state reports (Christian and Thomas Report No. NC-WRRI-325-F 2000, Christian *et al.* Report No. NC-WRRI-343-E 2004) delve into the daunting task of investigating the consequences of nitrogen loading in the Neuse River Estuary. The earlier report (2000), utilizes the seasonal nitrogen models of their own design. They employed a technique from NEA as well as structural analysis and matrices from NETWRK 4. They followed a single unit of input currency as it moved through the network, and observed the magnitudes of the processes it encountered. In NEA this is referred to as output environ analysis. Using this methodology they reported the fate of one unit of each of the forms of nitrogen in the model (DON, PN, NO_X, NH_4). In the earlier study there was no significant use of ascendency, however in the later study (2004), the Neuse River Estuary was abstracted as a detailed 30 compartment carbon model dominated by trophic interactions in the form of a food web. NETWRK 4.2 was used to perform network analyses including ascendency analysis. Values for ascendency and the A/C ratio are reported although the conclusions are dominated by their sensitivity analysis results of simulated fish kills. In the 2000 study, that includes the same suite of 17 models analyzed here, the authors conclude this regarding ascendency analysis:

"Ulanowicz has developed a theory as to the nature of systems' growth, development and maturity. The ideas are captured in several indices including ascendency, developmental capacity and overhead. As we did not use these, we will not expand on these rather complex concepts but refer the reader to the cited references. These indices have not been widely used as yet in environmental management, but are promising in their ability to capture the broader aspects of the ecosystem."

(Christian and Thomas Report No. NC-WRRI-325-F 2000)

CHAPTER 3

METHODOLOGY

3.1 CALCULATING ASCENDENCY

Ascendency is an ecological indicator that cannot be empirically gleaned from an ecosystem but rather is the product of the systems average mutual information (AMI) and total system throughput (TST).

$$Ascendency = TST * AMI \qquad (3.1)$$

Note that total system through*put* is notated the same (TST) as total system through*flow* from environ analysis literature. The first is the simple sum of all the flows in the system. The second is oriented – the summation of the sums of flows into (input analysis, TST^{in}) or alternatively, out of (output analysis, TST^{out}) each compartment. At steady state, $TST^{in} = TST^{out}$. This distinction is often overlooked in considering the two analysis methodologies.

The AMI of the system is calculated by first determining the potential contribution to complexity of each compartment of the system. A compartment with a single output, which enters another compartment or leaves the system, contributes nothing to the system's complexity. Conversely, a compartment with multiple, less probable, outputs increases the complexity of the system. The flows leaving the compartment, which are the least likely to happen, contribute the most to the system's complexity. However, the frequency at which these flows occur must be taken into account; therefore, averaging the mutual information of the system becomes necessary (Ulanowicz and Abarca-Arenas 1997). Equation 3.2 sums each compartment's contribution to the system complexity after being weighted by its respective probability yielding the system AMI. The second contributor to ascendency, TST, is the summation of all imports (D), usable (E) and unusable exports (R), as well as all internal flows (T_{ij}). Determining the general inputs

$$AMI = k \sum_{ij} \frac{T_{ij}}{T_{..}} log(\frac{T_{ij}T_{..}}{T_{i.}T_{.j}}) \tag{3.2}$$

(equation 3.3) and outputs (equation 3.4) to each compartment we can then sum all flows in the system (equation 3.5). TST is a measure of aggregate system activity, which has been suggested

$$T_i' = D_i + \sum_{j=1}^{n} T_{ji} \tag{3.3}$$

$$T_i = \sum_{k=1}^{n} T_{ik} + E_i + R_i \tag{3.4}$$

$$TST = \sum_{j=1}^{n} \sum_{i=1}^{n} T_{ij} + \sum_{i=1}^{n} (E_i + R_i) + \sum_{j=1}^{n} D_j \tag{3.5}$$

as the primary indicator of ecosystem growth (Ulanowicz 1997). This is an alternative to associating growth directly with stock magnitude or biomass.

The advantage of applying ascendency as an ecological indicator lies in understanding what an increase or decrease in the indicator functionally means. The principle of increasing ecosystem ascendency suggests that an ecosystem struggles towards increased growth and development. Their opposition in this endeavor, termed overheads, are comprised of internal redundancies, dissipations, exports, and decentralized inputs (Ulanowicz 1986). Without these overheads an ecosystem would be unconstrained and able to reach its full capacity for ascendency (Figure 3.1). At this maximum ascendency the weighted probabilities that determine the system's internal transfers would approach unity and the entire system would achieve a mechanical efficiency (Ulanowicz 1997).

This mechanistic simplicity is not observed in ecological networks. Often the contrary situation seems to persist. Deeply connected biotic and abiotic system components seem standard. Simply put, systems are subject to more requirements than operational efficiencies alone. Their stability determines whether they proceed, efficiently or not, into the future. Mechanical processes, such as those required to achieve maximal ascendency, are subject to catastrophic failure when a component is removed or disabled. The inefficient system waits to be pruned or replaced while the fragile mechanistic system succumbs to a recent perturbation. The system must strike a balance between these goals. The degree to which a living system is allowed to favor one goal over another is determined not only by its internal structure but is influenced by its external environment.

3.2 CHANGES IN ASCENDENCY

To employ ascendency as an ecological indicator is to presuppose that ascendency is in flux. Theoretically a static ascendency may speak as much about an ecosystem as a dynamic one yet due to the nature of the indicator, change is the typical empirical observation. As with any value which resides between its upper and lower bounds, ascendency's options are limited; to rise, to fall, or to stubbornly stay put. To investigate these options completely, remembering that ascendency is the multiplicative product of the total system throughput (TST) and average mutual information (AMI), lays our framework. Assuming that in the ever-changing world of an ecosystem flux is inherent, two options remain. Ascendency can advance towards its upper bound, developmental capacity, or regress based on the interaction of the before mentioned components. Whereas ascendency can only travel in two basic directions, and both TST and AMI are required to be positive real numbers, we can establish six possible combinations of change in ascendency, TST, and AMI (Figure 3.2).

Ascendency theory is considered applicable to all living and non-living systems, encompassing a spectrum of measurable currencies. While the overall concepts of growth and development seem applicable regardless of the currency, some differences surface. Interpretation of something as simple as a change in TST varies dependent on currency. While an increase in energy input, and corresponding rise in TST, may contribute to stable growth, an analogous spike in nitrogen input tends to create eutrophic conditions in aquatic ecosystems. Ecological managers, whose goals often favor conservation over growth, will require the ability to recognize the difference between sustainable growth and simply an increase in TST.

3.3 NETWRK 4.2

Decisions regarding which analysis software package to employ for our treatment of ascendency focused around EcoPath, NETWRK, and EcoNetwrk (NETWRK's Windows compatible counterpart). EcoPath is a commonly used software package for ascendency analysis of aquatic, biomass-driven, food web models (www.ecopath.org). It simulates biomass dynamics using coupled differential equations including variables such as consumption, emigration and fishing mortality. Although some aspects of the Christian and Thomas nitrogen model incorporate trophic interactions, many flows are physical or chemical transformations that do not mesh easily with EcoPath's framework.

The decision to ultimately employ EcoNetwrk's predecessor NETWRK 4.2 as our analysis software, was primarily for the sake of simplicity and to facilitate consistency with the multitude of studies referenced in this document which use NETWRK 4 or NETWRK 4.2, including both Christian *et al.* North Carolina state reports (2000, 2004). Therefore, information indices, flow structure, cycling and connectance values were calculated using the software package NETWRK 4.2 (Ulanowicz 1986, 1987). Input files for each of the seventeen (sixteen seasons, four year average) models were constructed from previously published Christian and Thomas data. Information indices including TST, ascendency, redundancy, overhead and developmental capacity are reported in the following chapter. FCI and connectance indices were also calculated and similarly reported. AMI is not directly included in the output of NETWRK 4.2, and was calculated as ascendency/TST.

3.4 FIGURES

Figure 3.1: The relationship between overheads, ascendency and developmental capacity (Ulanowicz 1997).

Figure 3.2: Characterization of the six possible scenarios of change in ascendency. The associated signs +/–) indicate an increase or decrease in magnitude. All values are positive.

Figure 3.1

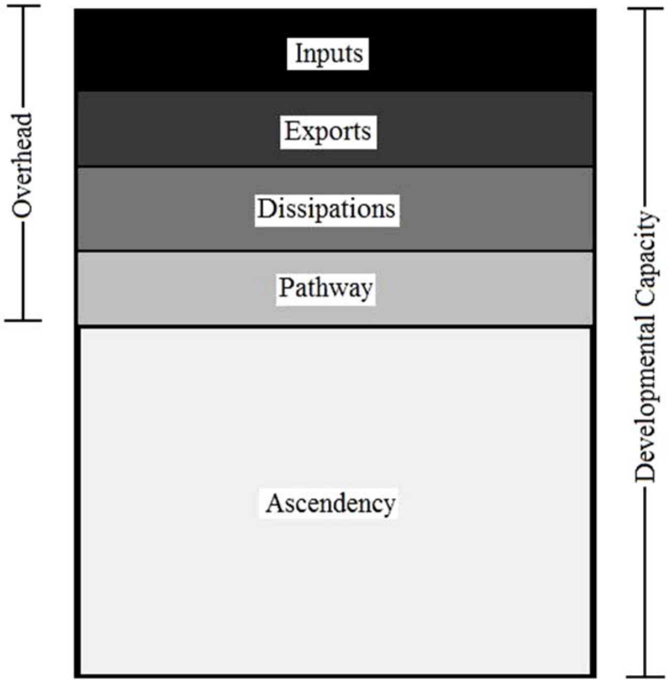

Inputs
Exports
Dissipations
Pathway
Ascendency
Overhead
Developmental Capacity

Figure 3.2

1	Ascendency	+	**4**	Ascendency	—
	TST	+		TST	–
	AMI	+		AMI	
2	Ascendency	+	**5**	Ascendency	—
	TST	+		TST	+
	AMI	–		AMI	
3	Ascendency	+	**6**	Ascendency	–
	TST	–		TST	+
	AMI	+		AMI	–

CHAPTER 4

RESULTS AND DISCUSSION

4.1 THROUGHPUT, INFORMATION, AND ASCENDENCY

Throughput in the form of TST was calculated using the previously described methods. The results for the sixteen seasons appear in tabular format in Table B1 (Appendix B). Calculated values range from 5,860 to 20,301 mmol of nitrogen per square meter per season. The mean value for the sixteen seasons is 10,569 (mmol N/m^2 season). Values appear to correlate highly with temperature and the resulting biological activity, with few exceptions. Figure 4.1 illustrates seasonal changes in TST for 1985, finding its minimum in winter, its maximum in summer and exhibiting intermediate values in the transitional seasons. However, Figure 4.2 shows depressed summer values replacing the expected seasonality with a slow decrease in TST for the duration of the year. In addition, Figures 4.3 and 4.4 reveal winter's ability to overtake the previous fall's TST values, if only marginally. Similarly, AMI was calculated as described before for the same sixteen seasons and the results also appear in Table B1. AMI values range from ~1.0 to ~1.5 bits with a mean of 1.225 bits. A bit is defined as the amount of information required to perform a single binary decision. Correlation of AMI values to seasonal changes remains unclear.

Ascendency values for each of the sixteen seasonal models appear in Table B1 (Appendix B). Values range from 7,704 to 22,170 mmol of nitrogen per square meter per season times bits of information. The sixteen season mean was 12,782 (mmol N bits/m^2 season). Ascendency values, similarly to TST, appear to correlate with temperature and biological activity. Changes in ascendency parallel changes in TST in most cases. Figure 4.1 illustrates how a rise or fall in TST corresponds to a simultaneous, analogous shift in ascendency. In a less observed scenario, Figure 4.4 shows a waxing TST accompanying a waning ascendency. Also included in Table B1 are the calculated A/C ratios for each season.

4.2 DEVELOPMENTAL CAPACITY AND CONSTITUENTS

The developmental capacity values for each season appear in Table C1 (Appendix C). Ranging from 20,433 to 69,012 mmol N bits/m^2 season it shares ascendency's units and in fact functions as its upper bound. Since our model has no compartmental dissipations (dissipations equivocate to unusable exports in ascendency theory), overheads and pathway redundancy make up the difference between developmental capacity and ascendency. In fall 1988 redundancy is at its minimum for our four year study, still comprising 52% of developmental capacity. Redundancy ranges from 10,600 to 45,229 (mmol N bits/m^2 season) with a mean of 22,072. In terms of magnitude, overheads in this model play a secondary role to redundancy. The mean values of overhead on imports and exports are 987.9 and 887.1 (mmol N bits/m^2 season) respectively. Seasonal values for redundancy and overheads are listed in Table C1 (Appendix C).

4.3 CONNECTANCE AND CYCLING

Seasonal connectance was calculated for sixteen seasons and the results are listed in Table C2 (Appendix C). Overall connectance values ranged from ~2.0 to ~2.7, with compartmental connectance values from ~1.8 to ~2.3. A connectance of 2.0 is interpreted as there being on average, two connections between any two arbitrary compartments. Overall connectance includes the effects of exogenous transfers, where compartmental connectance only considers transfers between compartments. Seasonal results for Finn's Cycling Index also appear in Table C2. The index ranges from 74% to 98% and represents the fraction of the system flow that is recycled. Peak cycling seasonally appears each summer while spring and winter typically exhibit lower values.

4.4 TEMPORAL COMPARISONS

Any quantitative calculations seem on the surface to be grossly inadequate at capturing the ever-changing complexities of an ecosystem. However, understanding and insight can come in many guises and it is in that vein that we push forward. Here we have applied Ulanowicz's indices regarding growth and development outside their primary application to biomass-driven food webs. We've calculated ascendency in the Neuse River Estuary based on nitrogen data abstracted into sixteen seasonal models. Ascendency values are typically compared temporally with previous values from the same ecosystem. In the Neuse River Estuary we identify two types of change in ascendency. The first is the short-term seasonal variability readily observable in the four years of data. Values in the Neuse exhibited strong seasonal variation, derived primarily from their TST component. As a measure of system activity, TST (and therefore ascendency) varies substantially between ecosystems (Table 4.1). Although it may be argued that these seasonal changes encompass an oscillating growth of the ecosystem, they hardly fit Ulanowicz's characterization of ecosystem development. A second form of change in ascendency must exist. Comparing the same season from year to year reduces the seasonal interference and brings us closer to our intended subject, long-term ecosystem development (Figure 4.5). While no published standards of what constitutes the minimum time frame required for observing and evaluating ecosystem development, the author must concede that a four year span seems too short.

4.5 SPATIAL COMPARISONS

Beyond evaluating an ecosystem referenced to its previous self, ascendency facilitates comparison between spatially distinct ecosystems. Ascendency however, is not created equal. Comparison between ecosystems is complicated when the models involved utilize different currencies. Ascendency is after all not dimensionless, and its formulation (flow × information) assures the model's currency is included in the units. Although relationships have been established to convert some common currencies (e. g., carbon to energy), Table 4.1 illustrates how ascendency units appear comparable, but ultimately are not. There is an information index generated in this analysis that has potential for global comparison. The A/C ratio is a dimensionless value that represents a system’s success at reaching the maximum ascendency for that moment in time. While this theoretical maximum does change with time, it allows us a dimensionless comparison between ecosystems with different units. Table 4.1 shows A/C values for seven aquatic ecosystems. Neuse River Estuary A/C values are amongst the lower percents listed, yet the Swartkops and Ems estuaries are similarly so, indicating some possible relationship of ecosystem classification via A/C rankings.

4.6 MODEL CONSIDERATIONS

The Neuse River Estuary models evaluated in this study contain four significant differences in comparison with typical ecosystem models used in ascendency analysis. Most notable, upon initial inspection is the degree of aggregation due to the compartment selection. Containing seven compartments, aggregation in the Neuse River Estuary model can be observed even among different forms of nitrogen. (e. g., NO_x compartment combines NO_2 and NO_3). Abarca-arenas and Ulanowicz (2002) described a “monotonic” decline in ascendency as they further aggregated a 50 compartment model of the Chesapeake Bay. Thus, we may consider our ascendency calculations in the Neuse to be somewhat depressed due to the simplicity of our model. However, a question more fundamental than, "What role aggregation plays in our calculations?" may be, "What should be considered comparing ascendency values between a system of primarily trophic interactions and a system of primarily chemical transformations?".

Our ascendency analysis focused on internal (compartmental) and external (import/export) nitrogen flux. Traditionally, ascendency analyses are performed on biomass and energy models. In particular aquatic carbon models are common, utilizing conversions between carbon and biomass or carbon and energy. While the formulation of ascendency is carefully constructed to retain applicability to all systems, including non-living systems, interpretation of changes in ascendency may however differ based on something as simple as currency. In a nitrogen model, an increase in ascendency and TST coupled with a falling AMI (Figure 3.2, scenario #2) may represent an eutrophication scenario. However, the same conclusion may not hold for an energy model.

Qualitative differences in model transfers should also be considered during ascendency analysis. While the Neuse River Estuary model contains examples of trophic interactions such as grazing, (PN-phyto → PN-hetero) its structure is dominated by chemical transformations (e. g., nitrification $NH_4 \rightarrow NO_x$). In a quantitative sense flows, regardless of the details, are comparable. However, considerations regarding the types of flow are required when addressing concepts such as Ulanowicz's pruning, the removal of weaker pathways in favor of more efficient and conservative trophic pathways. Furthermore, concepts of establishing or eliminating redundant flows in a food web model seem reasonable, while conceptualizing the Neuse River Estuary's nitrogen flow developing a "new" pathway between two chemical forms of nitrogen seems unreasonable.

Finally, regardless of how they interact, the dominance of biotic or abiotic compartments may be important to interpretations of ascendency. The Neuse River Estuary model contains primarily abiotic compartments representing stocks of nitrogen separated by their chemical form. In contrast, the typical models analyzed using ascendency are dominated by trophic interactions between biotic compartments. Living compartments inherently have certain predictable flows that non-living compartments do not. While abiotic model compartments are required to minimally exhibit a single output, biotic compartments in an ascendency analysis are required to have both an unusable export in the form of respiration, and a usable export in the form of excretion. Ascendency analysis differentiates between usable and unusable exports and therefore biotic and abiotic compartments will always have an inherent difference in ascendency theory.

4.7 INTERPRETING CHANGES IN ASCENDENCY

Changes in ascendency in the Neuse River Estuary model paralleled changes in TST in most cases. Equation 3.1 illustrates how TST (typically in the 10^3 to 10^5 range) simply dominates AMI (typically single digits) in the ascendency calculation. To characterize flux in ascendency, the six possible scenarios of change in TST and AMI were constructed (Figure 3.2). The difference between an increase in system ascendency where both constituents rise (scenario #1) and an increase in system ascendency at the expense of order (scenario #2) is qualitatively significant to an ecological manager. Simply observing change in ascendency will not address such differences.

Since we have no reference point leading into spring 1985, we had 15 opportunities to observe change in ascendency between seasons. Increase in ascendency (scenarios 1, 2, or 3) was observed six times. We only observed one occurrence of scenario 1, where ascendency and both of its constituents increased simultaneously. As scenario 1 represents Ulanowicz's concept of growth and development we suggest that a simple ratio (A_{g+d}) relating the number of times scenario 1 is observed (S_1) to the total number of observations (S_{total}) lends insight into short-term changes in ascendency (equation 4.1). While this is no substitute for long-term

$$A_{g+d} = \frac{S_1}{S_{total}} \qquad (4.1)$$

observations, it does differentiate between an orderly increase in system activity and growth at the expense of order. The A_{g+d} value in the Neuse River Estuary (~0.0667) is only of particular use in spatial and temporal comparisons and therefore retains the same limitations as described in previous sections.

No observations of scenario #3 were observed. This scenario represents a reasonable goal for an ecological manager facing the effects of eutrophication. In this observation you have an ecological indicator that identifies that the summation of all flows of nitrogen (including nitrogen loading) for this period are reduced and a simultaneous increase in AMI, interpreted as structure and order, is observed. The majority of changes in ascendency between seasons can be characterized as a loss of ascendency due to reduced TST and do not warrant comment, with the exception of fall to winter 1988. During this period we observed a reduction in ascendency despite an increase in TST. The change is subtle, and due to a ~14% decrease in AMI (scenario #6).

4.8 FIGURES

Figure 4.1: Seasonal changes in ascendency and its primary constituents (TST, AMI) in the Neuse River Estuary nitrogen cycle for 1985; based on nitrogen data abstracted into a compartmentalized model (Christian and Thomas 2003). Ascendency (mmol N bits/m^2 season) and TST (mmol N/m^2 season) values are read using the y-axis. AMI (bits) values are read off the alternate y-axis.

Figure 4.2: Seasonal changes in ascendency and its primary constituents (TST, AMI) in the Neuse River Estuary nitrogen cycle for 1986; based on nitrogen data abstracted into a compartmentalized model (Christian and Thomas 2003). Ascendency (mmol N bits/m^2 season) and TST (mmol N/m^2 season) values are read using the y-axis. AMI (bits) values are read off the alternate y-axis.

Figure 4.3: Seasonal changes in ascendency and its primary constituents (TST, AMI) in the Neuse River Estuary nitrogen cycle for 1987; based on nitrogen data abstracted into a compartmentalized model (Christian and Thomas 2003). Ascendency (mmol N bits/m^2 season) and TST (mmol N/m^2 season) values are read using the y-axis. AMI (bits) values are read off the alternate y-axis.

Figure 4.4: Seasonal changes in ascendency and its primary constituents (TST, AMI) in the Neuse River Estuary nitrogen cycle for 1988; based on nitrogen data abstracted into a compartmentalized model (Christian and Thomas 2003). Ascendency (mmol N bits/m^2 season)

and TST (mmol N/m^2 season) values are read using the y-axis. AMI (bits) values are read off the alternate y-axis.

Figure 4.5: Comparison of fall ascendency values (1985, 1986, 1987, 1988). Seasonal changes in ascendency are reduced and a year-to-year pattern is established.

Figure 4.1

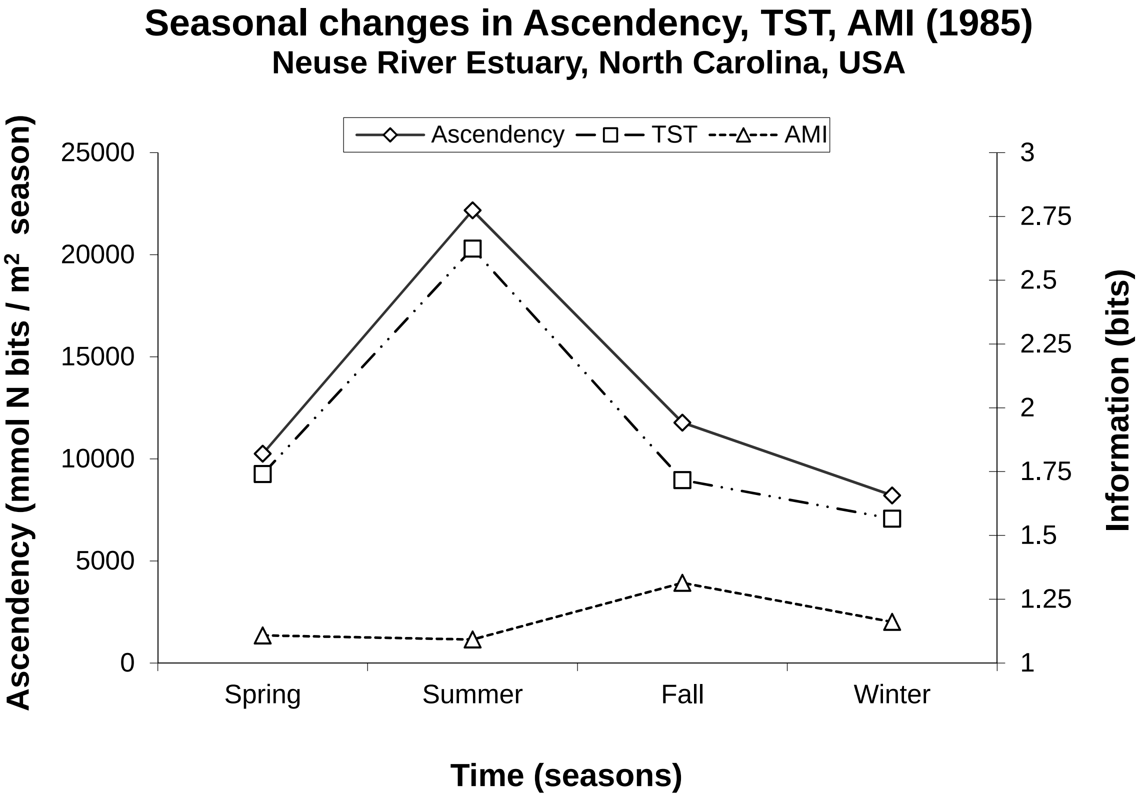

Seasonal changes in Ascendency, TST, AMI (1985)
Neuse River Estuary, North Carolina, USA
Ascendency
TST
AMI
Ascendency (mmol N bits / m2 season)
0
5000
10000
15000
20000
25000
Information (bits)
1
1.25
1.5
1.75
2
2.25
2.5
2.75
3
Spring
Summer
Fall
Winter
Time (seasons)

Figure 4.2

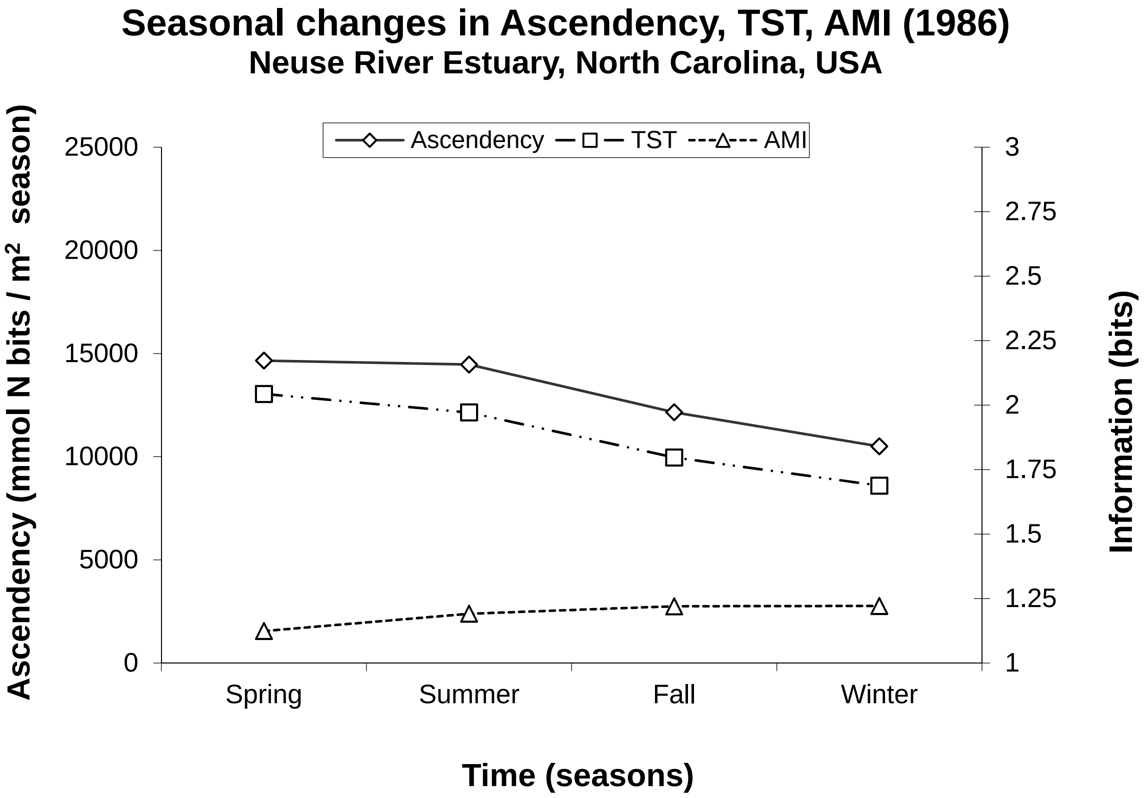

Seasonal changes in Ascendency, TST, AMI (1986)
Neuse River Estuary, North Carolina, USA
Ascendency
TST
AMI
Ascendency (mmol N bits / m² season)
25000
20000
15000
10000
5000
0
3
2.75
2.5
2.25
2
1.75
1.5
1.25
1
Information (bits)
Spring
Summer
Fall
Winter
Time (seasons)

Figure 4.3

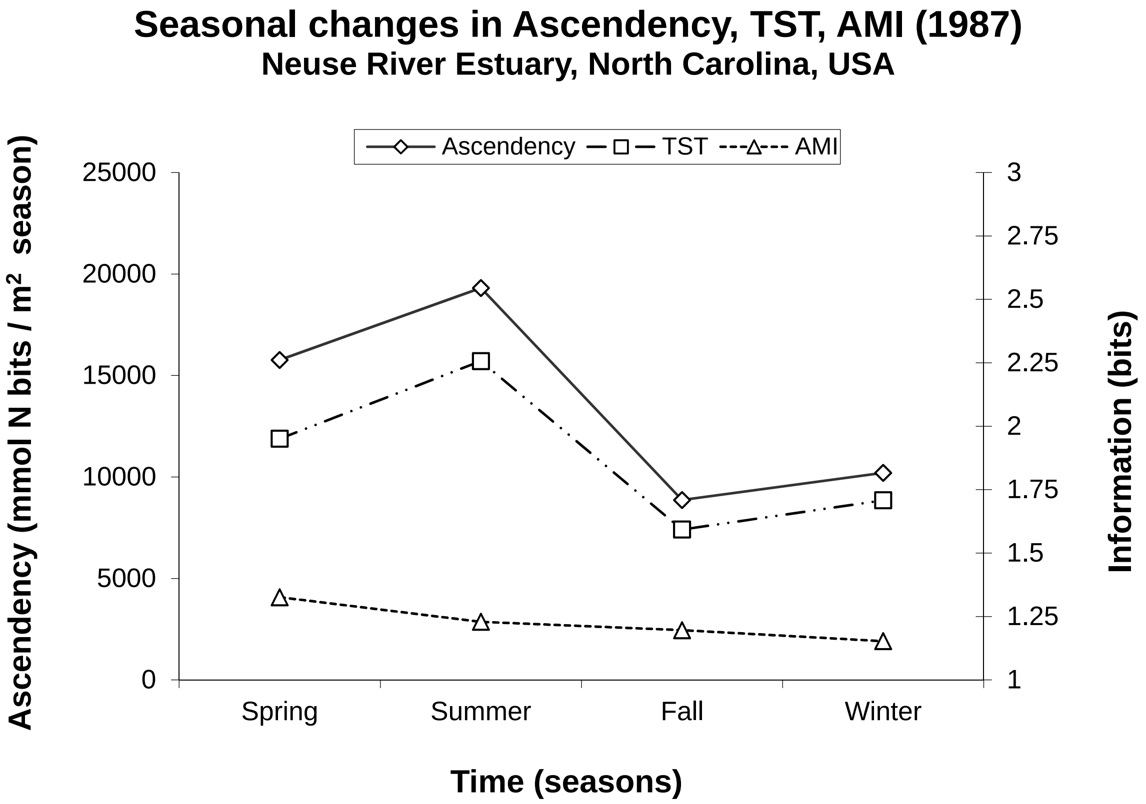

Seasonal changes in Ascendency, TST, AMI (1987)
Neuse River Estuary, North Carolina, USA
Ascendency
TST
AMI
Ascendency (mmol N bits / m^2 season)
25000
20000
15000
10000
5000
0
3
2.75
2.5
2.25
2
1.75
1.5
1.25
1
Information (bits)
Spring
Summer
Fall
Winter
Time (seasons)

Figure 4.4

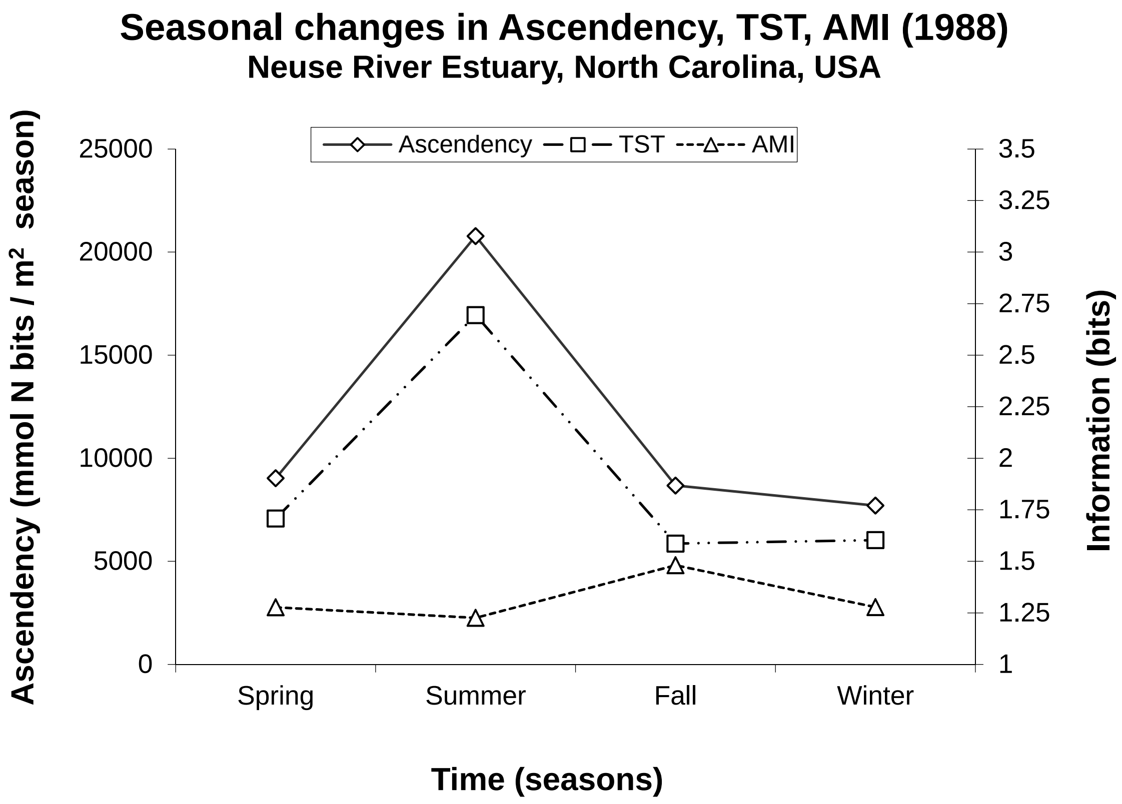
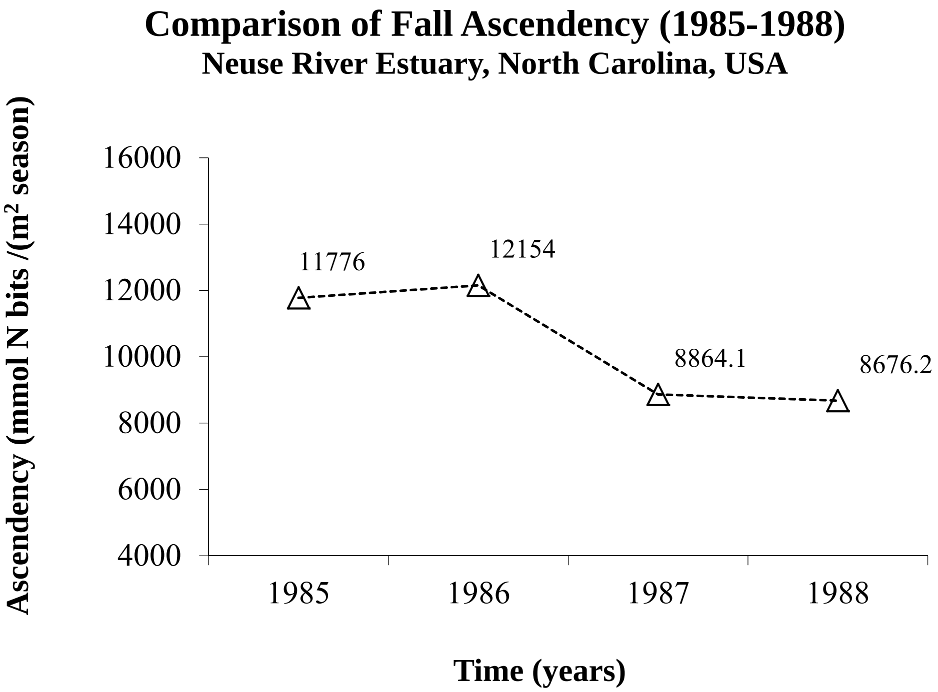

Seasonal changes in Ascendency, TST, AMI (1988)
Neuse River Estuary, North Carolina, USA
Ascendency
TST
AMI
Ascendency (mmol N bits / m² season)
Information (bits)
25000
20000
15000
10000
5000
0
3.5
3.25
3
2.75
2.5
2.25
2
1.75
1.5
1.25
1
Spring
Summer
Fall
Winter
Time (seasons)

Figure 4.5


Comparison of Fall Ascendency (1985-1988)
Neuse River Estuary, North Carolina, USA
Ascendency (mmol N bits /(m2 season)
16000
14000
12000
10000
8000
6000
4000
11776
12154
8864.1
8676.2
1985
1986
1987
1988
Time (years)

4.9 TABLES

TABLE 4.1: Ascendency and A/C values in geographically diverse ecosystems. Ascendency values seem comparable, however the Neuse River Estuaries currency and rate (nitrogen, season) differ from the other entries (carbon, day) taken from a previous study (Baird *et al.*, 1991). Values for the A/C ratios however are comparable despite the previous incongruity.

Table 4.1: Example of incomparable ascendency values, and comparable A/C values between various ecosystems. Neuse River Estuary values are mmol N bits/m^2 season), while Baird *et al.* values are mg C bits/m^2 day. The A/C (ascendency/developmental capacity) ratio is dimensionless.

Marine Ecosystem	Ascendency	A/C
Ems Estuary	2,307†	38.6†
Baltic Sea	4,452†	55.6†
Benguela Upwelling Region	5,593†	50.6†
Neuse River Estuary	12,782‡	35.1‡
Chesapeake Bay	16,335†	49.5†
Swartkops Estuary	17,565†	28.0†
Peruvian Upwelling Region	90,789†	47.6†

† Values from previously published data (Baird et al. 1991).

‡ These values represent average ascendency and A/C ratios for the Neuse River Estuary from 1985-1989.

CHAPTER 5

CONCLUSIONS AND FUTURE DIRECTIONS

5.1 OBJECTIVES

The objectives of the study encompassed interpretation of short term changes in ascendency in the Neuse River Estuary's nitrogen flow, evaluation of ascendency's performance outside its typical model applications, and investigation of spatial comparisons in the Neuse River Estuary's nitrogen flow and their implications to ascendency theory. Addressing goals regarding short-term changes in ascendency requires a novel outlook compared to traditional long-term concerns. Concepts of development and maturation are not readily apparent on the small time scale. To facilitate understanding of the importance of short-term changes, we've identified the 6 scenarios representing possible change in ascendency. The frequency of appearance of these scenarios speaks to ecosystem status and flux in ways that tracking short-term changes in ascendency cannot. As a specific application of the characterizations of change in ascendency we've suggested the use of the growth and development index which identifies and isolates the scenario where an ecosystem exhibits an increase in ascendency coupled with growth in both of its components.

The second objective focused on how ascendency performed in the Neuse River Estuary analysis. Focusing on four factors that set the Neuse River Estuary's nitrogen model apart from typical ascendency model applications, we investigated why changes in currency, structure, aggregation, or biotic compartments require special considerations with ascendency analysis.

Findings parallel concerns from NEA studies using the same Neuse models (Whipple *et al.* 2007). Our final objective involves the comparison of the Neuse River Estuary model with other spatially distinct models using ascendency analysis. The units of ascendency inherently include the model's currency units due to its formulation (flow × information). Therefore direct comparisons of ascendency values to facilitate ecosystem comparison when model currencies differ, becomes difficult. The A/C ratio, known as relative ascendency, does however support ecosystem comparison as does the growth and development index suggested herein.

5.2 FUTURE DIRECTIONS

In consideration of the work presented here, a number of future directions emerge. As presented, the author believes that numerous model factors must be considered during an ascendency analysis. Further complicating the process is the difference of magnitudes between the TST and AMI in ascendency's formulation. Future progress to reduce either of these hindrances would be advantageous. As previously stated, the A/C ratio allows comparison between unique ecosystems. Goal functions in ascendency analysis still revolve around maximizing or optimizing the ascendency index. Determination of a goal function in terms of the A/C ratio, rather than ascendency, may impart the power of ecosystem comparison to the goal function arena. Rather than ecosystem models progressing towards a model specific goal, in effect the modeled ecosystems would be "allowed" to chase the same goal.

In addition, applications further developing the six characterizations of change in ascendency (Figure 3.2) seem viable. Where a rise in ascendency and its components (scenario #1) may represent Ulanowicz's growth and development, what predefined ecosystem stages, changes, or perturbations characterize the five remaining possibilities? Do ecosystem concepts such as succession or maturation have a propensity to exhibit one of these scenarios?

Classification of internally or externally driven changes using the provided scenarios may facilitate understanding of ecosystem status and direction.

5.3 CONCLUSIONS

In conclusion, we analyzed a series of models of the Neuse River Estuary's nitrogen cycle using ascendency analysis. Focusing on ascendency as an ecological indicator, we briefly investigated short-term and long-term ascendency observations and their interpretations to an ecological manager. We identified four areas separating the Neuse River Estuary model from models traditionally analyzed using ascendency. Our analysis supports the use of the A/C ratio when comparing ecosystems internally or externally. The six possible combinations of change in ascendency and its components are identified and presented as means of comparing ascendency values. Taking into account observations of coupled growth and development, we've suggested an indicator ratio (A_{g+d}) preferable to ascendency in the short-term, in hopes of strengthening the approach. Ascendency is after all a functional, useful ecological indicator. It does however require more interpretation than preferable for a single value. By deconstructing it one level and observing the secondary dynamics, its flexibility and applicability are reinforced.

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APPENDICIES

Appendix A

Neuse River Estuary's nitrogen flow data: Input, output, and intercompartmental flows of nitrogen, including storages, for the period spring 1985 to winter 1988 (inclusive) in the Neuse River Estuary (Christian and Thomas, 2003). All units are in mmol of nitrogen per square meter per season (mmol N/m^2 season).

Table A1: Average compartmental nitrogen flow for a sixteen season period (spring 1985 to winter 1988) in the Neuse River Estuary, NC, USA (Christian and Thomas 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	1176	918	4816	0
PN-Hetero	4859	0	555	1388	583	5999	1605
Sediment	611	7	0	0	66	80	463
DON	1363	1138	0	0	0	0	0
NO_X	0	0	123	0	0	1037	0
NH_4	0	11714	159	0	0	0	0
PN-Abiotic	57	2005	0	0	0	0	0
Input	16	24	28	187	419	82	39
Output	37	148	418	124	11	23	31
Storage	85	64	5200	270	59	36	61

Table A2: Compartmental nitrogen flow for spring 1985 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	1176	918	4816	0
PN-Hetero	4859	0	555	1388	583	5999	1605
Sediment	611	7	0	0	66	80	463
DON	1363	1138	0	0	0	0	0
NO_X	0	0	123	0	0	1037	0
NH_4	0	11714	159	0	0	0	0
PN-Abiotic	57	2005	0	0	0	0	0
Input	16	24	28	187	419	82	39
Output	37	148	418	124	11	23	31
Storage	85	64	5200	270	59	36	61

Table A3: Compartmental nitrogen flow for summer 1985 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	508	366	1621	0
PN-Hetero	1706	0	323	1221	101	3897	731
Sediment	264	2	0	0	2	54	228
DON	499	1222	0	0	0	0	0
NO_X	0	0	33	0	0	386	0
NH_4	0	5820	119	0	0	0	0
PN-Abiotic	23	937	0	0	0	0	0
Input	4	5	8	26	50	20	6
Output	7	3	8	1	0	1	7
Storage	29	22	1300	68	6	5	25

Table A4: Compartmental nitrogen flow for fall 1985 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	238	238	1298	0
PN-Hetero	1237	0	128	176	103	960	335
Sediment	167	2	0	0	1	7	134
DON	355	16	0	0	0	0	0
NO_X	0	0	31	0	0	231	0
NH_4	0	2468	7	0	0	0	0
PN-Abiotic	15	452	0	0	0	0	0
Input	4	7	9	51	80	23	7
Output	4	8	154	8	0	2	5
Storage	23	18	1300	35	4	9	17

Table A5: Compartmental nitrogen flow for winter 1986 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	108	108	448	0
PN-Hetero	458	0	0	366	184	1517	232
Sediment	64	1	0	0	26	5	41
DON	133	347	0	0	0	0	0
NO_X	0	0	22	0	0	204	0
NH_4	0	2143	15	0	0	0	0
PN-Abiotic	8	263	0	0	0	0	0
Input	1	7	6	55	92	20	6
Output	2	10	106	61	0	4	4
Storage	14	12	1300	48	17	17	9

Table A6: Compartmental nitrogen flow for spring 1986 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	260	260	1034	0
PN-Hetero	1111	0	169	684	21	2721	463
Sediment	116	2	0	0	37	14	124
DON	311	625	0	0	0	0	0
NO_X	0	0	37	0	0	226	0
NH_4	0	3966	18	0	0	0	0
PN-Abiotic	15	573	0	0	0	0	0
Input	3	5	5	36	57	17	5
Output	4	8	74	28	2	6	6
Storage	16	18	1300	89	5	13	17

Table A7: Compartmental nitrogen flow for summer 1986 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	379	379	1416	0
PN-Hetero	1453	0	233	383	131	1432	427
Sediment	264	2	0	0	2	54	182
DON	435	292	0	0	0	0	0
NO_X	0	0	33	0	0	414	0
NH_4	0	3178	119	0	0	0	0
PN-Abiotic	18	589	0	0	0	0	0
Input	3	5	8	55	67	21	6
Output	7	3	127	20	2	2	4
Storage	29	18	1300	99	14	8	20

Table A8: Compartmental nitrogen flow for fall 1986 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	364	250	1370	0
PN-Hetero	1446	0	153	263	100	992	453
Sediment	124	2	0	0	1	7	109
DON	397	229	0	0	0	0	0
NO_X	0	0	31	0	0	275	0
NH_4	0	2628	7	0	0	0	0
PN-Abiotic	14	548	0	0	0	0	0
Input	1	4	9	19	49	14	4
Output	4	4	61	18	4	5	4
Storage	17	15	300	73	16	17	15

Table A9: Compartmental nitrogen flow for winter 1987 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	326	326	636	0
PN-Hetero	903	0	1	263	322	992	317
Sediment	96	2	0	0	26	5	59
DON	258	266	0	0	0	0	0
NO_X	0	0	22	0	0	195	0
NH_4	0	1791	15	0	0	0	0
PN-Abiotic	12	383	0	0	0	0	0
Input	12	15	6	146	464	37	11
Output	31	371	156	81	7	15	30
Storage	21	18	1300	51	84	14	1

Table A10: Compartmental nitrogen flow for spring 1987 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	580	273	1868	0
PN-Hetero	1980	0	103	215	87	690	599
Sediment	153	2	0	0	37	14	109
DON	544	224	0	0	0	0	0
NO_X	0	0	37	0	0	197	0
NH_4	0	2740	18	0	0	0	0
PN-Abiotic	14	715	0	0	0	0	0
Input	15	7	5	93	179	28	7
Output	45	0	162	66	16	17	28
Storage	21	16	1300	40	18	7	15

Table A11: Compartmental nitrogen flow for summer 1987 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	333	333	2424	0
PN-Hetero	2211	0	329	244	176	1782	623
Sediment	300	2	0	0	2	54	182
DON	558	12	0	0	0	0	0
NO_X	0	0	33	0	0	441	0
NH_4	0	4569	119	0	0	0	0
PN-Abiotic	18	786	0	0	0	0	0
Input	2	4	8	19	38	15	4
Output	5	0	67	12	0.1	2	3
Storage	33	18	1300	94	7	11	20

Table A12: Compartmental nitrogen flow for fall 1987 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	61	61	819	0
PN-Hetero	602	0	202	122	220	1518	124
Sediment	153	2	0	0	1	7	124
DON	168	18	0	0	0	0	0
NO_X	0	0	31	0	0	213	0
NH_4	0	2540	7	0	0	0	0
PN-Abiotic	15	232	0	0	0	0	0
Input	1	4	9	16	39	12	4
Output	4	0	56	19	1	2	3
Storage	21	18	1300	108	4	5	1

Table A13: Compartmental nitrogen flow for winter 1988 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	74	74	475	0
PN-Hetero	360	0	39	385	207	2469	216
Sediment	127	1	0	0	26	5	32
DON	125	348	0	0	0	0	0
NO_X	0	0	22	0	0	169	0
NH_4	0	3094	15	0	0	0	0
PN-Abiotic	6	240	0	0	0	0	0
Input	4	7	6	4	123	21	6
Output	9	0	121	18	7	12	4
Storage	28	8	1300	15	17	3	7

Table A14: Compartmental nitrogen flow for spring 1988 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	386	172	950	0
PN-Hetero	1116	0	50	182	102	449	339
Sediment	80	1	0	0	37	14	87
DON	302	245	0	0	0	0	0
NO_X	0	0	7	0	0	179	0
NH_4	0	1551	18	0	0	0	0
PN-Abiotic	11	414	0	0	0	0	0
Input	3	5	5	36	96	26	5
Output	2	32	119	15	1	3	4
Storage	11	12	1300	84	10	3	12

Table A15: Compartmental nitrogen flow for summer 1988 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	446	446	2438	0
PN-Hetero	2419	0	260	372	34	203	696
Sediment	218	2	0	0	2	54	218
DON	666	151	0	0	0	0	0
NO_X	0	0	33	0	0	386	0
NH_4	0	4772	119	0	0	0	0
PN-Abiotic	22	894	0	0	0	0	0
Input	1	4	8	27	64	23	5
Output	6	0	90	26	1	2	7
Storage	24	22	1300	78	7	5	24

Table A16: Compartmental nitrogen flow for fall 1988 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	261	3	1061	0
PN-Hetero	951	0	68	42	304	172	242
Sediment	95	1	0	0	1	7	87
DON	265	30	0	0	0	0	0
NO_X	0	0	31	0	0	213	0
NH_4	0	1434	7	0	0	0	0
PN-Abiotic	11	318	0	0	0	0	0
Input	1	4	9	30	65	15	4
Output	4	0	94	22	1	3	4
Storage	13	12	1300	71	9	5	12

Table A17: Compartmental nitrogen flow for winter 1989 in the Neuse River Estuary, NC, USA (Christian and Thomas, 2003). All units are in mmol N/m^2 season.

	PN-Phyto	PN-Hetero	Sediment	DON	NO_X	NH_4	PN-Abiotic
PN-Phyto	0	0	0	190	190	679	0
PN-Hetero	748	0	1	174	137	625	269
Sediment	91	1	0	0	26	5	41
DON	212	79	0	0	0	0	0
NO_X	0	0	22	0	0	180	0
NH_4	0	1457	15	0	0	0	0
PN-Abiotic	12	294	0	0	0	0	0
Input	6	8	6	94	152	19	6
Output	2	131	132	21	1	2	2
Storage	20	13	1300	47	12	6	9

Appendix B

Neuse River Estuary's ascendency, total system throughput, average mutual information and A/C ratio; Tabular results from ascendency analysis of 16 seasons of nitrogen flow in the Neuse River Estuary, NC, USA using the NETWRK 4.2 software package. Results include ascendency, ascendency's primary components (TST, AMI), and the A/C ratio (ascendency/developmental capacity).

Table B1: Seasonally calculated ascendency values and its primary constituents (TST, AMI). Units for TST are mmol N/m^2 season, AMI is measured in bits, and ascendency units are mmol N bits/m^2 season. The A/C ratio (ascendency /developmental capacity) is dimensionless.

Seasons	TST	AMI	Ascendency	A/C ratio
Spring 1985	9,253	1.108	10,252	0.315
Summer 1985	20,301	1.092	22,170	0.321
Fall 1985	8,962	1.314	11,776	0.377
Winter 1986	7,067	1.161	8,207	0.339
Spring 1986	13,043	1.124	14,657	0.339
Summer 1986	12,145	1.191	14,467	0.325
Fall 1986	9,963	1.220	12,154	0.348
Winter 1987	8,598	1.221	10,502	0.305
Spring 1987	11,885	1.326	15,764	0.364
Summer 1987	15,710	1.229	19,310	0.369
Fall 1987	7,410	1.196	8,864	0.377
Winter 1988	8,851	1.153	10,203	0.377
Spring 1988	7,074	1.277	9,031	0.340
Summer 1988	16,946	1.226	20,776	0.363
Fall 1988	5,860	1.481	8,676	0.425
Winter 1989	6,030	1.278	7,704	0.336

Appendix C

Neuse River Estuary's supplementary indices; Tabular results from ascendency analysis of 16 seasons of nitrogen flow in the Neuse River Estuary, NC, USA using the NETWRK 4.2 software package. Results include overheads (import, export), redundancy, developmental capacity, connectance and cycling indices.

Table C1: Seasonally calculated overhead, redundancy, and capacity indices for the Neuse River Estuary. Import overhead, export overhead, redundancy, and developmental capacity all have units of mmol N bits/m^2 season.

Seasons	Import Overhead	Export Overhead	Redundancy	Developmental Capacity
Spring 1985	836	923	20,524	32,535
Summer 1985	938	675	45,229	69,012
Fall 1985	1,047	535	17,915	31,273
Winter 1986	967	681	14,344	24,199
Spring 1986	856	749	27,026	43,289
Summer 1986	1,069	722	28,218	44,476
Fall 1986	675	576	21,550	34,956
Winter 1987	2,078	3,133	18,771	34,484
Spring 1987	1,584	1,699	24,234	43,281
Summer 1987	707	474	31,895	52,387
Fall 1987	567	403	13,685	23,519
Winter 1988	756	641	15,435	27,035
Spring 1988	926	725	15,896	26,578
Summer 1988	908	675	34,950	57,308
Fall 1988	714	443	10,600	20,433
Winter 1989	1,180	1,140	12,880	22,905

Table C2: Seasonally calculated connectance and cycling indices in the Neuse River Estuary. Connectance indices have the units of “connections”. Finn’s cycling index is a ratio and is dimensionless.

Seasons	Overall Connectance	Compartmental Connectance	Finn's Cycling Index
Spring 1985	2.358	2.176	0.957
Summer 1985	2.253	2.172	0.980
Fall 1985	2.165	2.023	0.914
Winter 1986	2.230	2.056	0.904
Spring 1986	2.174	2.061	0.960
Summer 1986	2.402	2.259	0.952
Fall 1986	2.246	2.128	0.969
Winter 1987	2.688	2.295	0.737
Spring 1987	2.273	2.064	0.899
Summer 1987	2.100	2.026	0.981
Fall 1987	2.017	1.904	0.952
Winter 1988	1.961	1.846	0.911
Spring 1988	2.417	2.220	0.894
Summer 1988	2.140	2.052	0.966
Fall 1988	2.043	1.889	0.911
Winter 1989	2.456	2.177	0.817