

INDIRECT EFFECTS AND DISTRIBUTED CONTROL IN ECOSYSTEMS. TEMPORAL
VARIATION OF INDIRECT EFFECTS IN A SEVEN-COMPARTMENT MODEL OF
NITROGEN FLOW IN THE NEUSE RIVER ESTUARY, USA: TIME SERIES ANALYSIS

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ABSTRACT

Indirect effects, the ability of one element in a system to impact another without direct interaction, are critical components of complex adaptive systems. Network Environ Analysis (NEA) is an environmental extension of economic Input-Output Analysis that characterizes and quantifies indirect effects transmitted by a specific currency (e.g., carbon, nitrogen) within a steady state system. Previous NEA results suggest that indirect effects tend to dominate direct effects in ecosystems. Although steady state models may be useful, ecologists are often interested in system dynamics. In this article, we use NEA to investigate the temporal dynamics of indirect effects in sixteen steady state models of nitrogen cycling in the Neuse River Estuary, USA. These models were originally constructed by Christian and Thomas (2003. *Network analysis of nitrogen inputs and cycling in the Neuse River Estuary, North Carolina, USA. Estuaries* **26**:815-828.). Our work had two primary objectives: 1) describe and quantify the temporal dynamics of indirect flows and 2) identify the importance of model factors in determining the magnitude of indirect flows. Our results indicate that indirect flows transmitted by the network of nitrogen transactions, especially microbial transformations, dominated direct flows in the Neuse River Estuary between spring 1985 and winter 1989. When we examined the indirect flow index (ratio of indirect to total system throughflow), we were surprised by the relatively small amount of temporal variation within the Neuse River Estuary. In all seasons, indirect flow was more than 80% of TST, and there was no significant interannual variation. Our analysis also revealed no clear relationship between boundary or direct flow and indirect flow, but a strong association between cycled and indirect flow. We conclude that while an increase in boundary, direct, and cycled flows can influence indirect flows, in the Neuse River Estuary models indirect flows are predominantly due to cycling. If nitrogen loading had been reduced

during our study period, this system likely would have remained eutrophic for an extended period of time. If we assume the system remained similar in 1997, we would expect the legislated reduction of nitrogen loading to have little immediate effect, although this action will be important for long-term change. Dominance of indirect flow due to cycling makes this system state relatively difficult to change rapidly by external forcing. In this sense the indirect effects stabilize the system, making it more resistant to external perturbations, though it may be more sensitive in the long-term.

“We are far less powerful than we think, but have much more impact than we perceive.”

Mitchel Thomashow (2002)

1. INTRODUCTION

Indirect effects, the ability of one species or system element to influence another without directly interacting with it, appear to have a significant role in the organization and transformation of biological systems. They have long been recognized by biologists (Darwin, 1959), and the challenge they pose for environmental management helped spark the environmental movement (Carson, 1962). Though challenging to investigate, ecologists are increasingly recognizing the significance of indirect effects as components of ecological interactions (Patten, 1983; Andrewartha and Birch, 1984; Patten, 1984; Miller and Kerfoot, 1987; Strauss, 1991; Wootton, 1994, 2002) and evolution (Miller and Travis, 1996; Laland et al., 1999; Odling-Smee et al., 2003). Wootton (2002) recently argued that indirect effects are “...a fundamental cause of ecosystem complexity.” In this article, we characterize the temporal variation of indirect effects in sixteen seasonal models of nitrogen cycling for the Neuse River Estuary, USA.

Part of the challenge of analyzing indirect effects is that there appear to be multiple types that ecologists have struggled to classify and empirically demonstrate (Miller and Kerfoot, 1987; Strauss, 1991; Wootton, 1994; Abrams, 1995). Here, we adopt the categorization scheme of Wootton (1993; 1994; 2002) that begins with two categories: interaction chains and interaction modifications. Interaction chains occur when one species impacts another by affecting a third. This occurs by linking two or more direct interactions together. For example, in the chain $A \rightarrow B \rightarrow C$, A indirectly influences C by directly influencing B. As ecologists are often interested in the abundance or density of species, these have also been labeled ‘density mediated interactions’

(Abrams et al., 1996). Several commonly studied ecological interactions arise from this type of indirect interaction including keystone predation, trophic cascades, apparent competition, indirect mutualisms, and exploitative competition (Wootton, 2002). Interaction modifications, on the other hand, occur when a species modifies the interaction between two species. At least two types of interaction modifications have been identified. ‘Trait-mediated indirect effects’ (Abrams, 1995; Abrams et al., 1996; Peacor and Werner, 1997; Bolker et al., 2003; Luttbeg et al., 2003; Werner and Peacor, 2003) occur when one species changes the traits or behavior of a second that alters how it interacts with a third. For example, Pacific killifish (*Fundulus parvipinnis*) parasitized by the trematode *Euhaporchis californiensis* tend to exhibit conspicuous behavior making them more susceptible to predation by avian predators than unparasitized killifish (Lafferty and Morris, 1996). ‘Environment-mediated indirect modifications’ occur when one species changes the environmental context in which two species interact. Ecosystem engineers, such as beavers that construct ponds providing habitat for aquatic organisms, are one example (Jones et al., 1997).

In ecosystems, organisms and elements of their abiotic environments are coupled together through an intricate network of energy–matter exchanges (Patten et al., 1976; Ulanowicz, 1986; Higashi and Burns, 1991). While observation and analysis of these transaction networks cannot identify specific mechanisms or depict all types of indirect interactions (Loehle, 1990; Wootton, 1994), they do capture many types of indirect interactions that are reflected in trophic dynamics and biogeochemistry (Patten, 1990; Higashi and Burns, 1991). These include some indirect interactions from each of the three broad categories identified earlier. Therefore, analysis of these flow–storage networks may illuminate the consequences of particular system organizations, especially the indirect effects mediated by this transaction network.

One purpose for developing input–output analysis (IOA) in economics was to trace indirect effects through the network of economic transactions (Leontief, 1966). Network environmental analysis (NEA) is an environmental application and extension of economic IOA. Through NEA, Patten and colleagues (Patten, 1984, 1985; Higashi and Patten, 1986, 1989; Patten, 1991) characterized indirect flows transmitted through the network of energy–matter exchanges in an ecosystem. At the whole-system level, the relative significance of indirect flows is indicated by the ratio of indirect to direct flow (Indirect/Direct). This ratio indicates the significance of indirect flows within a system's *environs*, which are within system, compartment-specific, input and output oriented environments (Patten, 1978, 1981, 1982, 1992). Previous results suggest that the Indirect/Direct flow ratio tends to be greater than unity in model ecosystems, implying that indirect effects are dominant (Patten, 1984; Higashi and Patten, 1986, 1989; Patten, 1991; Fath, 2004). This has led Patten (in prep.) to hypothesize that the natural world is unified through indirect effects.

Applications of NEA have been limited to steady state models (e.g., Dame and Patten, 1981; Patten and Matis, 1982; Flebbe, 1983; Gattie et al., in press). Though these models can be useful, ecologists are often interested in system dynamics. In this paper we use NEA to investigate the temporal dynamics of indirect flows in the Neuse River Estuary. We take a small step toward a true dynamic NEA by investigating both the seasonal and interannual variation in indirect effects in a discrete–time sequence of steady state models. Further, while past work indicates that aspects of both system structure and function influence the degree of indirect effects (Patten et al., 1990; Patten, 1991; Fath, 2004), the relative importance of various factors is unknown. This knowledge is crucial to our understanding of how indirect effects integrate ecological systems and alter their responses to environmental impacts. The Neuse River Estuary

data set provides an opportunity to begin to address these questions. Understanding the causes and consequences of indirect effects is necessary for sustainable management of ecosystems and the services they provide, a critical mission for ecological sciences (Palmer et al., 2004; Palmer et al., 2005).

The Neuse is a large river in North Carolina draining a 16,000 km² watershed. Water leaving the river enters the Neuse River Estuary and then flows into Pamlico Sound. This estuary has received a great deal of political and scientific attention in the last two decades because it has become highly eutrophic and at times hypoxic (Christian et al., 1986; Baird et al., 2004). In 1997, the State of North Carolina legislated a thirty percent reduction in nitrogen loading to the estuary. In addition, the US EPA required the state to develop a total maximum daily load (TMDL) of nitrogen entering the estuary by the summer of 1997. The sixteen seasonal nitrogen models were originally constructed by Christian and Thomas (2000; 2003) as part of the larger Neuse River Modeling and Monitoring (ModMon) program to study the estuary's response to new environmental management (Reckhow and Gray, 2000). Their analysis using a complementary type of ecological network analysis indicated that nitrogen dynamics in the estuary are dominated by internal recycling (Christian and Thomas, 2003).

Our first objective was to characterize the temporal dynamics of indirect flows transmitted through the nitrogen transaction networks. We used NEA to describe and quantify the indirect flows because it decomposes observed throughflows into their boundary, direct, and indirect portions. Although ecosystems are open thermodynamic systems that eventually dissipate imported energy–matter, indirect flows tend to dominant direct because of the large number of indirect pathways available in cyclic systems (Patten et al., 1982; Patten, 1985; Borrett and Patten, 2003). As the Neuse River Estuary nitrogen models are cyclic and well

connected, we expected indirect flows to be dominant. We also anticipated the proportion of indirect flow to vary seasonally, contributing more in the spring and summer when biological activity increases, and less in the winter when biological activity slows and physical processes are more pronounced. River discharge and nutrient loading tend to be high and flushing times short during colder months (Christian et al., 1991). Alternatively, more biological activity might have decreased the proportion of indirect flow.

Our second objective was to determine the relative importance of factors determining indirect flow in the Neuse models. Higashi and Patten (Higashi and Patten, 1986; Patten et al., 1990; Patten, 1991) showed algebraically that the ratio of indirect-to-direct effects should increase as model size (number of nodes, n), connectivity (proportion of possible links connected, $C = L/n^2$), strength of direct flows (Direct), and magnitude of cycling (Cycled) increase. This algebra, however, does not determine the relative importance of these factors or indicate whether this is a complete set of factors. Other attributes such as network topology (Borrett and Patten, 2003) or boundary flow also might be influential. In the model ecosystems we analyzed, network structure (n , C , and topology) was constant for the 16 seasons, but functional attributes (Direct, Cycled, and Boundary flow) varied. Given Higashi's algebra, we expected Direct and Cycled flow to significantly influence the magnitude of indirect effects. Further, we expected cycling to be the most significant factor as it establishes the feedbacks, amplifying direct flows into indirect components.

2. MATERIALS AND METHODS

2.1 NEUSE RIVER ESTUARY NITROGEN CYCLING MODELS

For our investigation, we used sixteen seasonal network models of nitrogen cycling in the Neuse River estuary from Spring 1985 to Winter 1989 originally constructed by Christian and

Thomas (2000; 2003). Each model has the same basic structure (Figure 1), with seven compartments ($n = 7$), 22 within-system observed flows, and boundary loading to and losses from each compartment. Compartments, or network nodes, represent nitrogen storage (mmol N m^{-2}) in phytoplankton (PN-Phyto), heterotrophs (PN-Hetero), detritus (PN-Aerobic), sediments, dissolved organic nitrogen (DON), nitrate and nitrite (NO_x), and ammonium (NH_4). Nitrogen flows ($\text{mmol N m}^{-2} \text{ season}^{-1}$) are represented by directed arcs in the network. Each compartment has nitrogen imports from upstream and the watershed as well as boundary losses due to denitrification and exports downstream into Pamlico Sound. The sediment compartment has an additional boundary loss due to sediment burial. Baird et al. (1991) suggested this structural consistency is critical for the type of model comparisons we make in this paper.

{INSERT FIGURE 1}

As reported in Christian and Thomas (2003), nitrogen flow and storage data for the models were drawn largely from a four year study of the Neuse River Estuary (Christian et al., 1991; Christian et al., 1992; Rizzo et al., 1992; Boyer et al., 1993; Boyer et al., 1994; Rizzo and Christian, 1996). The least well known data, including sediment-water column interactions, burial, and denitrification, were estimated based on related studies; sediment burial rates were adjusted to balance the model to a steady state¹ (i.e., inputs equal outputs for each node). See Christian and Thomas (2000; 2003) and Christian et al. (1992) for additional model details.

¹ The model for Summer 1987 was not exactly at steady state. However, the difference between input and output throughflow in NO_x , the only compartment not at steady state, was only $0.9 \text{ mmol N m}^{-2} \text{ season}^{-1}$. Analysis of an adjusted model (data not shown) showed this had no significant impact on our results.

2.2 NETWORK ENVIRON ANALYSIS AND INDIRECT EFFECTS

2.2.1. ENVIRON INDIRECT EFFECTS

Empirically measured or observed energy–matter flows from compartment j to i ($F_{n \times n} = (f_{ij})$, $i, j = 1, \dots, n$) in natural systems are comprised of both direct and indirect flows (Patten et al., 1976; Whipple and Patten, 1993; Whipple, 1999; Gattie et al., in press). NEA (Patten et al., 1976; Patten, in prep.) is a family of input–output methods descended from economics (Leontief, 1965, 1966) that analytically decomposes observed flows to identify their origins or fates within the system of interest (see Fath and Patten, 1999 for review). NEA includes structural analysis for path enumeration as well as functional analyses to investigate flow, storage, utility, and control. In this work, we focused on the output oriented throughflow-specific flow analysis. NEA methods are extensively described in the literature (Patten et al., 1976; Matis and Patten, 1981; Fath and Patten, 1999; Patten, in prep.) and were recently collected into a single MATLAB® function to facilitate its application (Fath and Borrett, in press). We will briefly review the NEA elements we used, and define the response variables for this study.

There are several basic steps to output oriented throughflow-specific flow analysis in NEA. Given the observed intercompartmental flows ($F_{n \times n}$) and boundary inputs ($z_{n \times 1}$) and outputs ($y_{1 \times n}$) of an n node system, we first define the total amount of energy–matter flowing

into and out of each node as $T_k^{(in)} \equiv \sum_{j=1(\neq k)}^n f_{kj} + z_k$ and $T_k^{(out)} \equiv \sum_{i=1(\neq k)}^n f_{ik} + y_k$ respectively, where

$T_k^{(in)} = T_k^{(out)} = T_k$ ($k = 1, \dots, n$) at steady state. Total system throughflow ($TST = \sum T_k$) is a

system-level measure of activity and is often used to characterize ecosystem models (Finn, 1976; Ulanowicz, 1986).

In the second step, observed flows (F) are normalized by the donor compartment throughflow. The resultant matrix, $G_{n \times n}$, represents the donor-specific direct flow intensities from j to i ($G = (g_{ij}) = \left(\frac{f_{ij}}{T_j} \right)$). Elements of G are interpreted as the probability that boundary material entering j will flow to i over a direct path (i.e., path length, $m = 1$). Next, flow from j to i over indirect pathways ($m > 1$) is determined by raising G to the m^{th} power, G^m . The elements of G^m are interpreted as the fractional transfer coefficient for boundary material entering j flowing over all pathways of length m between any j and i . Finally, total node throughflow is recovered by post multiplying the sum of the infinite power series of flow intensities by the boundary inflows:

$$T = \left(\underbrace{I}_{\text{Boundary}} + \underbrace{G^1}_{\text{Direct}} + \underbrace{G^2 + \dots + G^m + \dots}_{\text{Indirect}} \right) * z, \quad (1)$$

where $I = G^0$ is the matrix multiplicative identity. In open, dissipative, thermodynamic systems like ecosystems, $0 \leq g_{ij} < 1$ ($\forall i, j$) and at least one column (or row) sum is less than unity ensuring that the dominant eigenvalue of G is less than one (Berman and Plemmons, 1979). This criterion ensures that the power series converges to the transitive closure matrix $N = (n_{ij}) = (I - G)^{-1}$, where (n_{ij}) represents the integral (boundary + direct + indirect) throughflow from j to i generated by an input to j . Thus, $T = Nz$. The analysis used here only incorporates flow over pathways that Higashi and Patten (1989) termed procedurally indirect. Pathways with adjacent repeated nodes (e.g., $i \rightarrow i \rightarrow i \rightarrow i \rightarrow j$) that create only temporal indirectness are included as direct flows.

We can rewrite the throughflow decomposition in (1) by distributing z across the flow intensity partition, and summing the elements of each $n \times 1$ resultant vector to derive the following restatement in terms of TST:

$$\text{TST} = \underbrace{\sum \text{Iz}}_{\text{Boundary}} + \underbrace{\sum \text{Gz}}_{\text{Direct}} + \underbrace{\sum (\text{N} - \text{I} - \text{G})z}_{\text{Indirect}}. \quad (2)$$

This equation identifies the dimensionalized flow variables for the whole system scaled by the model inputs that we used as response variables: Boundary ($\sum \text{Iz}$), Direct ($\sum \text{Gz}$), and Indirect ($\sum (\text{N} - \text{I} - \text{G})z$). Dividing both sides of (2) by TST generates:

$$1 = \frac{\sum z}{\text{TST}} + \frac{\sum \text{Gz}}{\text{TST}} + \frac{\sum (\text{N} - \text{I} - \text{G})z}{\text{TST}}. \quad (3)$$

Elements of the right-hand side of (3) represent the portion of TST derived from each of the three categories of flow. From (2) the ratio of indirect-to-direct flows (Indirect/Direct) can be constructed as

$$\text{Indirect/Direct} = \frac{\sum (\text{N} - \text{I} - \text{G})z}{\sum \text{Gz}}. \quad (4)$$

Indirect/Direct is a system-level indicator of the relative significance of indirect flow in TST.

To address our first objective, we calculated this ratio and the TST partition in (3) for the Neuse River Estuary models using a modification of NEA.m (Fath and Borrett, in press). Further, we

compared the mean indirect flow index ($\text{IFI} \equiv \frac{\text{Indirect}}{\text{TST}} = \frac{\sum (\text{N} - \text{I} - \text{G})z}{\text{TST}}$, $0 \leq \text{IFI} < 1$),

averaging first across seasons, and second across four years. Year classes were constructed by grouping spring, summer, and fall of a year with the following winter (e.g., year class 1985,

$\text{yc1985} = \{\text{Spring 1985, Summer 1985, Fall 1985, and Winter 1986}\}$). Following a

Kolmogorov-Smirnov test to insure IFI was normally distributed, we analyzed statistical

significance of season and year class using a two-way ANOVA (Dalgaard, 2002). When necessary, multiple pairwise comparison t-tests were evaluated with Bonferroni adjusted p-values. We calculated all statistics with R (version 1.7.3, R Development Core Team, 2004).

Finn (1976) proposed an alternative partition of TST into portions from acyclic throughflow and cycled flow. Cycled flow, calculated as $\text{Cycled} \equiv \sum_{i=1}^n ((n_{ii} - 1)z_i)$, was an additional response variable in this study. The Finn cycling index (FCI), the ratio of cycled flow to TST, is another common metric used to characterize ecosystem organization. Allesina and Ulanowicz (2004) show that FCI does not account for all recycling, and introduce a new measure called the comprehensive cycling index (CCI). In their analysis of 23 ecosystem models, however, they found CCI to be linearly related to FCI by a factor of 1.14. As CCI is computationally intensive to determine and appears to be a linear multiple of FCI, we focus on FCI.

2.2.2. *DETERMINANTS OF INDIRECT EFFECTS*

To evaluate the relative influence of system attributes in determining the portion of indirect flow, we constructed a series of ordinary least squares regression models. While we could not evaluate the role of factors such as n and C because structure was constant in these networks, flow variability allowed us to consider the role of direct and cycled flow identified by Higashi and Patten's algebra as important determinants of indirect flows. We also considered boundary flow as a potential factor as it is a component of TST (2). We first examined the independent relationship between Indirect and Boundary, Direct and Cycled. We further considered additional pairwise combinations and multiple regression where appropriate.

3. RESULTS

The sixteen seasonal models of nitrogen cycling in the Neuse River Estuary demonstrate an expected seasonality in TST (Figure 2). TST varies from a minimum of 5,732 mmol N m⁻² season⁻¹ in fall 1988 to a maximum of 20,182 mmol N m⁻² season⁻¹ in summer 1985. Mean TST was 10,373 mmol N m⁻² season⁻¹ ($\pm 4,207$ SD). There appears to be a seasonal trend to the TST data with highs in summers and lows in winters. These results match our expectation that biogeochemical activity increases in spring as temperature and light levels increase, reaching a maximum in summer, and then declining through the fall to a minimum in winter. One exception to this general pattern is the summer of 1986. It is lower than the previous spring and is surprisingly lower than that found in the other four years. The cause of this deviation is unknown. The Finn Cycling Index (FCI) was high in these models with a mean of 88% ($\pm 9\%$ SD). Though we used a different set of algorithms, our TST and FCI values appear similar to those reported by Christian and Thomas (2003), demonstrating analytic consistency. Further, they showed that the values of nitrogen cycling found in the Neuse River Estuary are some of the highest reported in the literature. While there appears to be some seasonality to FCI, its regression with TST does not explain much of the variation ($R^2 = 0.31$).

{INSERT FIGURE 2}

In summary, nitrogen fluxes in the sixteen seasons of the Neuse River Estuary analyzed here were large and varied in a seasonal manner consistent with ecological expectations. More surprising was the magnitude of nitrogen recycling in the estuary. TST and the cycling index provide the starting point for our analysis of indirect flows in this system.

3.1 INDIRECT EFFECTS IN THE NEUSE RIVER ESTUARY MODELS

Nitrogen flux in the Neuse River Estuary was dominated by indirect flows in all sixteen seasons (Figure 3). Indirect/Direct consistently exceeded unity, ranging from 9.9 in winter 1987 to 174.4 in summer 1987 (Figure 3A). Indirect/Direct is linearly associated with TST ($R^2 = 0.72$), indicating that it is influenced by variation in TST. The fractional decomposition of TST using equation (3) again shows the dominance of indirect flows (Figure 3B). In all sixteen seasons indirect flow was more than 80% of TST. This partition also hints at a strong similarity in the amount of nitrogen loading or boundary inputs and the direct flows in the system.

{INSERT FIGURE 3}

There were small but not significant seasonal and interannual variations in the indirect flow index (IFI), where indirect flows were normalized by TST (Figure 4). Seasonal means ranged from 0.98 (± 0.01 SD) in summer to 0.91 (± 0.06 SD) in winter (Figure 4A). Year class means ranged from 0.97 (± 0.02 SD) in yc1985 and yc1987 to 0.94 (± 0.07 SD) in yc1986 (Figure 4B). Winter and yc1986 were the most variable groups, as they contained winter 1987 which had the lowest IFI. This may be because winter 1987 had the highest loading of nitrogen, resulting from extensive rainfall that season, and shortest flushing time within the estuary (Christian et al., 1991, Christian and Thomas, 2000). A two-way ANOVA suggests that seasonal variation is significant at $\alpha = 0.1$ but not $\alpha = 0.05$, and there is no significant difference between year classes (Table 1). We used a multiple pairwise t-test with Bonferroni corrected p-values to examine the potential seasonal differences suggested by the ANOVA. As the seasonal variances were not equal, violating the assumptions of the traditional t-test, we used a modified test in which standard deviations are not pooled (Dalgaard, 2002). These results suggest that there are no significant differences between the paired seasons (Table 2). Thus, the marginal statistical

significant difference among seasons that appears in the two-way ANOVA probably results from unequal variances.

{INSERT FIGURE 4}, {INSERT TABLE 1}, {INSERT TABLE 2}

We were surprised at the relatively small amount of temporal variation in indirect flows when normalized by TST within the Neuse River Estuary. We expected more pronounced seasonal variation, increasing with biological activity in the spring, climaxing in summer and then declining to a minimum in the winter. This pattern occurs but the difference between seasons was small; all were over 90%.

3.2 DETERMINANTS OF INDIRECT FLOW

The first step of this analysis was to investigate the pairwise relationship between Indirect and 1) Boundary, 2) Direct, and 3) Cycled. An initial scatter plot of Boundary and Direct versus Indirect revealed no clear relationship with Indirect (Figure 5A). However, it did reveal a strong linear relationship between Boundary and Direct. When the regression was forced through the origin (by definition direct is zero if there is no boundary flow), it was $\text{Direct} = 0.96 * \text{Boundary}$ ($R^2 = 0.99$, $p < 0.001$; Figure 5B). Thus, boundary and direct flow were nearly identical in this model. This occurs because each model compartment has high transfer efficiency. Little nitrogen is lost from the system at each node, allowing most of the boundary inputs to pass into the model over paths of length one, which is how Direct was defined. There was also a strong linear relationship between Indirect and Cycled (Figure 6). The regression equation was $\text{Indirect} = 906 + 0.98 * \text{Cycled}$ ($R^2 = 0.99$, $p < 0.001$), where both coefficients were statistically significant. The large intercept suggests that a portion of indirect flow occurs without cycling. This is understandable as interaction chains can create indirect flows without cycling. In these models,

cycled flow by itself explains nearly all of the variation in indirect flow; a multiple factor investigation was unnecessary.

{INSERT FIGURE 5}

{INSERT FIGURE 6}

4. DISCUSSION

We make two primary contributions with this work. First, we used a sequence of seasonal network models to investigate the discrete-time dynamics of indirect flows. In its present form, the mathematics of NEA requires input data from a steady-state system. Due to this analytical constraint, NEA characterizes the organizational complexity of ecosystems, but not their dynamic complexity that is frequently of ecological interest. However, the seasonal networks we analyzed provide a temporal sequence of snapshots that begins to reveal system dynamics, much like constructing a motion picture film from a series of still frames. Contrary to our expectations, our results revealed no significant seasonal or interannual variation in indirect flow as a fraction of TST; it was constantly larger than 80%. While there are temporal changes in nitrogen loading and total nitrogen flux, the macro organization of the estuary ecosystem with respect to nitrogen flux was remarkably constant.

The consistency of IFI results from the overwhelming dominance of indirect and recycling flows in determining TST. There are several features of the Neuse River Estuary that contribute to this. First, boundary inputs are minor components of TST. Christian and Thomas (2003) calculated that TN loading averaged 2% of TST, ranging from <1% to the unusually high value of 8% during the winter of 1987. Second, the importance of indirect flows and cycling of nitrogen is directly related to differences in the time scales of physical and biological processes. The flushing time of freshwater is of the order of weeks to months with an average of about 7

weeks (Christian et al., 1991). The turnover of dissolved nitrogen due to biological uptake and release is of the order of hours to days (Boyer et al., 1994). Phytoplankton turnover occurs in days (Boyer et al., 1993). Thus, there is considerable opportunity for imported nitrogen to be cycled through biological components numerous times from entry to exit from the system (Christian and Thomas, 2003). Third, the biological activity is largely microbial and potentially rapid, resulting from planktonic uptake and release of nitrogen and benthic biogeochemical processes. Cycles with quantitatively important, and biologically mediated, indirect flows thus control the overall dynamics of nitrogen. Biological processing is highly variable among seasons and is such a dominant part of TST that the resultant indices of FCI and IFI show little variation.

Second, we evaluated the relative contribution of several system attributes to the development of indirect flow. Higashi and Patten (Higashi and Patten, 1986; Patten et al., 1990; Patten, 1991) demonstrated algebraically that indirect flows could be influenced by n , C , cycling, and direct flows, but this work did not evaluate the relative contribution of these variables or determine if it was a complete set. We used linear regression models to evaluate the factors most significant in determining indirect flows. This statistical analysis supported and extended our findings for an explanation of consistency in IFI and FCI. We discovered that in the sixteen Neuse River Estuary models cycled flow was indeed the most important factor in explaining variation in indirect flow. Boundary and direct flows were only important in that they are necessary for cycling to occur. Though indirect flows are composed of both cyclic and acyclic flows such that $IFI > CCI > FCI$, cyclic flows appear to be dominant in these models. This occurs because the model compartments have high transfer efficiencies with respect to nitrogen use; only a small fraction of nitrogen imports are immediately lost to the system boundary. In this study, we were unable to appraise the relative significance of the model structure, including

n, C, and network topology, as structure was constant. Unfortunately we cannot generalize from these observations – they are particular to our study system. However, they are the first results to begin to address this question.

Ultimately, the Neuse River Estuary was very retentive of nitrogen between spring 1985 and winter 1989. The system was dominated by internal, biological processes. If nitrogen loading had been significantly reduced during this period, this ecosystem likely would have remained eutrophic for an extended period of time. If we assume that the system organization remained similar in 1997, we would expect the legislated reduction of nitrogen loading to have little immediate effect, though this action may be important for long-term change. This conclusion is consistent with that of Christian and Thomas (2003).

It is difficult to compare our results with previous reports of indirect flows determined by NEA for two reasons. First, previous publications usually do not report the same statistics we use in this paper. Higashi and Patten (1989) reported a measure of total indirect-to-direct flows for several ecosystem models taken from the literature. A five node model of energy flux ($\text{kcal m}^{-2} \text{y}^{-1}$) in a cold spring and a five node network of nitrogen flux ($\text{g N m}^{-2} \text{y}^{-1}$) in a Puerto Rico mountain rainforest had total indirect flow factors of 2.2 and 12.8 respectively (models reported in (Patten et al., 1976)). They also reported a total indirect flow measure for a six compartment oyster reef model of energy flux ($\text{kcal m}^{-2} \text{day}^{-1}$) as 3.3 (model from Dame and Patten (1981)). Unfortunately, they do not provide a clear description for how these total indirect flows were calculated. However, we suspect the calculation 1) is based on an alternate formulation for the indirect-to-direct flow ratio presented in Fath and Patten (1999) – $\text{Indirect/Direct} =$

$$\frac{\sum \sum (n_{ij} - i_{ij} - g_{ij})}{\sum \sum (g_{ij})}$$

, where i_{ij} are the elements of the identity matrix I, and 2) includes indirect

flows from both the input and output orientations. Using Fath and Patten's alternative formulation the indirect-to-direct ratios in the three models are 0.91, 6.18 and 1.53 respectively; when calculated as in equation (4) we found them to be 1.02, 6.14, and 1.58 respectively. Regardless of how calculated, the Indirect/Direct ratios for the Neuse River Estuary are substantially larger. Fath (2004) reported an indirect-to-direct ratio for 250 large-scale cyber-ecosystem models of trophic dynamics with 30, 60, 120, 300, or 600 nodes, with varying connectivity, cycling, and TST. His results, again using the alternative formulation, show that Indirect/Direct increases in these models with the number of nodes from approximately 8-10 for models with 30 nodes to 80-95 in models with 600 nodes. It also tends to increase with the Finn cycling index (FCI), though this had a restricted range (0.14 – 0.26) in these models. Given these results, the magnitudes of the Indirect/Direct ratio in the Neuse River Estuary models are quite surprising. Some of these very small models display much larger indirect flows than even the largest cyber-ecosystem models. We suspect that this difference is a reflection of the differences in compartment efficiencies and cycling, which result from distinctions between models of trophic processes and biogeochemistry. Christian et al. (1996) discussed the ramifications of the differences between trophic and biogeochemical networks. Biogeochemical networks, such as analyzed here, may be minimally dissipative, highly aggregated in biological nodes and disaggregated in chemical nodes, focused on microbial processes, and inclusive of inorganic components instead of treating them as external to the system (e.g., CO₂ in food web networks). These attributes generally foster cycling and resultant indirect flow.

The second difficulty however is perhaps more important. Our results show that the Indirect/Direct ratio increases linearly with TST. Thus, when we compare Indirect/Direct ratios between systems, we cannot be sure if we are identifying differences in indirect flows or

variation in TST. However, if we normalize the magnitude of indirect flow by TST as in the indirect flow index (IFI) we should remove the effects of TST variation. This creates an indicator of indirect flows that is more comparable across systems, similar in form to FCI or CCI. This should facilitate comparative ecosystem analysis of indirect flows in the spirit of Baird et al. (1991) and Krivtsov (2004).

Strong indirect influences in the Neuse River Estuary with respect to nitrogen, made possible by strong cycling, appear to make this system initially more resistant to external manipulations to manage the desired change of state (less eutrophic). In this sense, indirect flows seem to be a stabilizing force, making the system more resistant to external perturbations, an idea consistent with previous theoretical and empirical ecological investigations of nutrient cycling (DeAngelis et al., 1989 and references therein). However, this may be a short-term or transient dynamic. Systems tightly integrated or strongly connected by network indirect flows may ultimately be more vulnerable due to their interconnectedness (Barabási, 2002; Gunderson and Holling, 2002). The system transformation may take a long time to be fully expressed, but we suspect that systems like the Neuse River Estuary that are highly integrated will be more sensitive to both external and internal perturbations including internal changes such as alterations in a lower hierarchical level like an individual node becoming more or less dissipative (efficient) or disappearing completely. This is because system integration through indirect flows creates what is known as the multiplier effect in economics (Samuelson, 1948). The multiplier effect is indicated by the number of times an input is expected to be used or travel through the system before it exits. Ecologists have termed this average path length (Finn, 1976) or more recently network aggradation (Jørgensen et al., 2000). We expect perturbations to be multiplied more in more integrated systems, making them more sensitive or less stable. This increasing sensitivity

with increasing connectedness has been described as a loss of ecological resilience in the general model of system transformations or adaptive cycle at the heart of Panarchy Theory (Holling, 1973, 2001; Gunderson and Holling, 2002). This potential loss of stability is one argument for a modular or hierarchical arrangement of system components, allowing the potential benefits of increasing system integration while localizing instabilities (Simon, 1962; Krause et al., 2003). This potential increased sensitivity to perturbations suggests that targeted attacks on the most well connected nodes (as in Albert et al., 2000; Dunne et al., 2002) or nodes with the largest throughflow might rapidly generate system wide changes. If true this suggests that management actions to increase the nitrogen dissipation from Sediment (most well connected) or PN-Hetero (most throughflow) might initiate a more rapid system transformation. Control analysis (Schramski et al., In press) of this system, however, suggests that NO_x may be a better management target. Further investigation is required to understand these conflicting possibilities.

In conclusion, nitrogen flux in the Neuse River Estuary between spring 1985 and winter 1989 was dominated by indirect flows. The indirect flow index – total indirect nitrogen flow normalized by total system throughflow – showed little seasonal and no significant interannual variation. Nitrogen cycling was the overriding factor determining the magnitude of indirect flows. The Neuse River Estuary was highly nitrogen retentive, ensuring that the same atom of nitrogen revisited individual compartments multiple times before exiting the system. Our analysis suggests that because this system is dominated by internal processes management efforts focused on decreasing nitrogen loading would not have rapidly impacted the eutrophic state of the estuary. In this sense indirect flows seem to be a stabilizing force, making it more resistant to external perturbations. This may be a transient effect, however, as indirect flows may make the

system more sensitive in the long-term, as perturbations are propagated and potentially magnified. This prediction may currently be in operation as the ecosystem commonly experiences periods of anoxia and hypoxia with subsequent fish kills linked to the substantial microbial processing of energy (Baird et al., 2004).

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7. TABLES

Table 1: Results of two-way ANOVA indicating temporal variation (seasonal and interannual) of indirect flow index (IFI)

source of variation	df	SSE	MSE	F value	Pr(>F)
Season	3	0.012119	0.00404	3.67	0.05637 •
Year Class	3	0.002369	0.00079	0.7174	0.56616
Residuals	9	0.009906	0.001101		

• indicates significance at $\alpha = 0.1$ level.

Table 2: Results of a pairwise comparison (t-test with non-pooled SD) of seasonal mean indirect flow index (IFI) indicating no significant differences. Values in the table are Bonferroni corrected p-values.

	Fall	Spring	Summer
Spring	1	-	-
Summer	0.89	0.52	-
Winter	0.81	1	0.55

8. FIGURE LEGENDS

Figure 1: Nitrogen cycling model of the Neuse Estuary (modified from Christian and Thomas (2000)).

Figure 2: Seasonal total system throughflow (TST, $\text{mmol N m}^{-2} \text{ season}^{-1}$, left axis) and proportion of total system throughflow due to cycling (Finn Cycling Index, FCI, right axis) in the Neuse Estuary from spring 1985 to winter 1989. The mean cycling index was 0.88 (± 0.09 SD) and the mean total system throughflow was $10,373 \text{ mmol N m}^{-2} \text{ season}^{-1}$ ($\pm 4,207$ SD).

Figure 3: Indirect effects in sixteen seasonal models of nitrogen cycling of the Neuse River Estuary (Spring 1985 to Winter 1989). A) Ratio of indirect-to-direct flow partitions of TST. In all seasons, the Indirect/Direct ratio is substantially greater than one (marked by thin horizontal line), indicating the dominance of indirect effects. B) Seasonal partition of TST into boundary, direct, and indirect flow components.

Figure 4: Temporal variation in indirect flow index (IFI = Indirect/TST). A) Seasonal. B) Interannual, based on year classes grouping 4 sequential seasons to form a year class (i.e., $\text{yc1985} = \{\text{spring 1985, summer 1985, fall 1985, and winter 1986}\}$). There are no statistically significant differences between seasons or year classes.

Figure 5: Relationship between flow types in 16 seasonal nitrogen cycling models of the Neuse River Estuary (1985-1989). A) Indirect flow shows no clear relationship with either boundary or direct flow; however, B) there is a strong linear relationship between boundary and direct flows ($\text{Direct} = 0.96 * \text{Boundary}$, $R^2 = 0.99$, $p < 0.001$).

Figure 6: Relationship between indirect and cycled flows in the 16 seasonal nitrogen cycling models of the Neuse River Estuary (Indirect = $906 + 0.98 \cdot \text{Cycled}$, $R^2 = 0.99$, $p < 0.001$).

Figure 2

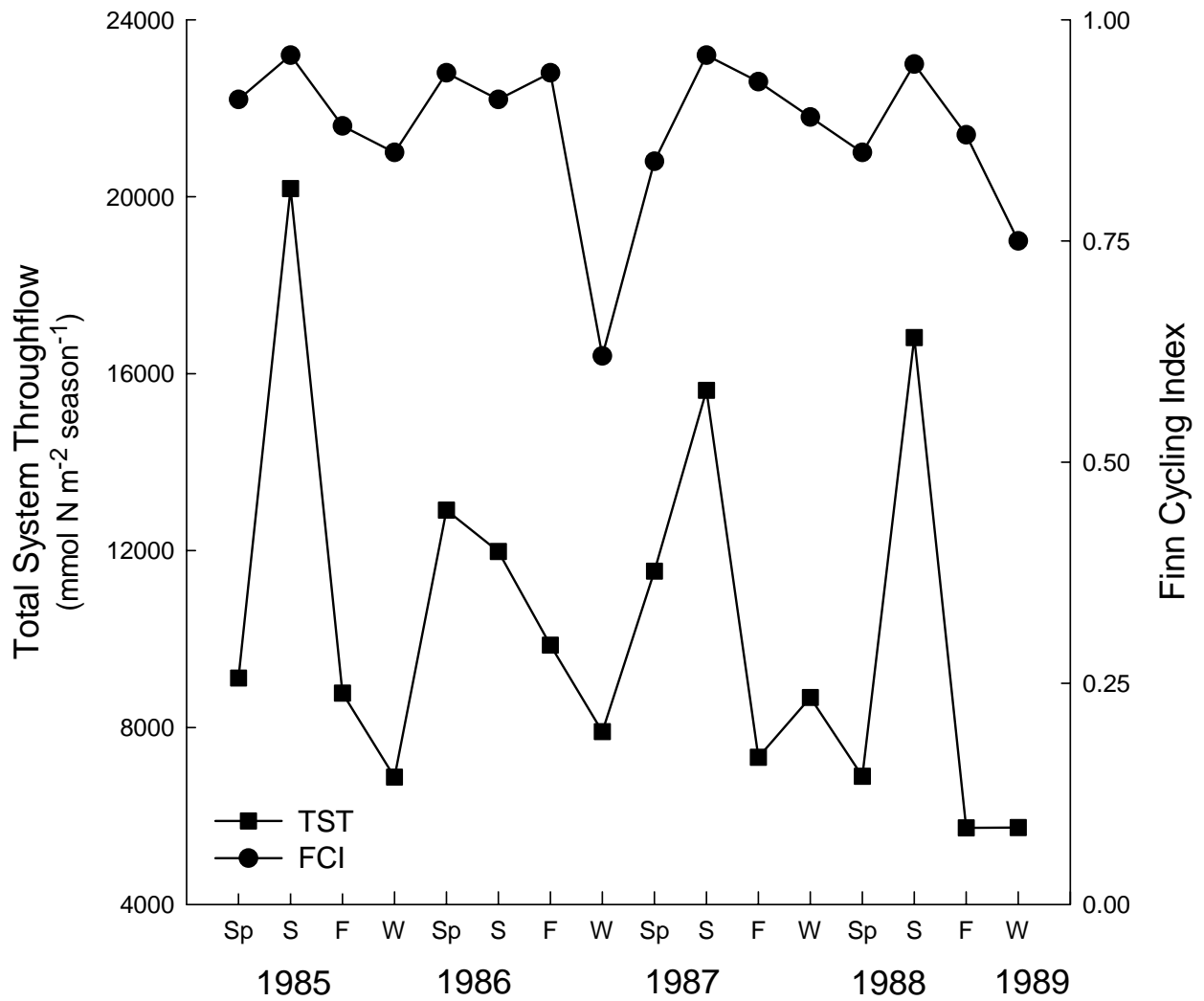


Figure 3

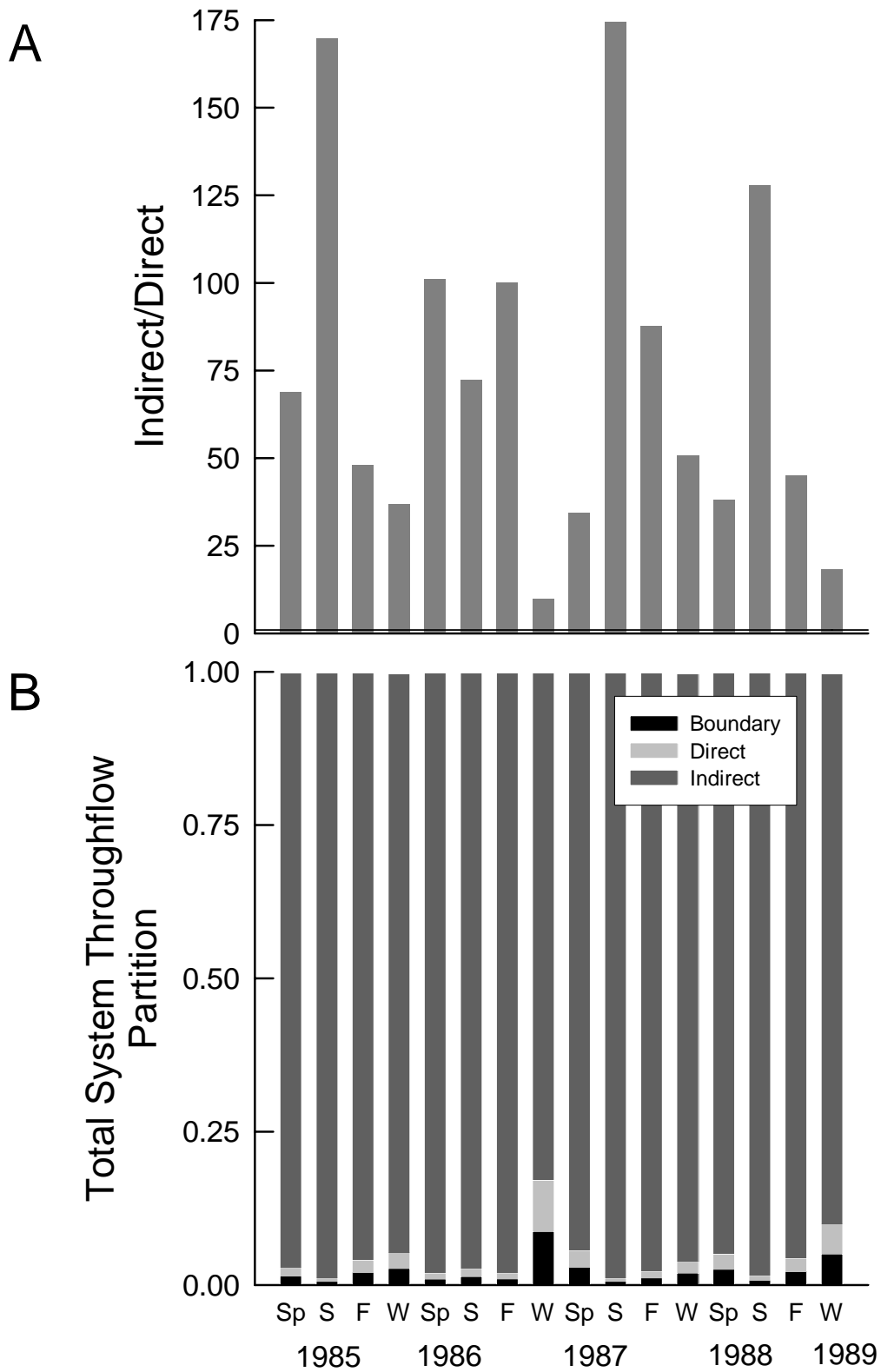


Figure 4

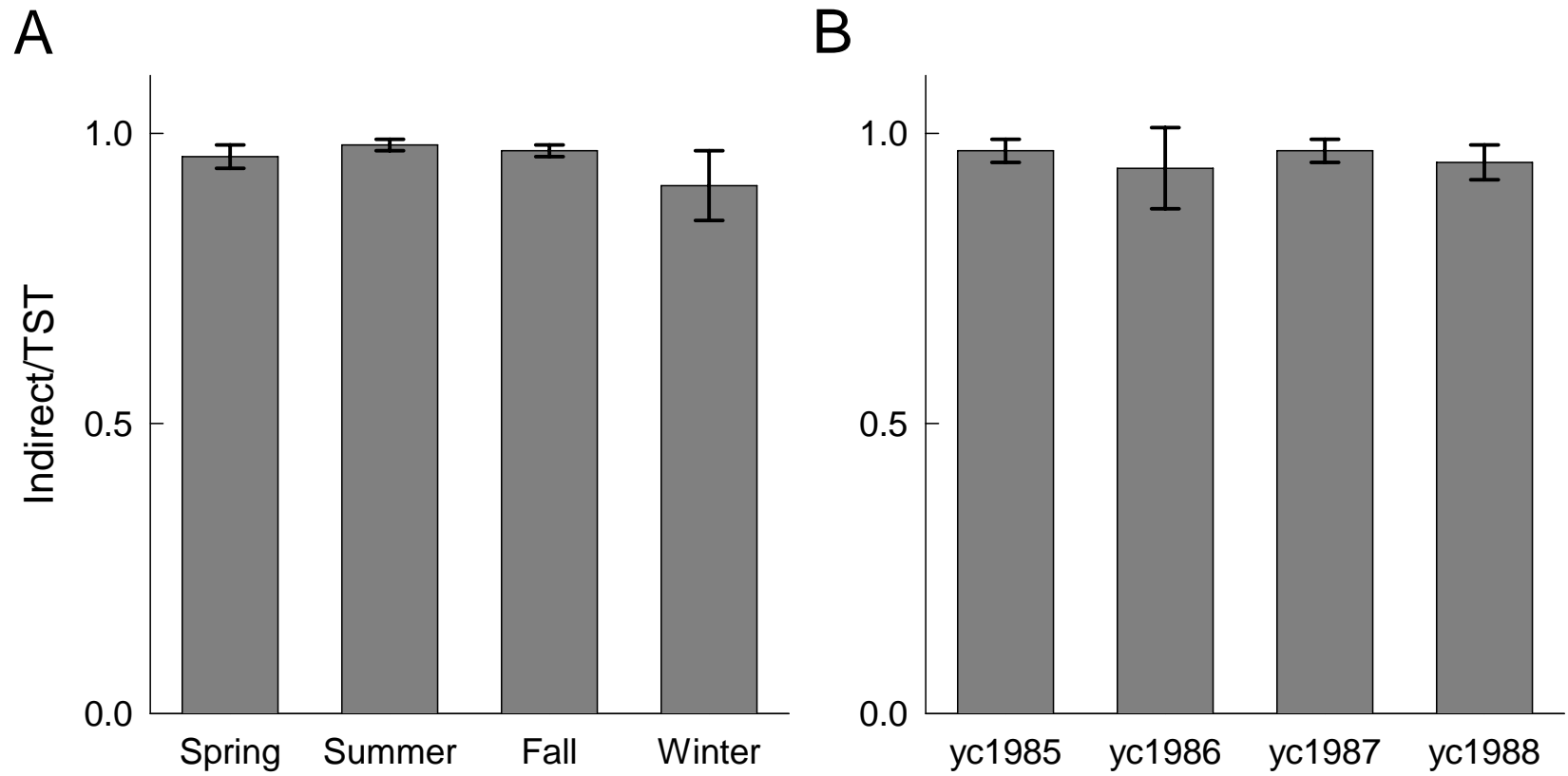


Figure 5

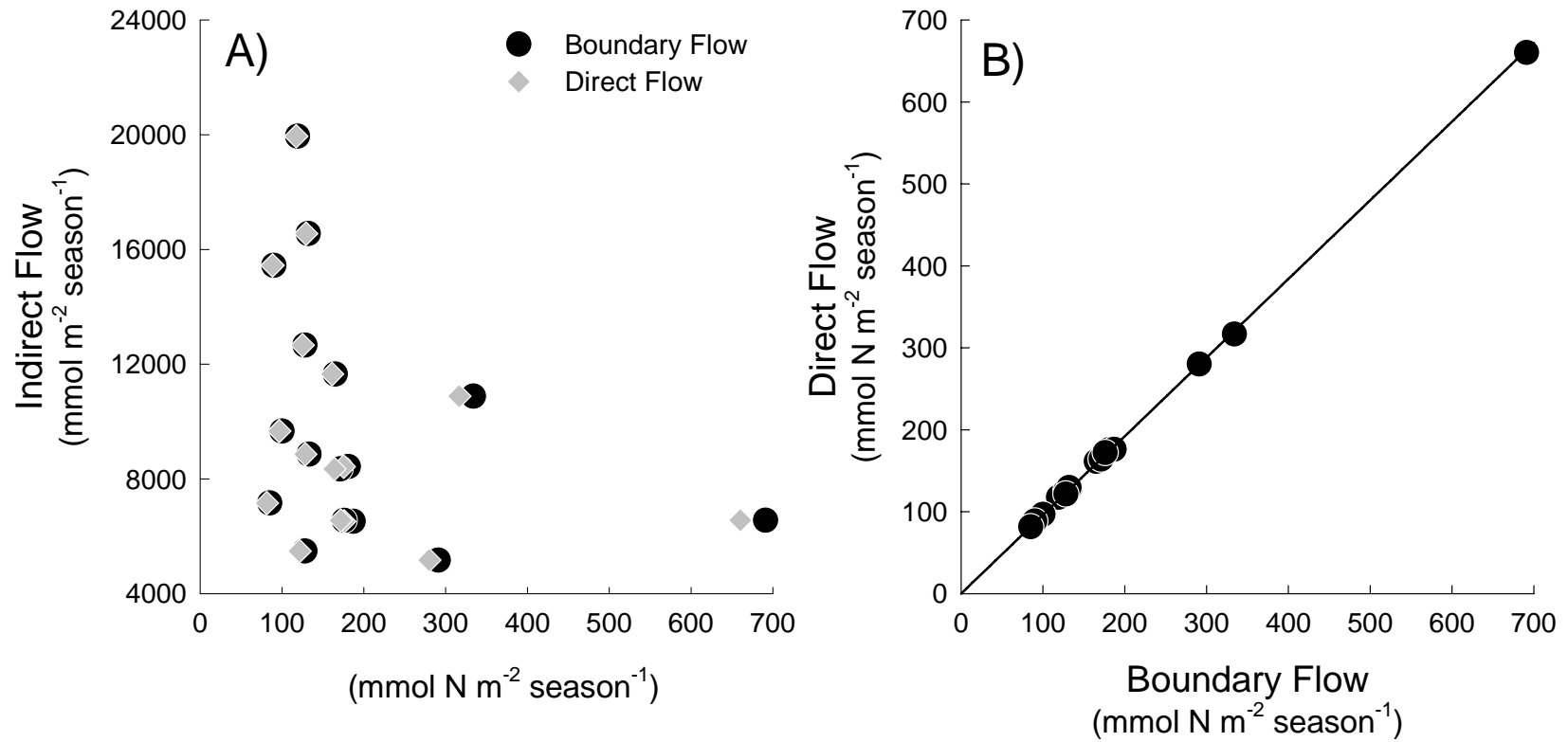


Figure 6

