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Network Analysis of Trophic Dynamics in South Florida Ecosystems, FY 96: The Cypress Wetland Ecosystem

Robert E. Ulanowicz, Cristina Bondavalli, Michael S. Egnotovich

University of Maryland System, Chesapeake Biological Laboratory, Solomons, MD 20688-0038

E-mail: ulan@cbl.umces.edu
Tel: (410) 326-7266
FAX: (410) 326-7378

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EXECUTIVE SUMMARY

A 68- component budget of the carbon exchanges occurring during the wet and dry seasons in the cypress wetlands of South Florida has been assembled. These networks of exchange will serve as independent benchmarks against which the performance of the ATLSS multi-model, now under construction, will be assessed. During the construction of these networks, it soon became clear that the received wisdom, that these systems are driven by cypress litterfall, is simply not true. Less than half the carbon reaching the higher trophic levels has spent any time in the form of detritus. Production by the understory of vines, epiphytes and aquatic vegetation play the key roles in sustaining the system, and phytoplankton is especially important during the dry season. The structure of the lower trophic level ATLSS module for the cypress wetlands will need to be revised in the light of these new findings.

The middle trophic level fish and amphibians appear to exhibit the highest trophic efficiencies found in the cypress ecosystem. Taxa at either end of the trophic chain appear less efficient by comparison. The result is a peak in trophic efficiency at trophic level four. The trophic levels of most taxa do not change appreciably between seasons. Most dietary replacements occur at the same trophic levels. In fact, the entire trophic structure does not change much between seasons, although the overall system activity during the dry season falls by some 25%.

One may employ the contributions by the various taxa to the overall measure of system ascendency to create an index of that compartment's "intrinsic value" to overall system performance. These new criteria nicely spotlight the potential values of rare and endangered species, such as the Florida panther, to system functioning.

Relatively little cycling takes place in the cypress ecosystems, even by comparison with physically more open systems, such as the Chesapeake estuary. What recycle as does occur, however, is exceedingly complex. In particular, the predation on eggs and juveniles of higher trophic elements by lower level species complicates the cycling structure enormously and provides tens of millions of new pathways for recycle. Such "ovi-predation" has been neglected in most trophic budgets, but it could be of enormous significance in forecasting the results of system impacts.

Finally, ecologists are accustomed to thinking that the norm for this ecosystem occurs during the wet season, because water level appears to be the limiting factor for the dominant vegetation, the cypress trees. Network analysis reveals, however, that the system is actually somewhat more organized during the dry season. Viewed with this as background, the high water levels of the wet season appear more in the light of a defining stress to the ecosystem.

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1. RATIONALE

A primary goal of coordinated research on South Florida's environmental resources is to understand those communities as whole ecosystems. Toward that end, the Across Trophic Levels System Simulation (ATLSS) project is an attempt to simulate the interactions of the various elements of wetland biotic communities within the framework of a single, encompassing computational scheme.

The resulting ATLSS model is one of the most complex and sophisticated models ever attempted. It will consist of simulation modules of varying, and often very high complexity that represent the important components of all the wetland ecosystems of South Florida. It follows that the output from ATLSS will be exceedingly complicated, and it may not be a straightforward task to elucidate the causal origins of any particular model behavior. Such uncertainty could become problematical, especially if the initial trials of ATLSS should behave "pathologically" (as is highly probable during the initial runs of such a complex model). Even should outputs not appear unrealistic, the difficulty remains that there exist no precedents for evaluating how well such a "multi-model" performs as an analog of the real system. I.e., there are no set protocols for "calibrating" such complex simulations. ATLSS, therefore, requires a partially independent benchmark against which one may gauge the plausibility of its outputs; and, towards that end, ATLSS investigators have chosen to create a suite of trophic flow networks that estimate material exchanges in the ecosystems being modeled. These will serve as calibration standards. In addition, these networks will be analyzed by a set of quantitative methods called Network Analysis (NA) that will serve as a guide for calibrating and debugging the initial modeling trials.

Trophic flow networks are graphical and mathematical depictions of the answers to the questions, "Who eats whom, and by how much?" Typically, diagrams of flow networks are comprised of boxes that represent the major components of the ecosystem. The boxes are connected by arrows, which indicate the transfers of material or energy between the components. Usually, each arrow is labelled with the magnitude of its transfer as averaged over a prescribed period of time.

Accordingly, the University of Maryland contingent of ATLSS investigators is assembling very detailled networks of carbon exchanges as they normally occur in the ecosystems of the South Florida wetlands. Networks consisting of some 60 - 70 important compartments are being estimated for each of four habitats, using existing data and ongoing field work. Separate networks for wet and dry seasons are being created for the ecosystems of the forested wetlands, the gramminoid marshes, the mangrove estuaries, and the shallows of Florida Bay. Each network will be a snapshot of the trophic flows and biomasses as averaged both over the hydroperiod in question and over the spatial domain of that particular biotope.

Analyses are to be performed on the resulting networks at several scales. The key questions that can be answered for any fully- quantified trophic network include: (1) To what extent does each taxon depend upon (or contribute to) all other taxa over all trophic pathways, both direct and indirect? (2) What are the efficiencies with which material is being transferred up the trophic ladder? (3) What are the pathways by which material is being recycled within the system? and (4) What is the current organizational status of the ecosystem? Any or all of these answers can be used to debug an ATLSS model that is not performing realistically.

Below, we present the estimation and analysis of the first of these four habitats -- the cypress wetland ecosystem. In the ensuing two annual reports we will present the corresponding results for the networks of Florida Bay, the estuarine mangroves, and the gramminoid wetlands (or Everglades proper.).

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2. STUDY AREA

2.1 Physical Characteristics

The 295,000 hectare wetlands of the Big Cypress Natural Preserve and the adjacent Fakahatchee Strand State Preserve in southwest Florida have been described by the US Forest Service (1996) as a flat, gently sloping limestone plain. During the rainy season (June through September) water flows slowly southward over this plain into the mangrove swamps bordering the Gulf of Mexico. This flow rate, however, is slower than what occurs in the sheet flow that originates from Lake Okechobee and flows southwestward through the (mostly) Cladium-dominated (gramminoid) prairies. During low water periods there may be no discernible flow through the cypress wetlands. In places, the flow of water has cut channels into the limestone, allowing deep organic soils to develop. These channels, or drainage sloughs, are occupied by tall, dense, elongated swamp forests that stand out on the horizon in contrast to the open terrain that borders them. The local term for this type of elongated swamp is "strand."

Another type of deepwater, cypress-dominated swamp, is called a "dome". Cypress domes are generally small in size, usually 1 to 10 hectares and consistof poorly-drained to permanently wet depressions that are dominated by pondcypress. They are called "domes" because, when viewed from the side, the larger trees in the middle and the smaller trees toward the edges present a vaulted profile. This domed appearance has been attributed variously to a deeper deposit of peat in the middle, fire that is more frequent around the edges, or a gradual increase in water level that causes the dome to "grow" from the center outward. But a definite reason for this profile has not been determined yet, nor do all domes display the characteristic shape (Mitsch and Gosselink, 1993).

During periods of low water levels, water is impounded in numerous ponds. Elevation ranges from 3.6-12 m above mean sea level in the northern part of Big Cypress to sea level where it grades into mangrove swamps.

The climate of southern Florida is moist and mild; it is frost-free nearly all year. Mean annual precipitation is around 1,500 mm, 80 percent of which falls from May to October, creating distinct wet and dry seasons. Precipitation received in 1 year has ranged from 760 to 2,540 mm. Occasionally, drought in summer (normally the wet season) can result in complete cypress defoliation, which otherwise would not occur until fall.

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2.2 Vegetation

Baldcypress (*Taxodium distichum*) and the almost- indistinguishable pondcypress (*T. ascendens*) dominate the alluvial floodplain forests. Plant associates in cypress swamps vary with depth, duration, and frequency of flooding, soil type, geographic location, and stand density. Cypress domes and strands have few associates in the center; most of those present are shade-tolerant species of epiphytic bromeliads, orchids, ferns, and nettles, or aquatic macrophytes such as tall flag (*Thalia geniculata*) and arrowhead (*Sagittaria* spp.) Associates on the perimeter of cypress domes and strands include buttonbush (*Cephalanthus occidentalis*), redbay (*Persea borbonia*), sweetbay (*Magnolia virginiana*), magnolia (*Magnolia* spp.), cocoplum (*Chrysobalanus icaco*), dahoon (*Ilex cassine*), myrsine (*Myrsine florida*), southern bayberry (*Myrica cerifera*), Coastal Plain willow (*Salix caroliniana*), and Florida poisontree (*Metopium toxiferum*). Red maple (*Acer rubrum*), pond apple (*Annona glabra*), strangler fig

(*Ficus aureus*), water ash (*Fraxinus caroliniana*), swamp bay (*Persea palustris*), and paurotis palm (*Paurotis wrightii*) are frequently found in cypress domes and strands.

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2.3 Faunal Characteristics

Cypress swamps do not have a distinct fauna, but share many species with adjacent plant comunities. Most species and individuals spend only part of their lives in the swamp. Benthic invertebrates form the heterotrophic base of the food chain. A high diversity of invertebrates has been recorded for cypress domes and strands. This is strongly related to water quality. Parameters such as oxygen concentration and pH, play an important role in shaping benthic community (composition and abundance).

During summer, reptiles and amphibians dominate cypress swamp vertebrate communities, while in winter birds become more abundant. Reptiles and amphibians are prevalent in cypress swamps because of their ability to adapt to the fluctuating water regime. In addition, the relatively high winter temperatures allow them to remain active through the cooler seasons. Among amphibians, the ranid frogs showed the highest numbers: common species also included southern leopard frog (*Rana utricularia*), cricket frogs (*Acris* spp.), oak toad (*Bufo quercicus*), and green treefrog (*Hyla cinerea*). Two of the most interesting reptiles are the well known American alligator (*Alligator mississippiensis*) and the cottomouth mocassin (*Agkistrodon piscivorus conati*), a poisonous water snake. Other water snakes, such as several species of Natrax, are usually more important in terms of number and biomass.

The reason why bird densities are higher in cypress swamps during winter is due largely to the presence of wintering birds. Birds that use cypress swamps include wild turkey (*Meleagus gallapaio*), ibis (*Plegadis* spp.), double-crested cormorant (*Phalacrocorax auritus*), herons (*Ardea herodias*, *Butorides striatus*, *Nycticorax nyticorax*, and *Nyctorax violaceus*), snowy egret (*Egretta thula*), great egret (*Casmerodius albius*), anhinga (*Anhinga anhinga*), and belted kingfisher (*Ceryle alcyon*). The limpkin (*Aramus guarauna*) is a characteristic occupant of cypress swamps due to the availability of snails. Canopy- feeding passerines are common, but there usually are only few mid-story species, such as red-bellied woodpecker (*Melanerpes carolinus*), pileated woodpecker (*Drycopus pileatus*), tufted titmouse (*Parus bicolor*), and great crested flycatcher (*Myiarchus crinitus*). The wood duck (*Aix sponsa*) is common in the larger cypress domes that contain sufficiently large trees. Prothonotary warbler (*Protonotaria citrea*) is also a typical member of the cypress swamp avian community.

Most mammals occurring in cypress swamps occupy ecotones. Mammals include white-tailed deer (*Odocoileus virginiana*), gray fox (*Urocyon cinereoargenteus*), fox squirrel (*Sciurus niger*), raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis marsupialis*). River otter (*Lutra canadensis*) and bobcat (*Lynx rufus*) are common residents of large cypress domes. There are many rodents and shrews including short-tailed shrew (*Blarina brevicauda*), cotton mouse (*Peromyscus gossypirus*) and hispid cotton rat (*Sigmodon hispidus*), which nests in trees to avoid floodwaters. Away from the center of cypress domes one finds small mammals such as the marsh rabbit (*Silvilagus palustris*) in addition to species mentioned previously. Arboreal mammals include the eastern gray squirrel (*Sciurus carolinensis*), and several species of bats. Rare and endangered species, and species whose ranges formerly included cypress swamps, include mangrove fox squirrel (*Sciurus niger avicenna*), black bear (*Ursus americanus*), Florida panther (*Felis concolor*) and mink (*Mustela vison*).

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3. PARSING THE NETWORK

As with most analyses, some of the most important assumptions in Network Analysis are made at the very beginning. They concern decisions as to what the elements of the network will be and how these taxa are to be connected. In this project, these decisions are simplified somewhat by the requirement that the network be comparable to the ATLSS simulation. That is, each state variable of the ATLSS model must have a counterpart in the accompanying network.

Network analysis, however, can treat far more complicated webs of interaction than are possible using simulation modeling. Keeping the simulation dynamics of many coupled processes from becoming pathological is a difficult balancing act. Because NA does not deal explicitly with dynamics, far greater taxonomic resolution becomes possible with this form of analysis. As a result, some taxa in the ATLSS model will be represented by several compartments in the cypress network. In addition, compartments can be added to the network with relative ease. For example, the creation of an individual- based model for one of the less "charismatic" mammals, like opossum, would entail significant effort. As will be described below, it requires nowhere near as much work to include the opossum compartment into the quantified trophic web.

Although the primary purpose for creating the cypress networks is to serve as a calibration benchmark for ATLSS, it should be mentioned that the network and its ensuing analysis can also serve independent purposes. For example, some biologists will be curious to know how their particular species of interest, which might not appear in ATLSS, will fare under the proposed hydrological scenarios. With regard to trophic interactions at least, the results of NA should allow those investigators and managers to make some educated guesses about how the excluded population might change. For example, NA quantifies the direct and indirect trophic interactions of each compartment with all other compartments in the web. In particular, the stocks and activities of each compartment not appearing in ATLSS can be compared with all those that do participate through NA, and such coefficients and ratios as may result can be applied to the predicted outputs from ATLSS to estimate the accompanying trophic status of the non-included species. In other words, after calibration NA can serve to expand the scope of predictions from ATLSS.

From an ecological viewpoint virtually all the important trophic components (i.e., those comprising at least 5% of the standing biomass or activity) have been written into ATLSS. These include: macrophytes, periphyton, terrestrial invertabrates, crayfish, prawns, apple snail, piscivorous fish, planktivorous fish, frogs, lizards, snakes, turtles, salamanders, the American alligator, wading birds, and white-tailed deer.

It happens, however, that data exist to make at least crude estimates of the stocks and activities of a number of other ecosystem members. For example, there exist census figures on most of the mammals that occur in the cypress swamps (Environmental Impact of the Big Cypress Jetport, 1969; Sowde and Woodall, 1985; Smith and Bass, 1994) Using these figures it becomes possible to estimate the standing stocks of carbon in these populations; and, using techniques described in the next section, to approximate as well the magnitudes of their transfers with predators, prey and detritus. Hence, it was decided to include these "parallel" species into the NA.

One major lexical question involved how to treat the manifold species that comprise such functional groups as the heterotrophic microorganisms and the benthic meiofauna, for which data at the level of individual species are not available. As a result it was decided to create two general compartments called "living particulate organic matter (POC)" and "living sediment" to include these poorly resolved parts of the ecosystem. The "living POC" include bacteria, microprotozoa and zooplankton; while "living sediment" brings together bacterioplankton, microfauna and meiofauna.

In the end, the network consisted of a total of 68 separate components. Only those species closely associated with the dominant patterns have been retained in this model. Hence, only reptiles, amphibians, birds and mammals commonly found in cypress forest and mixed swamp forest made the final list of species. Some additional species have been included following suggestions by experts. Once completed, the list was aggregated somewhat according to criteria, such as species sharing same diet, available data and the goals of ATLSS. For example, most species to be included in ATLSS as individual-base models have been maintained as separate compartments in the network.

The final list of species, along with a very brief description of what they entail, includes:

1. Living Particulate Organic Carbon (See description above.)

2. Living Sediment (See description above.)

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3.1 Primary Producers

A description of the dominant primary producers is reported in the "study area" section of this report. They have been divided as follows:

3. Phytoplankton - A single compartment has been used as representative of the whole phytoplankton community, because available data relate only to aggregate clorophyll-a concentration.

4. Floating Vegetation - Such as pond lillies and duckweed

5. Periphyton - Most diatomaceous forms of algae

6. Macrophytes - Such as *Utricularia* and *Bacopa*

7. Epiphytes - Bromileads, orchids, ferns, etc.

8. Understory - Mostly forbs, such as redbay, willow and bayberry

9. Vines and associated Leaves - Such as strangler fig

10. Hardwood Leaves - From maples, bays and ashes

14. Roots - Roots found in the first 5-19 cm soil horizon have been included in this compartment.

Taxodium spp. are included as a separate compartment, because they comprise a major percentage of the total biomass and also serve as major source of detritus. Furthermore, the leaves and woody parts of the trees have been relegated to separate compartments to follow better the role of production by cypress and other trees in the domes and strands.

11. Cypress Leaves

12. Cypress Wood

13. Hardwood Wood

14. Roots - Roots found in the first 5-19 cm soil horizon have been included in this compartment.

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3.2 Invertebrates

The macro invertebrates of the cypress sytems were divided into five categories. Crayfish, apple snails, and prawns, appear as distinct compartments in order to distinguish their separate contributions to higher trophic levels, which are thought to be substantial.

15. Crayfish (*Procambarus alleni*)

16. Apple Snail (*Pomacea paludosa*)

17. Prawns (*Palaemonetes paludosus*)

18. Aquatic Invertebrates - This compartment includes all the other aquatic invertebrates not listed above; the most representative are:

Annelida (*Nais obtusa*), Arachnoida (*Hydrachna* sp), Amphipoda (*Hyalella azteca*), Isopoda (*Ascellus militaris*, *Lirceus lousianae*), Coeloptera (*Agabus* sp, *Bidessus* sp. *Halipus mulcheri*), Diptera (*Brillia alticola*, *Chaoborus albides*, *Chironomus* sp, *Glyptotendipes lobiferous*, *Goeldichironomus* sp *Polypedilum convictus*, *Procladius culiciformis Stichtochironomus exquisitus*, *Tanypus punctpennis T. stellatus,* Hemiptera (*Neocorixa snowi*), Odonata (*Anomalagrion hastatum*, *Enallagma triviatum*, *Erythrodiplax minscula*, *Ischnura posita*, *Libellula depressa*, *Orethmis ferraginea*, *Pachydiplax longipennis*) Mollusca *(Lioplax subcarinata*)

19. Terrstrial Invertebrates - Studies of terrestrial invertebrates in cypress systems are sorely lacking (especially for BCNP). Hence, no single species have been compartmentalized. The most representative groups are: Coeloptera (beetles), Non-chironomid diptera, Tricoptera (caddisflies), Turbellaria, Lumbriculidae (earthworms), Nematoda (roundworms), Odonata (dragon and damsel flies), Spiders, Mites, Collembola (springtails), Orthoptera (grasshoppers crickets), Psocoptera (bark lice), Homoptera (leafhoppers and aphids), Lepidoptera (moths butterflies), Hymemoptera (ants and bees), Centipedes, Millipedes, Psuedoscorpions.

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3.3 Fishes

The fish community has been partitioned into three components, based on feeding behavior and size. The grouping is based on Kushlan's (1976) catergorization of fish community structure. The three compartments are :

20. Small Fish, herbivorous and omnivorous. This is the largest of the three categories defined in the

fish community. The most representative species are: *Gambusia affinis* (mosquitofish), *Poecilia latipinna* (sailfin molly), *Heterandria formosa* (least killifish), *Cyprinodon variegatus* (sheepshead minnow), *Jordanella floridae* (flagfish), *Adinia xenica* (diamond killifish), *Erymizon succetta* (Eastern chubsucker), *Lucania goodei* (bluefin killifish), and larval fish of the two following compartments while they are herbivores and omnivores.

21. Small Fish, primarily carnivores. The most representative species are: *Fundulus confluentus* (spotfin killifish), *Fundulus chrysotus* (golden topminnow), *Fundulus seminolus* (Seminole killifish), *Notemigoneus crysoleucas* (Golden shiner), *Labidesthes sicculus* (brook silversides), *Notropis petersoni* (coastal shiner), *Notropis maculatus* (tailight shiner), and larval fish that are carnivorous.

22. Large Fish, primarily carnivores. The most representative species are: *Lepisosteus platyrhincus* (florida gar), *Ictaluris* sp. (catfish), *Micropterus salmoides* (large-mouthed bass), *Ennacanthus gloriousus* (blue spotted sunfish), *Lepomis gulosus* (warmouth), *L. macrochirus* (bluegill), *L. microlophus* (read ear sunfish), *L. punctatus* (spotted sunfish), *and Amia calva* (Bowfin).

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3.4 Reptiles

Reptiles have been devided into four different compartments:

23. American alligator - (Alligator mississippiensis)

24. Turtles - The most representative species are:

Florida snapping turtle (*Chelydra serpentina osceola*), Stinkpot or Common musk turtle (*Sternotherus odoratus*), Striped mud turtle (*Kinosteron baurii*), Florida red-bellied turtle *(Pseudemys nelsoni*), Florida chicken turtle (*Deirochelys reticularia chrysea*), Florida soft shelled turtle (*Apalone ferox*)

25. Lizards - The most representative species are: Green anole (*Anolis carolinensis*), Southeastern five-lined skink (*Eumeces inexpectatus*)

26. Snakes - The most representative species are: Florida green water snake (*Nerodia floridiana*), Florida banded water snake (*Neridoa fasciata compressicauda*), South Florida black swamp snake (*Seminatrix pygaea*), South Florida ribbon snake (*Thamnophis sauritus*), Eastern mud snake (*Farancia abacura*), Rough green snake (*Opheodrys aestivus*), Yellow rat snake (*Elaphe obsoleta quadrivittata*), Everglades rat snake (*Elaphe obsoleta rossalleli*), Florida kingsnake (*Lampropeltis getula floridiana*), Florida cottonmouth (*Agkistrodon piscivorus conati*)

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3.5 Amphibians

27. Salamanders - The most representative species are: Two-toe amphiuma (*Ampiuma means*), Greater siren (*Siren lacertina*), Everglades dwarf siren (*Pseudobranchus striatus belli*), Peninsula newt

(*Notophtalnus viridesens pianopicola*)

Frogs were subdivided into three components, based on size:

28. Large frogs

29. Medium frogs

30. Small frogs

The most representative species are:

Southern toad (*Bufo terrestris*), Oak toad (*Bufo quercicus*), Green tree frog (*Hyla cinerea*), Barking treefrog (*Hyla gratiosa*), Squirrel treefrog (*Hyla sqirrella*), Little grass frog (*Pseudacris ocularis*), Eastern narrow-mouth toad (*Gastrophryne carolinensis*), Southern leopard frog (*Rana utricularia*), Pig frog (*Rana grylio*), Florida chorus frog (*Pseudacris nigrita verrucosa*)

31. Salamander larvae. This compartments include the first stages of salamander life cycle

32. Tadpoles. This compartments include the first stages of frogs life cycle.

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3.6 Birds

33. Pelecaniformes - The most representative species are: Double crested cormorant (*Phalacrocorax auritus*) and Anhinga (*Anhinga anhinga*).

34. Anseriformes - The most representative species is the wood duck (*Aix sponsa*).

35. Vultures - The most representative species are: Turkey vulture (*Cathartes aura*) and Black vulture (*Coragyps atratus*).

36. Kites & Hawks - The most representative breeding species are:Swallow-tailed kite (*Elanoides forficatus*), Red-tailed hawk (*Buteo jamaicensis*), Red shouldered hawk (*Buteo lineatus*), Short-tailed hawk (*Buteo brachyurus*). The most representative nonbreeding species are: Cooper's hawk (*Accipiter cooperii*), Sharp-shinned hawk (*Accipiter striatus*), Broad-winged hawk (*Buteo platypterus*).

37. Galliformes - The most representative species is the turkey (*Meleagris gallopavo*)

38. Egrets -The most representative species are: Great egret (*Casmerodius albus*) and Snowy egret (*Egretta thula*).

39. Great Blue Heron - (*Ardea herodias*)

40. Other Herons - The most representative species are: Little blue heron (*Florida caerulea*), Green heron (*Butorides virescens*), Black-crowned night heron *(Nycticorax nycticorax*), Yellow-crowned night heron (*Nyctanassa violacea*).

41. Woodstork - (*Mycteria americana*)

42. White Ibis - (*Eudocimus albus*)

43. Gruiformes - The most representative specie is: Limpkin (*Aramus guarauna*)

44. Owls - The most representative species are: Great horned owl (*Bufo virginianus*), Barn owl (*Tyto alba*), Barred owl (*Strix varia*)

45. Caprimulgiformes - The most representative breeding species are: Chuck-will's-widow (*Caprimulgus carolinensis*) and Common nighthawk (*Chordeiles minor*). The most representative nonbreeding specie is Whip-poor-will (*Caprimulgus vociferus*)

46. Hummingbirds - The most representative specie is: Ruby-throated hummingbird (*Archilochus colubris*)

47. Woodpeckers - The most representative breeding species are: Pileated woodpecker (*Dryocopus pileatus*), Red-bellied woodpecker (*Centurus carolinus*), Downy woodpeaker (*Dendrocopos pubescens*). The most representative nonbreeding species is: Yellow-bellied sapsucker (*Sphyrapicus varius*).

48. Passiformes, onnivorous - The most representative breeding species are: Tufted titmouse (*Parus bicolor*), Mockingbird (*Mimus polyglottos*), Brown thrasher (*Toxostoma rufum*), Common grackle (*Quiscalus quiscula*), Cardinal (*Richmondena cardinalis*). The most representative nonbreeding species are: Tree swallow (*Iridoprocne bicolor*), Catbird (*Dumetella carolinensis*), Robin (*Turdus migratorius*), Cedar waxwing (*Bombycilla cedrorum*), Solitary vireo (*Vireo solitarius*), Rusty balckbird (*Euphagus carolinus*), Swamp sparrow (*Melospiza georgiana*).

49. Passiformes, predatory - The most representative breeding species are: Eastern kingbird (*Tyrannus tyrannus*), Great-crested flycatcher (*Myiarchus crinitus*), Purple martins (*Progne subis*), Carolina wren (*Thryothorus ludovicianus*), Blue-gray gnatcatcher (*Polioptila caerulea*), Loggerhead shrike (*Lanius ludovicianus*), White-eyed vireo (*Vireo griseus*), Prothonatary warbler (*Protonotaria citera*), Parula warbler (*Parula americana*), Pine warbler (*Dendrocia pinus*). The most representative nonbreeding species are: Eastern phoebe (*Sayornis phoebe*), Solitary vireo (*Vireo solitarius*), Rusty blackbird (*Euphagus carolinus*) and many other migrating warblers.

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3.7 Mammals

50. Opossum - (*Didelphis marsupialis*)

51. Shrews - The most representative specie is: Short-tailed shrew (*Balarina brevicauda*)

52. Bats - The most representative species is: Evening bat (*Nycticeius humeralis*)

53. Black Bear - (*Ursus amaricanus*)

54. Grey Fox - (*Urocyon cinereoargenteus*)

55. Racoon - (*Procyon lotor*)

56. Mink - (*Mustela vison*)

57. Otter - River otter (*Luntra canadensis*)

58. Florida Panther - (*Felis concolor*)

59. Bobcat - (*Lynx rufus*)

60. Squirrels - The most representative species are: Eastern gray squirrel (*Sciurus carolinensis*) and Fox squirrel (*Sciurus niger*)

61. Mice & Rats - The most representative species are: Cotton mouse (*Peromycus gossypinus*), Hispid cotton rats (*Sigmodon hispidus*), Rice rat (*Oryzomys palustris*), Florida water rats (*Neofiber alleni*)

62. Rabbits - The most representative specie is marsh rabbit (*Silvilagus paulstris*)

63. White-Tailed Deer - (*Odocoileus virginianus*)

64. Hog - Feral Hog (*Sus scrofa*)

65. Armadillo - (*Dasypus novemcinctus*)

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3.8 Detrital Compartments

66. Refractory Detritus - Refractory detritus represents organic matter that decomposes at a relatively slow rate. For this network we use the information reported in Dierberg and Ewel (1986), where the decomposition rate for refractory detritus is 0.17/yr.

67. Labile Detritus -Liable detritus is organic matter that decomposes at a faster rate. The decomposition constant in this case is 5.7/yr (Dierberg and Ewel, 1986).

68. Vertebrate Detritus - Some of the species listed in this network, primarily vultures, feed on carrion. In the economy of this ecosystem this mode of feeding turns out to be very singular. A third derital compartment consisting of vertebtate bodies just after death was created so as to avoid vultures feeding directly on living species and thus acting as a top predators.

The stocks and activities of all 68 compartments vary during the course of the year. Seasonality at this latitude, however, is marked more by variations in water level than by changing temperature. Thus, seasonality is depicted in the form of two separate networks -- one for the wet season (from June to November) when water levels are high and another for the dry season (December to May), when water levels are relatively low and the canopy is more sparse, due to the deciduous habit of the cypress trees.

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4. METHODS

After the "lexical" phase of model building, the next step involves connecting the selected compartments to one another via feeding and detrital pathways. This topology is determined from information about the diets of each taxon. But the purpose here is not merely to formulate a qualitative "foodweb". We wish to *quantify* the connections as well. Toward this end, it is useful to concentrate first on assessing the densities, or stocks of the particpating taxa. Knowing the concentration of biomass is the key to scaling all the activities of a particular population.

4.1 Estimation Techniques

The biomasses of some species are known with reasonable precision. For example, the number of animals per hectare is available for many of the compartments. As the standard units used in NA are grams of carbon per square meter, the available data had to be transformed to maintain dimensional consistency. Towards this end, information on the average weight (grams) of animals was gathered from technical manuals. The percentage of carbon per gram of dry weight was then combined with wet weight/dry weight ratio to calculate the biomasses in gC/m^2. In the case of primary producers, most sources report data on biomass in grams per hectare. In this case only the wet weight/dry weight ratio and the percentage of carbon per gram of dry weight (Jorgensen et al., 1986) were necessary to convert the biomass into the correct units.

The conversions for phytoplankton were a little more complicated. Data from the area of the Big Cypress National Preserve were given in micrograms of chloropyll-a per litre. To convert these figures into carbon a C/chl-a ratio of 50/1 was assumed as representative of living phytoplankton (Strickland, 1965). By assuming an average water depth for the wet and dry seasons (Duever et al., 1986), the number of liters of water per square meter could be calculated. Multiplying gC/l by l/m2, yielded concentrations in gC/m2. For living POC, biomass was reported in gC/l, and the same procedure used for phytoplankton was followed.

Once the biomass had been approximated, information was sought on the consumption rate (or primary production rate) per unit biomass of each species. Multiplying a biomass density by this factor establishes the total input to the compartment in question. At this point, if one has solid data on the dietary proportions of heterotrophs, the total input can be apportioned among the various prey and the magnitudes of those tranfers can be set. Unfortunately, the dietary components of some taxa are available only as a list of species. In such cases we had no other option but to apportion the total input to the several prey in proportion to the standing stocks of these prey.

The two networks were assumed to balance over each season. While this is unlikely to be the actual case, balance is required for the critical input/output phase of NA (described below.) Furthermore, assuming balance facilitates the estimation of many rates. For example, when a component is balanced, its total output can be equated to its total input, as just calculated. It remains to apportion this compartmental "throughput" among the output processes —respiration, excretion, natural mortality and losses to predation. Fortunately, respiration and excretion rates per unit biomass are available from the literature for most species, so that these outputs can be immediately established. Most of the losses to predation are reckoned from the predator (input) side, as described above.

At this point, the balance is almost complete. It remains to estimate the exchanges of carbon with the outside world. Exogenous imports occur in three different ways: (1) Carbon from the atmosphere may be fixed as biomass through the process of primary production. The magnitude of this import is assessed by multiplying the standing stock of the autotroph by its primary productivity per unit carbon, as

mentioned above. (2) Biomass may enter or leave the system advected by water flow into and out of the study area. These exchanges can be estimated from the overall water budget for the swamp (Duever et al. 1986), which includes figures for gross advective water exchange with the surrounding areas. Multiplying these water exchanges by the concentrations of those species suspended in the water column will provide an approximation for these exogenous transfers. (3) Biomass may enter and leave the system as animal populations migrate across the boundaries of the study area.

Migration applies to many animals species in the model, and especially to birds. Wading birds might nest on the trees of a particular dome but may feed elsewhere. Such feeding could be classified as an import to the system. Furthermore, different types of birds have different feeding techniques. For example, some need high water level and others, low. It may also happen that birds nesting outside of a particular dome come to the dome to feed. This activity would constitute an export from the system. Due to a lack of detailed information on these aspects of feeding, it has been assumed that such imports and outputs balance. That is, all the birds in the model are assumed to feed inside the cypress and none come form outside just to feed there.

The techniques for estimating all the flows entering and leaving each compartment now have been described. Of course, uncertainties inherent in these partially independent estimations will keep many of the compartments from balancing exactly. The degree of imbalance can be computed by entering the existing flow estimates into a spreadsheet format. (EXCEL[TM] was used for this purpose.) One may compare marginal sums of inputs and outputs to identify those compartments that are most out-of-balance. The investigator has several options for treating an imbalanced compartment. If the imbalance is severe, it is probably best to recheck the sources and the arithmetic. Failing the discovery of an error, one might search for other references to cross-check the data being used.

If no amendments to a compartmental budget can be made on the basis of new data, some investigators prefer to bring the system nearly into balance by adjusting the least-well known flows. Others would rather maintain the flow proportions for each compartment as they appear in the literature and to rebalance the whole system under the covering assumption of linear, donor-control, which always maintains positive flows (Ulanowicz 1989) In this study all compartments could be balanced to within a few percent using literature values, and final balance was achieved using the program DATBAL, which assumes linear, donor control.

The resulting networks are too large and complicated to display easily as illustrations. Even a matrix representation of one such network spans several pages and is cumbersome to use. For these reasons, we have decided to present our detailed results in hypertext format. The user is strongly urged to access the results over the World Wide Web at <http://www.cbl.cees.edu/~bonda/ATLSS.html>.

There one may follow simple instructions to locate the estimated value of any stock or flow in either the wet or dry season. Furthermore, the entire rationale and associated references pertaining to the estimation of any particular value have been documented in hypertext. By pointing and clicking one may examine a trophic flow network in minute detail never before available for a network of such size and complexity.

The authors feel that this format for disseminating the network results should have important benefits for ecosystem science in general and for the visibility of the ATLSS endeavor in particular. We are aware of no other single source where the structural elements of an entire ecosystem can be examined and scrutinized so readily. Even if a user has no idea of the benefits of NA, he/she can begin with the species that interests them most and trace the sources and fates of material in that compartment -- simply by pointing and clicking. The presentation also makes it easier to critique the networks, and online suggestions for improvements and amendments are welcomed.

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4.2 Network Analysis

4.2.1 Background

Sometime during the mid-1970's it became apparent that ecological modeling in the form of a set of coupled, deterministic differential equations was a problematical undertaking that required support from other, independent methods for systems analysis. In the search for parallel methods of describing the behavior of total ecosystems, various computations performed on the underlying network of trophic flows have figured prominently (SCOR, 1981).

The original impetus for diverting attention from dynamics and concentrating analysis on flow structure came from the field of economics, where success in elucidating indirect economic effects had been achieved by manipulations on matrices of economic flows (Leontief, 1951; Hannon, 1973). Thereafter followed a number of other topological treatments of the underlying flow graph (e.g., Finn, 1976; Levine, 1980; Patten et al., 1976; Ulanowicz and Kemp, 1979). Eventually, Ulanowicz collected most of the methods for analysing flow networks into a single executable package, called NETWRK (Ulanowicz and Kay 1991)

Four types of analyses are performed by NETWRK. First, so- called input- output structure matrices are calculated. These allow the user to look in detail at the effects, both direct and indirect, that any particular flow or transformation might have on any other given species or flow. Next, the graph is mapped into a concatonated trophic chain (after Lindeman 1942). Then all the simple, directed biogeochemical cycles are identified and separated from their supporting dissipative flows. Finally, global variables describing the state of development of the network are presented. NETWRK and its accompanying documentation may be downloaded from the WWW at <http://www.cbl.cees.edu/~ulan/ntwk/network.html>.

In addition to NETWRK, a package called IMPACTS was used to gauge both the positive and negative, direct and indirect impacts that heterotrophic predation may cause. The method was described in Ulanowicz and Puccia (1990). Of particular interest is how negative impacts at one level can ramify to become positive indirect effects.

The data required to run either of these programs have already been discussed. Above it was detailled how, for each compartment, it is necessary to know: (1) all the inputs from outside the system, (2) all the various inputs flowing from other compartments of the system, (3) all the outputs which flow as inputs to other compartments, (4) all exports of useful medium outside the system, and (5) all rates of dissipation of medium. Each of these flows can be represented by a positive scalar element of a matrix or a vector; the absence of a flow can be represented by a zero.

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4.2.2 Input/Output Analysis

The initial section of the NETWRK package is founded upon an ecological variation of input-output

analysis. So- called "total contribution coefficients" (Szyrmer and Ulanowicz 1987) are calculated that describe exactly what fraction of the total amount leaving compartment i (prey or row designation) eventually enters compartment j (predator or column designation) over all pathways, both direct and indirect. Alternatively, the "total dependency coefficients" portray the fraction of the total ingestion by j which passed through compartment i along its way to j. The columns of this matrix are particularly useful in that they portray the "extended diet" of the species in question (or, correspondingly, the trophic "pyramid" that underlies each heterotroph.) As we hope to demonstrate, such indirect ratios can provide valuable information about how a system is functioning.

As an example of indirect diet coefficients, we consider the lizard compartment in the cypress swamps. These reptiles feed almost entirely on terrestrial invertebrates, so that the

"total dependency coefficients" of lizards on this the latter compartment is 100%. Because Terrestrial invertebrates feed, among other things, upon compartment 8, the understory, contributions from 8 will pass to the lizards through the invertebrates. This indirect contribution to lizards is about 20.6%. Some of the same material that was present in the understory, eventually became terrestrial invertebrates, and hence the sum of the numbers down a column in the "total dependency matrix" usually exceeds 100%.

Hannon (1973), Finn (1976), Levine (1980) and Patten et al. (1976) give various examples of how one may employ input-output analysis. One highly useful such application is the decomposition of the graph according to each input. That is, the eventual fate of each of the nonzero inputs to the system is traced independently of the other inputs to the system. Not only does this decomposition portray the isolated effects of the various inputs, but these sub-networks can be linearly recombined to recreate what the effects of any other combination of inputs would be, if the flow structure were kept the same.

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4.2.3 Trophic Aggregation

The second section of ourput from NETWRK interprets the given network according to the trophic concepts of Lindeman (1942). Of course, it is impossible to relegate omnivorous heterotrophs entirely to a single trophic level, but Ulanowicz and Kemp (1979) indicated how input-output techniques could be used to apportion the activities of omnivores among a series of integer trophic levels. This method has been expanded to include the effects of biogeochemical cycles by Ulanowicz (1995a).

In order for trophic aggregation to be meaningful, it is necessary that trophic pathways among living compartments remain finite in length, otherwise one is forced to interpret an infinite regress of trophic levels. Fortunately, Pimm (1982) states that cycles among living taxa are rare in ecosystem networks (although we shall encounter some interesting exceptions in the cypress networks.) The absence of such feeding cycles avoids trophic pathways of infinite length. As a preliminary to trophic aggregation, therefore, all cycles flowing only through active feeding links are first removed from the network. So long as the Finn cycling index for such heterotrophic cycling (see below) remains sufficiently small (say, below two percent or so), no appreciable distortion of results should ensue. The 2% requirement is more than satisfied by the cypress networks.

When the fractions by which each component feeds at a particular trophic level are weighted by the value of that trophic level and the results are summed, one arrives at the effective trophic level for the given species (Levine 1980) For example, if a species or compartment is receiving 15 units of medium

along a pathway of length 2 and 5 units along a pathway of length 3, then it is acting 75% as a herbivore (trophic level=2) and 25% as a carnivore (level=3). The effective trophic position becomes (.75 x 2)+ (.25 x 3)=1.75. It is often interesting to compare the average trophic position of species under different circumstances (as is done below for the wet and dry seasons.)

The section on trophic aggregation culminates with the partitioning of activity into a trophic "chain" of transfers along aggregations of heterotrophs. Each such integer aggregation feeds back into detrital return loops. Such a depiction of the underlying trophic dynamics has been termed "canonical" by Ulanowicz (1995), because any ecosystem can be mapped into this equivalent and simple form to allow the relative magnitudes of corresponding flows to be compared directly.

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4.2.4 System-Level Indices

The next section of output from NETWRK provides values for global attributes of the network that were defined by several information theorists to gauge the pattern of development in ecosystems (Ulanowicz, 1980,1986; Hirata and Ulanowicz, 1984; Ulanowicz and Norden, 1990). One begins by calculating the "total system throughput", or the gross sum of *all* transfers, to act as a measure of the size of the system. Multiplying the total throughput by the system indeterminacy (according to the Shannon Wiener formula) of the individual flows yields what has been termed the "development capacity" of the system. This quantity serves as an upper bound on the ascendency, which is a measure of the network's potential for competitive advantage over other real or putative network configurations. Ascendency is the product of a factor of size (total system throughput) times a factor representing the coherence of the flows (the average mutual information of the flow structure.)

The difference between the realized structure and its upper bound is the overhead (Ulanowicz, 1986) Overhead has conflicting interpretations. On one hand, it is a catchall for the system's innefficiencies in processing material and energy. What is a disadvantage under benign conditions can turn in the system's favor when it is perturbed in some novel way. Then, the overhead represents a "strength-in-reserve" of degrees of freedom which the system can utilize to adapt to the new threat. Overhead is generated in any of four ways: there is overhead due to indeterminacy of imports, exports, dissipations (respirations), and about which of several parallel pathways flow will proceed between any two nodes (redundancy.) The fractions of the development capacity encumbered by the ascendency and by each of the overhead components provide a profile of the structural composition of the system that often is useful for assessing the organizational status of a system.

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4.2.5 Cycles

Most networks of ecosystem flows contain cycles of material or energy, and the magnitude and structure of these cycles is fully described by NETWRK. The program enumerates all of the simple cycles in the given matrix of exchanges (an enormous task in the case of the cypress networks.) Furthermore, the simple cycles are grouped into "nexuses" of cycles all of which share the same "weak arc." A weak arc is defined here as the smallest flow in a given directed cycle. The assumption is that the weak arc is the

limiting or controlling link in a cycle, and that by grouping according to critical links, one identifies the domain of influence for each weak arc. Presumably, any change in a weak arc will propagate throughout its associated nexus. The nexuses are listed roughly according to ascending order of the magnitude of their defining weak arcs.

The cycles are then subtracted from the network in a fashion described in detail by Ulanowicz (1983). Briefly, the magnitude of flow in the smallest weak arc is distributed over the flows in that particular nexus and the resulting amounts are subtracted from each arc in that nexus. This process zeroes the weak arc, thereby eliminating all the cycles in that nexus, but it does not disturb the balance around any compartment, nor does it change any exogenous input, export or respiration. None of the remaining arcs of the nexus are driven negative. After that nexus has been removed, the next smallest weak arc is located; and nexuses are subtracted iteratively until all cycles have been removed from the network.

As each cycle is removed, the flow associated with that cycle is added to the magnitudes of other cycles of the same trophic length. The end result is a distribution of the magnitude of cycling according to the trophic length of cycles. This profile could be useful in assessing system response to perturbation. For example, cycling via the larger loops is often more sensitive to disturbance. The cycle distribution is then normalized by the total system throughput. Summing this normalized distribution yields the Finn cycling index, which is the fraction of total activity that is devoted to cycling (Finn 1976).

Finally, the separation of cycled from transient flow is reported in the form of separate matrices for each type of flow. The row sums and column sums of the matrix of aggregated cycles will always balance; no further reference to exogenous exchanges is necessary. The visual structure of the aggregated cycles existing in more complicated networks very often reveals separate domains of control in the network (e.g, Baird & Ulanowicz 1989) Finally, it should be remarked that the starting network has been neatly decomposed into an acyclic "tree" of dissipative flows and a wholly conservative nexus of cycled flows.

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4.2.6 Trophic Impacts

NETWRK treats only positive mass flows and does not consider the propagation of the negative effects that accompany predation. Ulanowicz and Puccia (1990) outlined how to treat the propagation of both positive and negative trophic effects, and their technique has been implemented in the algorithm, IMPACTS. For any particular component (designated as the "focal taxon"), IMPACTS provides a ranked listing of all the positive and negative impacts (both direct and indirect) upon that focal species. Also a ranked listing of all the direct and indirect trophic effects that focal species has upon all the other taxa is likewise presented. Of special interest are those predators that exert a direct negative impact upon a prey, but whose combined indirect positive influences more than compensate the prey for its direct losses. Such "beneficial predators" are more common than might be supposed and often highlight particular ecological roles that otherwise might have gone unnoticed. IMPACTS can be downloaded from <http://www.cbl.cees.edu/~ulan/ntwk/network.html>.

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5. RESULTS

5.1 Input/Output Analysis

Perhaps the most useful indices to result from the Input/Output section of NETWRK are the "total dependency coefficients" (Szyrmer and Ulanowicz 1987) or, more appropriately, the "indirect diets" of each taxon. By reading down the column of these dependency coefficients one notes the quantitative trophic history of material reaching that given taxon. For example, it is commonplace to think of forested wetlands as detritus-based ecosystems. The basis for this view is that the dense tree canopy does not allow a significant growth of understory (aquatic vegetation, periphyton, vines and epiphytes) so that litterfall, mainly from cypress, is the major source of energy for secondary producers. The total dependency coefficients calculated for the cypress swamps suggest that this picture is not entirely appropriate here. Dependencies on detritus (compartments 66, 67, 68, 1 and 2) are appreciable, but not as high as expected (Fig. 1).

Of the total amount of carbon reaching many top predator compartments, only a minor fraction transits through detrital pathways. In particular, for Florida panther, gray fox and black bear, the dependence on detritus is less than 40%, and the fraction for bobcat is extremely low. In addition, the total dependency matrix reveals that many species in this ecosystem are almost totally dependent on the *grazing* chain. White-tailed deer and squirrels, for example, receive almost no material from the detritus compartments (Fig. 2 and Fig. 3).

During the dry season, when the canopy is negligible, the importance of primary producers other than cypress, such as periphyton biomass and other subcanopy vegetation, grows considerably. Even during the high water period dependencies on these items are significant. Aquatic vegetation in considerable quantity can be observed in the middle of domes and strands where many big ponds provide holes in the canopy. We considered these open aquatic zones to be part of our forest wetland model. It should be noted that quantitative data on the subcanopy vegetation in the study site were not available, so the model was built by adapting information from the Everglades area. The adaptation of Everglades data to forested wetlands was guided by expert opinion (G. Dalrymple, J. Browder, J. Snyder), and personal observations.

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5.2 Trophic Impacts

The results of impact analysis reveal that primary producers have a surprisingly strong influence on top carnivores. The overall positive impact on bobcats by their prey is 94%, while the total positive impacts of primary producers on the same species is almost as great (91%.) Similarly, Florida panther benefits directly from prey and indirectly from primary producers by 90% and 74%, respectively. One of the main reasons behind these results is the importance of deer and other herbivores in the diets of these two top carnivores.

It is obvious that indirect effects can play important roles in ecosystem dynamics. Compartment 2, living sediment, for example, exerts a strong negative effect on the Florida panther, (Fig. 4). The same applies to black bear (53) and bobcat (59). The direct negative effects of the latter compartments on panther are due to competition for food, as they share many elements of their diets with the Florida panther. The reason why compartment 2 has a significant negative impact on Florida panthers and Black bears (but

not on bobcats) is not as straightforward. Living sediment negatively affects a great number of components (53, 23, 24, 26, to name only a few), that are not directly linked with them. The most intuitive explanation for such impact might be the competition for common resources by these species with the invertebrates and fishes, which are an important source of food for many other compartments. But this would not explain the positive indirect role played by living POC, the other segment of the microbial community. In contrast with "living sediment", POC has positive effects on many compartments (esp. 23, 24, 26). This suggests that living POC is more important as a prey, rather than as competitor, to many compartments, such as invertebrates, which are important energy sources for secondary producers. To explain better why living sediment and POC have opposite impacts would help to clarify trophic dynamics in this system. Direct and indirect effects between alligator (23), turtle (24) and snakes (26) are also significant and important. Snakes are part of the alligator diet, so that one would expect them to exert a positive impact on alligators. However competition between the two for invertebrates, fish, and many other species becomes a crucial factor, and the net effect of this asymmetric competition is negative. Much the same configuration explains the impact coefficient of alligators on snakes and those between turtles and snakes. The alligator diet includes turtles, making the effect of gators on this prey negative. Turtles impact alligators in a positive way, even though alligator (eggs) are one of their prey. In this case predation by alligator on turtles is stronger than the competition between the two for many common sources of food, and turtle predation on alligators is negligible.

Components with similar diets compete with each other, and the more the diets overlap, the stronger is the competition. In a complex network, such as the forested wetlands, one would expect this effect occur very often; and, in fact, the coefficients in the impacts matrix support this expectation (although there are interesting exceptions.) Mink and Otter, for example, feed on the same compartments, but seem not to compete with one another. The reciprocal negative impacts are less than 1%. Turtles seem to compete with otter and mink, although the intensity of this phenomenon is modest. No significant negative impacts have been observed between other pairs of animal groups that have similar diets, such as great blue herons and woodstork, kites hawks and owls. Significant competition seems to occur, however, between frogs (28, 29, 30) and fishes (20, 21, 22).

The direct impact of a predator on its prey is obviously negative; however, the overall effect can become positive, due to the multiplicity of interaction pathways involved. In such cases we speak of "beneficial predators". In the forested wetlands network a surprisingly large number of beneficial indirect links between predators and their prey exist, and the number of instances is higher during the wet season (78) than in the dry (67). Compartments that exert a positive effect on their prey are numerous: (21) small fish-primarily carnivorous, (36) kites & hawks, (44) owls, (42) white ibis, and, most significantly, (23) American alligator (Table 1). The alligator behaves as a beneficial predator to a conspicuous number of prey (Fig. 5): invertebrates (15, 16, 17, 18, 19), frogs (28, 29, 30), galliformes (37), and mice & rats (61). This behavior appears to be related to the combined effect of strong predatory and competitive releationships between the alligator and turtles and snakes, and these latter two are the most important predators of the compartments just listed.

Analysis of the total dependency matrix yields interesting information about differences between the two study periods. Some changes in direct diets could be related to changes in the availability of primary producers. Squirrels (60), for example, feed more on (8) understory, during the dry season, when the latter is more abundant, and less on (10), hardwoods; the opposite occurs during the wet season (Table 2). Primary producers also play a very important role on changes in indirect diet coefficients (Table 3). Of particular interest is the fact that phytoplankton, although not a direct source of food to many higher trophic taxa, becomes a key element in their indirect diets during the dry season. Of the 55 seasonal changes in indirect diet coefficients that exceed ten percent, thirty involve phytoplankton (although it forms only eight direct connections.)

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5.3 Trophic Levels

The changes in diet composition just discussed concern mainly primary producers and don't seem to induce big changes in the average trophic levels of most heterotrophs (Fig. 6). This relative constancy could be due to the fact that alternative food sources for a given compartment often belong to the same trophic level as the prey they replace. An example already cited is the squirrels' alternating preference for understory and hardwood leaves, both of which belong to trophic level one. The same compensation applies in some cases to indirect diets.

Those compartments that do undergo major dietary changes between seasons, such as living POC and living sediment, feed only on level-one compartments, so that any change in their diet distributions will have no effect on their trophic positions. The only compartments that show any significant diet modification are the Gruiformes, great-blue heron and woodstork. During the dry season they feed more on lower trophic levels, especially compartment 19, terrestrial invertebrates. During the wet season, however, they feed more on alligator eggs and lizards.

Trophic analysis also addresses ecological efficiency. Among the compartments with low production efficiencies were many mammals and birds (Fig. 7). These are mainly top predators, such as vulture, owls, panther, and black bear, whose productions go almost entirely to detritus compartments (Fig. 8) . The same applies to alligator. Although some predators feed on alligators eggs and juveniles, this predatory loss represents only a small proportion (0.2%) of alligator assimilation. The remaining reptiles exhibited ranges in efficiency from 10-17%. The significant predation on these taxa is more than balanced by the high amount of biomass they produce. They account for 50% of the total vertebrate biomass, which is due in part to moderate predation and in part to their low metabolic rates. Large biomasses and high secondary production likewise characterize invertebrates as having middle to low efficiencies (2-15%). They represent 88% of the total system animal biomass.

Amphibians and fishes are the most efficient compartments. The trophic efficiencies for fish range from 21 to 61%, and for amphibians, 46 - 87%. They sustain many compartments and their losses to predation are comparable to their productions. The high efficiencies reflect their importance in energy transfer.

The trophic efficiencies for each trophic level, for wet and dry season, are depicted in Fig. 9. The pattern in the efficiencies is quite unusual. In most other studies) efficiency decreased more or less monotonically along the tropic chain (Baird and Ulanowicz, 1989), while here the efficiency fluctuates markedly. For wet seasons, after an initial sharp decrease from 47.3% in level I to 2.64% at level II, trophic efficiencies rise over the next two steps, reaching 8.46 % at level III, and 15.1% at level IV. From this point onward efficiency decreases along the tropic chain. The low value for level II is attributable mainly to "living sediment". Only 0.69% of what goes into this compartment reaches the third level. Of the total amount of material entering the second tropic level , 90% passes through this "living sediment". Part of it is dissipated and part becomes detritus. This very low tropic efficiency also contributes to the strong negative effect that this compartment has on many other taxa, as described in Section 5.2. By way of contrast, the positive effect of compartment 1, living POC, likely results from a higher efficiency coefficient (14%). More than 50% of what comes out of level II and enters level III issues from the living POC. The efficiencies at levels III and IV rise, mostly due to the high efficiencies of the fishes and amphibians. Wet and dry seasons show similar trends in trophic efficiencies, but values are generally higher during the dry season. The same pattern applies to the efficiencies of single compartments: they are higher during the dry season, as shown in Fig. 9.

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5.4 System Level Indices

Perusal of the community organizational indices (Table 4) reveals a familiar story. Ulanowicz and Baird (1989), for example, examined how the system ascendency and related variables calculated for the Chesapeake mesohaline ecosystem varied over the four seasons of the year. They concluded that the magnitude of system activity (total system throughput) modulated almost all the seasonal variation in the ascendency-type variables. The seasonal variation in the informational factors (e.g, ascendency/ throughput, capacity/ throughput, etc.) was insignificant by comparison. In other words, the magnitudes of trophic processes changed markedly over the course of a year, but the kinetic relationships among them remained essentially the same. (The assumed topology was held invariant over the seasons, but the relative magnitudes of the flows still could have changed the values of the information indices. It did so only to a slight degree.) In evaluating the impacts of thermal additions to a tidal marsh ecosystem Ulanowicz (1984) also observed that the resulting change in activity level was strong, but the underlying trophic structure remained relatively unimpacted.

A comparison of the organizational status of the wet and dry season networks reveals this same pattern. The total system throughput falls by some 25%. This drop is repeated in virtually all the other indices, so that, proportionally, there is very little change in any of the information factors. The proportion of capacity that appears as ascendency (A/C) actually rises by 0.6% during the dry season. Somewhat noteworthy, the flow diversity (C/T) also rises from 4.64 to 4.71 bits. (If the dry season were the period of greatest system stress, one would expect both these values to fall instead of rise.) The proportion of internal ascendency (Ai/Ci) shows a bit more of an increase during the dry season (1.4%). (One must bear in mind that the information indices are logarithmic in nature, so that small differences in them reflect somewhat larger changes in the underlying kinetics.)

The connectance indices are the log- averaged number of connections per node (Ulanowicz, in press). The value for the overall connectance (includes all flows, internal as well as external) of ca. 1.9 links per node is somewhat low, indicating the system should possess a strong internal stability, but possibly will exhibit little resilience to externally imposed stress. Surprisingly, the intercompartmental connectance (includes only internal flows) is very high and exceeds the theoretical maximum (ca. 3.01) for a stable system. This high value is probably inflated by the large number of passive returns to the detrital compartments; because, when only feeding flows are included, the connectance drops to a very reasonable value of 2 - 2.3 links per node.

Heretofore, the information indices have been applied only to whole systems. Evidence is accumulating, however, that the various subcomponents of the ascendency-like variables can serve to gauge the contributions of individual system elements to the performance of the whole system (Ulanowicz 1996) For example, the ascendency is comprised of terms that are generated by each transfer in the system. If, for example, one sums up all the terms generated by the inputs to a given taxon (say, the jth one), the result is a measure of the contribution of that compartment to the full system ascendency (call it A_j). Because ascendency may be viewed as an indicator of efficient system performance (Ulanowicz 1997), the same partial-sum, A_j, represents the contribution of taxon j to overall system performance. Furthermore, if one then divides A_j by the corresponding throughput for taxon j (call it T_j), the ratio A_j/T_j will represent the contribution per unit of activity of j to the total system ascendency.

Calculating and ranking these "contribution coefficients" proves to be a most interesting exercise (Table 5). When the average trophic levels of the 68 compartments were presented (Fig. 6), it may have surprised some to see the alligators, snakes and wading birds feeding at trophic levels that are higher than some other "charismatic megafauna", such as the Florida panther, Bobcat, or Grey Fox. The relative contributions to ascendency by the latter, however, outweigh the former, as shown in the table. Perhaps even more surprising is the very high ranking of the Vertebrate Detritus (fifth). The relative values of these coefficients seem to accord well with most people's normative judgments of the specific "value" of the various taxa to the organization of the system as a whole.

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5.5 Cycling

In comparison with the gramminoid wetlands to the southeast, which are more rapidly flushed by sheet flow from Lake Okechobee, one expects the cypress wetlands to appear more like a closed system, with materials cycling within for long times. With respect to carbon, however, the numbers do not bear out this conjecture. The Finn cycling index, for example, measures the fraction of the total system throughput that is engaged in recycling. It is only 8.8% during the wet season and 9.2% in the dry. These values are less than half the relative amount of recycling that one encounters in the ecosystem of Chesapeake Bay (21%), which is flushed at a much higher rate (Baird and Ulanowicz 1989.)

This difference between the swamp and estuary seems to have its origin in the relative availabilities of material that falls to the sediment in each habitat. In Chesapeake Bay, carbon reaching the sediment is more likely to be reused and fed back up the trophic chain. In the cypress networks, by contrast, material reaching the bottom is more likely to stay buried. (These are muck - producing systems.) Also, material not reaching the bottom is likely to be respired sooner, due to the higher ambient temperatures.

Despite these low magnitudes of recycling, the structure of the recycle pathways that do exist is exceedingly complex. The wet season network, for example, possesses exactly 3,975,514 simple cycles of carbon. (A simple cycle is one in which no taxon is visited more than once.) The dry season configuration is even more complicated, possessing 27,084,903 cycles. The analysis of so many pathways for recycle was far beyond the capabilities of the version of NETWRK that was available at the beginning of the project year. The way that version was written, it was necessary to store the individual identities of all they before the cycles could be separated from the network. When only several thousand or fewer cycles were identified, this requirement proved to be no obstacle. There is simply no way, however, using most desktop computers, to store over 27,000,000 cycles (some up to 20, two- digit links long) in RAM, and even attempting a RAM-ROM tradeoff proved to be prohibitive.

It was obvious that the cycle identification routine of NETWRK needed to be rewritten, in order to treat the multitude of cycles in rigorous fashion. Eventually, a way was found to remove a very large number of cycles while staying within RAM during most of the procedure. In effect, speed of execution was sacrificed to avoid a massive need for storage. Thus, instead of storing the identities of all the cycles at any time, only summary information about the nexus (a group of cycles with the same limiting link) with the smallest link is stored during one pass through the identification routine. That nexus is then removed, and the whole procedure is started anew with the residual network. This amended algorithm requires many passes through a combinatorial search routine, all of which entails a prodigious amount of computation. This disadvantage is offset somewhat by the enormous speed of the newer PC's on today's market. Even so, the task remained daunting. It took a Sun- SPARC Ultra (TM), one of the fastest mid-range computers on the current market, over 177 hours to strip the 27M cycles from the dry season

network.

The big question is why do there exist so many more cycles in the dry season network than during the wet period? To answer this, it was necessary to examine the list of nexuses that were unique to each season. It turned out that there were roughly the same number of nexuses particular to each season; and, furthermore, most of the nexuses that exist only during the wet season contained more individual cycles than those unique to the dry season. There were, however, several overwhelming exceptions to this pattern. In particular, those nexuses unique to the dry season that involved as prey the 6 taxa, Woodstork, Other Herons, Egrets, Great Blue Heron, White Ibis, and Alligator, added over 15,500,000 cycles to the dry season count. (Presumeably, predation upon these taxa also inflated the numbers of cycles in the nexuses common to both seasons.)

The reader may already have noted that the taxa just named feed near the top of the foodchain, and as adults they rarely become prey for others. This is not true of their eggs or juveniles, however. "Ovi-predation" is quite common during the dry season, when the birds and gators are nesting, and it seems to be this type of feeding that creates an enormous number of new channels for recycle. Predation on large, energy rich eggs is common in terrestrial and freshwater communities, and the eggs of amphibians, reptiles and birds are the predominant prey. Nest predation seems to be consistently lower in the marshes and higher in the adjacent upland habitats. Deep water and dense vegetation plays an important role in restricting predation to only very water-adapted predators, such as mink. Moreover, nests became more vulnerable during the dry season, as they remain exposed to predators, such as raccoons and foxes. Because of the high bird density in this area during the dry season and because of the high energetic value of big wading bird eggs, we think that "ovi-predation" deserves particular attention in the cypress network.

The distribution of cycled flow among loops of different trophic lengths can provide clues to system performance. Presumeably, less impacted systems are able to cycle material over longer and slower routes. In comparing cycling during the wet and dry seasons, one observes that 6.9% of system activity consists of recycle over loops of trophic length two. This is slightly higher than the 6.7% that circulates over pathways of the same length in the dry season. (No single- link feedbacks are present in either network.) Because the Finn cycling index of the dry season is higher than that for the wet, one deduces that proportionately more material is cycling during the dry season over longer, slower cycles, and the output from NETWRK confirms that as fact. Once again, the dry season shows comparatively less evidence of impact.

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6. SUMMARY

The cypress swamp ecosystem of Southwest Florida provides probably the closest subtropical analog in the continental United States to the much- reputed complexity of the legendary tropical rainforest. It is a highly complex ecosystem, whose workings are not easily captured by simple models. The 68-compartment network of trophic exchanges developed in this ATLSS subproject is the most highly-resolved and complicated trophic budget ever to be assembled.

Previous studies of cypress- dominated ecosystems in Florida have characterized the biotype as being primarily detritus- based (Odum & Ewel 1984), so that the preliminary ATLSS model of the lower trophic level processes in this habitat were written according to this scenario

(Ulanowicz 1995b.) In light of this legacy, the most significant and surprising result to issue from the current work is the conclusion that the cypress ecosystem is *not* primarily a detritally- based ecosystem. To be sure, the input of carbon and energy from the cypress litterfall is significant, but available evidence and expert opinion point to the likelihood that most of this particular input ends up buried in the sediments. This is, after all, a peat- producing system.

There is ample evidence to support the contention that over half of the carbon reaching the higher trophic levels arrived there via the grazing chain, without passing through any detrital compartment. The understory vegetation of phytoplankton, periphyton, vines and epiphytes constitute the trophic foundations for most of the higher trophic level production. The production by phytoplankton is especially important to the sustenance of the system during the dry season, when the mostly deciduous canopy is relatively open. It will be necessary to rewrite the lower trophic level ATLSS module for cypress wetlands to accommodate this new scenario for trophic dynamics. In a sense, even before the preliminary ATLSS model has been assembled, network analysis already has begun to fulfill its purpose to serve as a benchmark against which to judge the performance of the ATLSS simulation.

Trophic efficiencies are greatest among the fish and amphibians. Predation on these groups comes close to matching their assimilation and growth. Efficiencies of the reptiles and mammals are low by comparison, with much of their assimilation being respired or going to detritus. The efficiency of the "living sediment" is especially low, causing it to exert a negative trophic impact upon a number of compartments. Trophic levels do not change much between the wet and dry seasons. Although several species showed significant dietary changes between seasons, these mostly involved replacement by alternate pray at the same trophic level. Trophic efficiencies at each level do not decline in monotonic fashion, as is usually the case, but rather fluctuate in magnitude. There is a sharp drop in efficiency from level I to II, followed by a gradual rise in production efficiency in the next two levels, which are dominated by fish and amphibians. The trophic level efficiencies during the dry season differ from those during the wet period only in being slightly higher.

Total system activity drops 25% during the dry season, but the accompanying trophic structure seems to change little between seasons. In fact, structural measures indicate a slightly higher level of system organization during the dry season. Experimentation with the terms of the system ascendency led to the discovery that the quotient of the contribution of a taxon to overall ascendency divided by the activity of the same compartment yielded a very useful index of the relative contribution by that taxon to overall system performance. According to this measure, taxa such as panther, bobcat and fox exhibited the highest "intrinsic values" in the ecosystem, despite their being lower on the trophic scale than reptiles, such as alligators and snakes.

Although the cypress swamps appear to be somewhat isolated as regards physical transport, there is

relatively little cycling of carbon in this system. The percentage of activity in cypress ecosystems that comprises cycling is less than half the corresponding fraction found in physically more open systems, such as the Chesapeake estuary. It appears that much of the carbon flow exits the system in the burial of cypress litterfall before it can be included into the trophic dynamics. Despite the low relative magnitude of cycling in cypress systems, the structure of cycling in these communities is exceedingly complex. For example there are over 27 million simple cycles in the dry season network, most of which owe their existence to "ovi-predation", or the consumption of nutrient rich eggs and juveniles of higher trophic species by populations lower on the trophic chain.

Although one is inclined to think of the wet season as being the normal configuration for the cypress ecosystem, this judgement is rendered on the basis of the dominant vegetation, not on the trophic status of the system as a whole. All indications issuing from this analysis suggest that the dry season configuration of trophic processes performs under less stress.

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Annual Report to the United States Geological Service Biological Resources Division University of Miami Coral Gables, FL 33124

Network Analysis of Trophic Dynamics in South Florida Ecosystem, FY 97: The Florida Bay Ecosystem

Robert E. Ulanowicz, Cristina Bondavalli, Michael S. Egnotovich

University of Maryland System, Chesapeake Biological Laboratory, Solomons, MD 20688-0038

E-mail: ulan@cbl.umces.edu
Tel: (410) 326-7266
FAX: (410) 326-7378

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EXECUTIVE SUMMARY

A 125- component budget of the carbon exchanges occurring during the wet and dry seasons in Florida Bay has been assembled. These trophic networks are the most highly-resolved and complete foodweb ever to have been assembled for any ecosystem. They will serve as independent benchmarks against which the performance of the ATLSS multi-model, now under construction, will be assessed.

As is the case with such detailed, quantitative descriptions of ecosystems, the overall configuration of trophic transfers yields numerous clues as to how the ecosystem is functioning. An analysis of indirect contributions reveals, for example, that seagrasses are the ultimate source of carbon for the system during the wet season, however, epiphytic periphyton becomes the foundation that sustains system activity during the dry period. These primary producers fuel ecosystem activity mostly via indirect routes involving passage through detrital links. There is some 37% more trophic activity during the wet season, as compared with the dry interval that follows. Nevertheless, more species appear to feed higher on the trophic ladder during the dry season than they do during the wet period. The taxon feeding highest on the trophic ladder are the raptors, which, on average, feed at level 4.6. Such averages hide the existence of some very long trophic feeding chains, which in a few instances reach 15 transfers in length. Such long concatenations, however, move only an insignificant amount of carbon along their whole length.

A remarkably high percentage of carbon is recycled by the Florida Bay ecosystem. Over 26% of total system activity involves recycling (a proportion exceeded only by coral reef ecosystems), and, quantitatively, most of these processes are carried out by the pelagic and benthic flagellates. The topology of the Florida Bay ecosystem is remarkably stable throughout the year.

PAST WORK

This report covers work done during the second year of a four year task under ATLSS to quantify the trophic processes in South Florida ecosystems. Last year, a 69-compartment network of trophic

exchanges in the cypress wetlands was constructed and analyzed. The results were communicated in last year's report to USGS/BRD and were elaborated in two manuscripts now under peer review for publication in the scientific literature. In particular, "Beneficial predators: The case for the American alligator" is in review with *Ecosystems*, and "Insights into whole ecosystem behavior of South Florida wetlands" has been completed and will be sent for review to the journal *Oecologia.* These manuscripts are being forwarded to USGS/BRD along with this report.

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1. RATIONALE

A primary goal of coordinated research on South Florida's environmental resources is to understand those communities as whole ecosystems. Toward that end, the Across Trophic Levels System Simulation (ATLSS) project is an attempt to simulate the interactions of the various elements of wetland biotic communities within the framework of a single, encompassing computational scheme.

The resulting ATLSS model is one of the most complex and sophisticated models ever attempted. It will consist of simulation modules of varying, and often very high complexity that represent the important components of the ecosystems of South Florida. It follows that the output from ATLSS will be exceedingly complicated, and it may not be a straightforward task to elucidate the causal origins of any particular model behavior. Such uncertainty could become problematical, especially if the initial trials of ATLSS should behave "pathologically" (as is highly probable during the initial runs of such a complex model). Even should outputs not appear unrealistic, the difficulty remains that there exist no precedents for evaluating how well such a "multi-model" performs as an analog of the real system. I.e., there are no set protocols for "calibrating" such complex simulations. ATLSS, therefore, requires a partially independent benchmark against which one may gauge the plausibility of its outputs; and, towards that end, ATLSS investigators have chosen to create a suite of trophic flow networks that estimate material exchanges in the ecosystems being modeled. These will serve as calibration standards. In addition, these networks will be analyzed by a set of quantitative methods called Network Analysis (NA) that will serve as a guide for calibrating and debugging the initial modeling trials.

Trophic flow networks are graphical and mathematical depictions of the answers to the questions, "Who eats whom, and by how much?" Typically, diagrams of flow networks are comprised of boxes that represent the major components of the ecosystem. The boxes are connected by arrows, which indicate the transfers of material or energy between the components. Usually, each arrow is labelled with the magnitude of its transfer as averaged over a prescribed period of time.

Accordingly, the University of Maryland contingent of ATLSS investigators is assembling very detailed networks of carbon exchanges as they normally occur in the ecosystems of South Florida. Networks consisting of more than 60 important compartments are being estimated for each of four habitats, using existing data and ongoing field work. Separate networks for wet and dry seasons are being created for the ecosystems of the forested wetlands, the gramminoid marshes, the mangrove estuaries, and the shallows of Florida Bay. Each network will be a snapshot of the trophic flows and biomasses as averaged both over the hydroperiod in question and over the spatial domain of that particular biotope.

Analyses are to be performed on the resulting networks at several scales. The key questions that can be answered for any fully- quantified trophic network include: (1) To what extent does each taxon depend upon (or contribute to) all other taxa over all trophic pathways, both direct and indirect? (2) What are the efficiencies with which material is being transferred up the trophic ladder? (3) What are the pathways by which material is being recycled within the system? and (4) What is the current organizational status of the ecosystem? Any or all of these answers can be used to debug an ATLSS model that is not performing realistically.

During Calendar Year 1997 we reported our findings on the cypress wetland ecosystems. Below, we present the estimation and analysis of the second of these four habitats -- the Florida Bay ecosystem. In next year's annual report we will present the corresponding results for the networks of the estuarine mangroves, and the gramminoid wetlands (or Everglades proper.).

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2. STUDY AREA

Florida Bay is a triangular, tropical lagoon/bay which occupies a shallow, rocky trough between the relic, exposed barrier reefs of the Florida Keys and a series of mangrove-lined bays and sounds at the southern end of the Florida peninsula (Surface water improvement and management plan for the Everglades, 1992). The western side opens directly to the Gulf of Mexico (Fig. 1). The bay is about 2200 km^2 in total area, with 1800 km^2 included within Everglades National Park (Tilmant, 1989; Robblee et al., 1991). Florida Bay is effectively divided into a series of basins by a complex network of anastomosing carbonate mud banks that restrict circulation (Sogard et al., 1989). Depths vary from only centimeters over the mud banks, to a few meters in the deeper basins.

Historically the bay has been described as varying between a positively functioning estuary and a tropical, hypersaline lagoon, depending up the season: a positively functioning estuary during periods of high rainfall (summer); a hypersaline lagoon when evaporation exceeds upland runoff and oceanic exchange (winter).

Due to the effects of water management the bay now functions more often as a hypersaline lagoon. Under pre-managed conditions, Florida Bay received its input of freshwater from sheet flow across the southern Everglades and Taylor Slough. In addition, freshwater flowed through Shark River Slough, into Whitewater Bay, and subsequently entered western Florida Bay via flow around Cape Sable (Fourqurean et al., 1993). Today, these areas, along with the C-111 canal, are still the major sources of freshwater inflow to coastal estuaries and Florida Bay. However, the current water management system has altered water delivery to the bay by constructing a series of canals, impounding water in the Water Conservation Areas, and diverting water eastward to urban areas and the Atlantic Ocean. Evidence from coral banding suggests that the overall volume of freshwater flow has been reduced by more than half in the past century (McIvor et al., 1994).

Currently, freshwater inflow to Florida Bay increases with the beginning of the rainy season in June from direct rainfall, surface flow and groundwater discharge (Mazzotti and Brandt, 1989). During normal rainy seasons, Florida Bay exhibits a pronounced gradient of salinity increasing from north to south across the entire bay. The causes of salinity patterns in Florida Bay include not only freshwater inflow but also circulation and flushing patterns. As mentioned above, the anastomosing shallow mud banks divide the bay into discrete basins. These banks act as barriers, effectively limiting water exchange between basins, particularly in interior sections of the bay. In addition, due to the absence of hurricanes for the last 32 years, both basins and banks undoubtedly have become shallower, further restricting circulation. Reduced circulation, when coupled with low freshwater inflow and high evaporation, leads to conditions of hypersalinity. In all but the years of highest rainfall, portions of Florida Bay, particularly in the central portion, have become hypersaline, with salinities greater than 35 parts per thousand (Fourqurean et al., 1993).

Florida Bay supports diverse biological communities that are interrelated in this complex ecosystem. The estuary contains two main types of marine (saltwater) habitats: mangrove areas and inshore marine areas (McIvor et al., 1994). Mangrove isles cover less than 2% of the area of the bay (Enos, 1989) and they will be the subject of the next network model. Inshore marine areas are of two types. The first are grass-bottomed areas, covered primarily with *Thalassia testudium*, *Halodule wrightii* and *Syringodium filiforme*. Seagrass meadows occupied more than 80% of the bottom of Florida Bay, prior to the die-off that began in 1987 (Zieman et al., 1989; Robblee et al., 1991), They are among the most productive ecosystems in the marine environment, rivaling those of tropical rain forest and tidal marshes (Odum and Hoskin 1958, Zieman and Wetzel 1980, McRoy and Helffrich, 1977). The importance of seagrasses is due to several factors. These include their function as nursery areas containing high densities and

diversities of fishes and invertebrates, which serve as feeding grounds for gamefish and waterfowl [Heck and Orth 1980]), and which cycle carbon and other elements via detrital processes (Klug 1980). Seagrasses also provide stabilization for coastal sediments and support dense epiphytic communities (Klug, 1980). Epiphytes are sessile plants and animals that grow attached to their seagrass host (Harlin 1980) and are a significative component of the production of the system (Frankovick and Fourqurean 1998).

The second type of inshore marine area consists of hard-bottom calcium carbonate rock, overlain by a thin layer of carbonate sediment. This habitat is most common in the southern portion of the bay and is home to sponges, octorals and macroalgal patches (Butler et al., 1992). Here the macroalgae, present also in seagrass beds, form large unattached masses, collectively known as drift algae. The species most representative of this environment are: *Batophora oerstedi*, *Laurencia poitei* and *Acetabularia crenulata* (Surface water improvement and management plan for the Everglades, 1992).

Florida Bay serves as a nursery ground for a variety of species of invertebrates and fish, including approximately 22 species with commercial and recreational value (Davis et al., 1994). Among the invertebrates are some of the most important commercial and recreational crustacean fisheries in the coastal Florida waters, in particular: pink shrimp, Florida lobster and stone crab (Cantillo et al., 1995).

Another species of shrimp, *Thor floridanus,* is numerically the dominant species of grass shrimp in Florida Bay, and thus an important food item for both the bay's juvenile gamefish and the less heralded resident fish populations (Holmquist et al 1989).

Crustaceans, like other groups of macroinvertebrates, play an important role in the ecosystem. They serve as the primary trophic pathway connecting the detrital and primary producer levels to the more charismatic gamefish, mammal and avifauna. Sessile organisms (Sponges and Corals), by contrast, are more important for their structural contributions than for their direct role in the system's trophic dynamics, and their effects on structure are particularly important in the hard-bottomed communities within Florida Bay (Chiappone and Sullivan 1994). Few organisms feed directly upon sponges, yet their presence is crucial for maintaining the spiny lobster population, as they represent the primary source of cover for juvenile lobsters (Butler et al., 1995). The juveniles develop while residing within the internal cavities of the sponges, until they are large enough to avoid most predation.

Florida Bay is a nursery ground also for many species of juvenile fishes, such as tarpon, snook, barracuda and mullet (Davis et al., 1994). Over the past 10 years, however, the structure of the entire fish community has undergone substantial changes, which appear coupled with new environmental conditions, primarily the dieoff of sea grasses. Since 1944, 38 fish kills have been recorded in Florida Bay; and most of these have occurred within the past 15 years (Cantillo et al. 1995). Harvest data for Monroe County, Florida, indicate substantial shifts in the dominance of several commercially important species (Bohnsack et al., 1994). For example, harvests of grouper and mackerel have declined substantially, while those of the yellow-tailed snapper have risen.

Historically, the forage fishes were dominated by several demersal and seagrass canopy species: gold spotted killifish (*Floridicthys carpio*), rainwater killifish (*Lucania parva*), pinfish (*Lagodon rhomboides*) and mojarras (*Eucinostomus* spp.). In recent years, following the seagrass dieoffs and massive algal blooms of the late 1980s and early 1990s, the previously described food fishes suffered a severe decline in numbers. The abundance of pelagic species, specifically anchovies (e.g., bay anchovy, *Anchoa mitchilli*) and sardines (e.g., scaled sardine, *Harengula jaguana*) has since increased, taking the place of the declining demersal and canopy fishes (Thayer et al. 1987; Hoss et al. 1996; Matheson et al. In Press).

The Florida manatee aside, gamefish are probably the most charismatic animals of Florida Bay. The spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), gray snapper (*Lutjanus grisseus*), sheepshead (*Archosargus probatocephalus*), black drum (*Pagonias cromis*) and snook (*Centropomus undecimalis*) are all persued by both sports and commercial fishermen. Tarpon (*Megalops atlanticus*), ladyfish (*Elops saurus*) and bonefish (*Albula vulpes*) are also highly prized game fish, but overall fishing pressure on these three is less intense, in that they are not fished commercially (Tilmant 1989; Schmidt et al 1997).

Florida Bay, the Everglades and the ecotonal areas between them are tightly linked through the interdependencies of many organisms. An obvious example is the wading birds that shift between foraging in freshwater and estuarine habitats, depending upon existing water levels (Bancroft et al., 1994). Herons, for example, forage primarily in seagrass flats, but during the summer, great white herons (*Ardea occidentalis*) and, to a lesser extent, great blue herons (*Ardea herodias*), wade (and feed) on the banks (Browder, pers. com.). One species of especial concern is the roseate spoonbill (*Ajaia ajaja*), which forages on the south Florida ecotone and which also nests in Florida Bay. Brown pelicans (*Pelecanus occidentalis*) and double-crested cormorants (*Phalacrocorax aurotus*) dominate the avifauna in the southcentral part of the bay, roosting in number on Arsenicker, Buchanan and Barnes Keys (Browder, pers. com.).

Although Everglades estuaries are not the dominant wintering area for waterfowl within the state, 22 species of ducks have been documented as occurring in this area. The most common are: blue-winged teal (*Anas discors*), lesser scaup (*Aythya affinis*), pintail (*Anas acuta*), American wigeon (*Mareca americana*), ring-necked duck (*Aythya collaris*) and shoveler (*Spatula clypeata*). Other birds that use the bay include loons (*Gavia immer* and *G. stellata*), greebs (*Podiceps aurotus* and *Podilymbus podiceps*), American coot (*Fulica americana*), numerous shorebirds (eg. sandpipers and plovers) and many gulls and terns (black skimmer, *Rynchops nigra*, laughing gull, *Larus atricilla* and ring-billed gull, *Larus delawarensis*.

Two important raptors live in the bay: osprey (*Pandion haliaetus*) and bald eagle (*Haliaeetus leucocephalus*). These two top level carnivores are residents of the area: they breed and forage in the estuary (Surface water improvement and management plan for the Everglades, 1992).

Another species at the top of the food chain is the American crocodile (*Crocodylus acutus*). About one-half of the entire U.S. population of crocodiles, a federally listed endangered species, nest in Florida Bay within Everglades National Park (Mazzotti and Brandt, 1994). Other important reptiles encountered within the study area include three species of sea turtles. Loggerhead turtle, *Caretta caretta*, green turtle, *Chelonia mydas* and hawksbill turtle, *Eretmochelys imbricata*, have been observed using Florida Bay. (Surface water improvement and management plan for the Everglades, 1992).

The Florida manatee (*Trichechus manatus latirostris*, a federally-designated endangered species) is a year-round inhabitant of Florida Bay, where submergent aquatic vegetation, such as seagrasses, forms the major component of their diet. Manatees are dispersed throughout Florida waters in the summer, but concentrate in warmer waters during winter (Irvine et al., 1982). Recent surveys revealed that Everglades National Park waters account for up to 20% of the west coast population and 9% of the state-wide population (Snow, 1991). Another charismatic marine mamma occurring in Florida Bay is the bottlenose dolphin, *Turpsiops truncatus* (Irvine et al., 1982).

In recent years, significant deteriorations in water quality and biodiversity have been observed in the Bay. The cause of such degradation is not well understood, and it is most likely a combination of factors resulting, both anthropogenic and natural. Ever since the recent loss of turtle grass from the majority of the mud banks, turbidity and phytoplankton production have increased in the northern Bay. Further

effects of loss of grasses include reduced recruitments of pink shrimp, snook, and redfish; lowered reproductive success of ospreys, great white herons, and roseate spoonbills; and shifts in the distributions of manatees, American crocodiles, and many of the wading birds that historically nested in the estuarine ecotonal area." (McIvor et al., 1994).

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3. PARSING THE NETWORK

As with most analyses, some of the most important assumptions in Network Analysis are made at the very beginning. They concern decisions as to what the elements of the network will be and how these taxa are to be connected. In this project, these decisions are simplified somewhat by the requirement that the network be comparable to the ATLSS simulation. That is, each state variable of the ATLSS model must have its counterpart in the accompanying network.

Network analysis, however, can treat far more complicated webs of interaction than are possible using simulation modeling. Keeping the simulation dynamics of many coupled processes from becoming pathological is a difficult balancing act. Because NA does not deal explicitly with dynamics, far greater taxonomic resolution becomes possible with this form of analysis. As a result, some taxa in the ATLSS model will be represented by several compartments in the FBayress network. In addition, compartments can be added to the network with relative ease. For example, the creation of an individual- based model for one of the lesser-known fishes (e.g., bonefish or tarpon) would entail significant effort. As will be described below, it requires nowhere near as much work to include theese two compartments into the quantified trophic web.

Although the primary purpose for creating the FBayress networks is to serve as a calibration benchmark for ATLSS, it should be mentioned that the network and its ensuing analysis can also serve independent purposes. For example, some biologists will be curious to know how their particular species of interest, which might not appear in ATLSS, will fare under the proposed hydrological scenarios. With regard to trophic interactions at least, the results of NA should allow those investigators and managers to make some educated guesses about how the excluded population might change. For example, NA quantifies the direct and indirect trophic interactions of each compartment with all other compartments in the web. In particular, the stocks and activities of each compartment not appearing in ATLSS can be compared with all those that do participate through NA, and such coefficients and ratios as may result can be applied to the predicted outputs from ATLSS to estimate the accompanying trophic status of the non-included species. In other words, after calibration NA can serve to expand the scope of predictions from ATLSS.

From an ecological viewpoint, virtually all the important trophic components (i.e., those comprising at least 5% of the standing biomass or activity) have been written into ATLSS. These include: detritus, microbes, aquatic/estuarine macrophytes, zooplankton, mesoinvertebrates, macroinvertebrates, piscivorus fish, planktivorous fish, wading birds, etc.

It happens, however, that data exist to make at least crude estimates of the stocks and activities of a number of some other ecosystem members. For example, there exist census figures (mainly harvesting data, Smith unpublished) on most of the fish that occur in the Florida Bay. Using these figures it becomes possible to estimate the standing stocks of carbon in these populations; and, using techniques described in the next section, to approximate as well the magnitudes of their transfers with predators, prey and detritus. Hence, it was decided to include these "parallel" species into the NA.

For many categories, such as phytoplankton, we have reserved compartments for each of the more abundant and better documented species and then created one box to receive all of the remaining species. Thus it is that we have the groupings "Other cnidaridae" among the invertebrates, or "other demersal fishes" and "other pelagic fishes".

In many networks the major lexical question involved how to treat the manifold species that comprise some functional groups for which data at the level of individual species are not available. In the Florida

Bay network this was the case especially for small benthic invertebrates. As a result it was decided to create one general compartment called "Meiofauna" to characterize this poorly-resolved part of the ecosystem.

In the end, the network consisted of a total of 125 separate components. Only those species closely associated with the dominant patterns have been retained in this model. Hence, only primary producers, invertebrates, fishes, reptiles, birds and mammals commonly found in Florida Bay made the final list of species. Some additional species have been included following suggestions by experts. Once completed, the list was aggregated somewhat according to criteria, such as species sharing same diet, available data and the goals of ATLSS. For example, most species to be included in ATLSS as individual-base models have been maintained as separate compartments in the network.

Hereupon follows the final list of the components, along with a very brief description of what they entail.

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3.1 Primary Producers

The first elements of the network are the primary producers.

Phytoplankton has been divided into seven different compartments; those species supported by sufficient information have been retained in separate compartments:

C 1. 2um Spherical Phytoplankton - Spherical cyanobacteria with an average dimension of 2um.

C 2. Synedococcus - *Synedococcus sp.*

C 3. Oscillatoria- *Oscillatoria sp.*

C 4. Small Diatoms (<20um) - All diatoms smaller than 20um.

C 5. Big Diatoms (>20um) - All diatoms larger than 20um.

C 6. Dinoflagellates - All dinoflagellates are included in this compartment. Among others we have: *Ceratium sp.*, *Dinophysis sp.* and *Prorocentrum sp.*

C 7. Other Phytoplankton - Contains all the lesser abundant or less-common species not included in the previous six compartments, in particular, some Cryptophyte and Euglenophyte.

C 8. Benthic microalgae - A single compartment has been used to represent the entire benthic microalgal community, because available data relate only to aggregate chlorophyll-a concentration.

Seagrasses play an important role in the economy of this ecosystem, so the three major species are represented by separate compartments. In addition, we identify another general compartment for all the

seagrass roots.

C 9. Thalassia - *Thalassia testudium.*

C 10. Halodule - *Halodule wrightii.*

C 11. Syringodium - *Syringodium filiforme.*

C 12. Roots - The aggregated roots.

C 13. Drift Algae - All macroalgae are include in this compartment, but most importantly *Batophora oerstedii*, *Acetabularia crenulata*, *Laurencia sp.* and *Penicillus sp.*

C 14. Epiphytes - All epiphytes have been grouped into this compartment. Most occur on Thalassia and are dominated by the coralline red algae *Melobesia membranacea* and *Fosliella farinosa* (Frankovich and Zieman, 1994).

C 15. Free Bacteria -All the heterotrophic free-living bacteria that occur in the water column.

C 16. Water Flagellates - All the flagellates found in the water column.

C 17. Water Ciliates - All ciliates inhabiting the water column.

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3.2 Invertebrates

Zooplankton has been divided into six different compartments Species supported by sufficient information have been keep separate:

C 18. Acartia tonsa - *Acartia tonsa.*

C 19. Oithona nana - *Oithona nana.*

C 20. Paracalanus - *Paracalanus crassirostris.*

C 21. Other Copepoda - Contain all the other less abundant copepods not listed as separate compartments; among them: *Tortanus setulosis*, *Euterpina acutifrons*, *Longipedia helgolandicus*, *Calanopia americana.*

C 22. Meroplankton - Includes all forms of planktonic larvae, both fish and macroinvertebrate. For many species, inputs into the system occur via this compartment (e.g.,*Callinectes* spp. and several of the fish compartments).

C 23. Other Zooplankton - Any isolated temporary residents of the zooplankton that do not

fit in any of the above compartments.

C 24. Benthic Flagellates - All flagellates living within the sediments.

C 25. Benthic Ciliates - All the ciliates living among the sediment.

C 26. Meiofauna - Very little information is available on meiofauna in Florida Bay, and all species have been grouped into a single compartment.

Macroinvertebrates are represented by 26 compartments. Taxonomy, feeding habits and the amount of available information determined the final composition of the list of compartments (Tabb and Manning, 1961; Hudson and Allen, 1970; Turney and Perkins, 1972; Holmquist et al., 1989; Cantillo et al., 1995). Species of ecological and commercial importance were assigned individual compartments (e.g., *Callinectes* spp., stone crab, spiny lobster and pink shrimp). The crustaceans are the most highly resolved portion of the macroinvertebrate network. The remaining macroinvertebrate compartments are resolved at best to functional groups within a given phylum. As mentioned above, the lack of ecological knowledge at the species level forced the aggregation into more general compartments. "Macrobenthos" represents the extreme in aggregation, while "Echinodermata" and "Other Cnidaria" represent somewhat better resolution. In the case of Macrobenthos, organisms from a wide range of phyla with similar trophic functionalities were grouped together whereas," Other Cnidaria" contains cnidarians, both free swimming organisms (jellies) and anemones, whose functional roles in the system differ greatly from their cnidarian counterparts in the Coral compartment.

Gastropod and Polychaete compartments were resolved only to the functional level. Due to the vast number of species and only a rudimentary understanding of their ecology, it was possible to sort these organisms based only on general feeding behaviors, rather than on species-specific characteristics (Tabb and Manning 1961; Turney and Perkins 1972; Fauchald and Jumars 1979).

C 27. Sponges -This compartment includes all species of sponges, both with and without commercial value. It includes species from families such as Spongiidae, Dysideidae, Haliclonidae, Callyspongidae, Tedanidae, Axinellidae and Placospongidae. Some dominant and important species are: *Spheciospongia vesparium*, *Tethya diploderma*, sheepswool sponge (*Hippiospongia lachne*), yellow sponge (*Spongia barbara*) and grass sponge (*Spongis graminea*).

C 28. Coral - All coral species, (primarily stony corals and octocorals) are included in this compartment. The stony corals are dominated by species such as: *Siderastrea radians*, *Porites porites*, *Solenastrea hyades*. The octocorals include the the following species: *Pterogorgia anceps*, *Pseudopterogorgia americana*, and *Briareum asbestinum*.

C 29. Other Cnidaria - Contains those cnidarians not in the coral compartment (i.e., free swimming [jellies] and anemone forms). Most species are from the order Actinaria.

C 30. Echinodermata -The dominants in this compartment are: Sea Cucumbers (various Hollothuroidean Synaptids and *Holothuria floridana*), brittle stars (*Ophiostigma isacanthum* , Amphiurids and *Ophiolephis elegans*), sea urchins (*Echinaster sentus* and *Echinaster spinulosus*) and sea stars (*Astropecten duplicatus*).

C 31. Bivalves -Molluscs of Class Bivalvia - Common and notable representatives are: eastern oyster (*Crassostrea virginica*), bay scallop (*Argopecten irradians*), *Nucula*

aegeenis , *Solemya occidentalis* , tellins (*Tellina* spp.), *Neaeromya floridana* , and scorched mussel (*Brachiodontes exustes*).

C 32. Detritivorous Gastropods - Gastropods whose primary food source is detrital material: Squilaridae (*Caecum pulchellum*, *C. nitildum*, *C. floridanum*, and *C. imbricatum*), Olividae (*Olivella* spp., *Oliva* sp.), Nassariidae (*Nassarius albus*) and Atydae (*Haminoea succinea*).

C 33. Epiphyte Grazing Gastropods - Gastropods whose primary food source is epiphytes: Cerithidae (*Cerithrum* spp.) and Crepidulidae (*Crepidula maculosa*)

C 34. Predatory Gastropods - Gastropods whose primary prey are living animals: Conidae (*Conus floridanus*, *Conus stearnsi* and *Conus jaspideus*), *Modulus modulus*, *Marginella eburneola*, *M. guttata*, and *Thais deltoidea*.

C 35. Detritivorous Polychaetes - Polychaetes whose primary food source is detrital material: Capitellidae (*Mediomastus* spp. and *Notomastus* spp.), Cirratulidae, Maldanidae, Magelonidae (*Axiothella mucosa*), Orbiniidae (*Scolopos* sp. and *Scoletoma verrilli*), Paraonidae, Pectanaridae, Syllidae (*Syllis broomensis* and *Grubeosyllis* sp.), Terebellidae (*Armandia* sp and *Terebellides parvus*) and *Cirrophorus* spp.

C 36. Predatory Polychaetes -Polychaetes who prey primarily upon living animals: Nereidae (*Nereis accuminata* , *Nereis* spp., *Certaonereis* sp. and *Platynereis* sp.), Amphinomidae, Goniadidae, Eunicidae (*Schistomeringos pectinatus*), Syllidae (*Syllis prolifera* , *S. cornuta* , *Exogone rolandi* , *E. dispar* , *E. laurei* , and *Spaerosyllis piriferopsis*) and Lumbrineridae (*Lumbrineris* sp.).

C 37. Pelagic Feeding Polychaetes -Polychaetes feeding primarily on material suspended in the water column: Sabellidae, *Branchiomma nigromaculata* , Dorvilleidae (*Protodorvillea kefersteini*), Trichobranchidae (*Trichobranchus glacialis* and *Dasybranchus lunulatus*), *Chone* spp., *Fabricinuda triloba* , *Prionospio* sp., *Paraeupolymnia* sp., and *Sabellestarte* sp.

C 38. Macrobenthos - Includes all other (primarily benthic) invertebrates that are larger than the organisms in the Meiobenthos compartment and not included in the other macroinvertebrate compartments: Marine Oligochaetes, Sipunculids, Platyhelminthes, Nemerteans, Bryozoans, etc.

C 39. Benthic Crustaceans - Primarily Cumaceans, Tanaidaceans and Ostracods (i.e., crustacean species too large to be included in smaller-sized benthic compartments): Cumacea (*Vaunthompsonia* spp., *Cumella* spp., *Oxyurostylis* spp. and *Cyclaspis* spp.), Tanaidacea (*Pseudoleptochelia* spp., *Leptochelia forresti* , *Kalliapseudes* spp. and *Pagurapseudes largoensis*) and Ostracoda (*Eusariella* spp., *Parasterope muelleri* , *Eusarsiella paniculata* and *E. cornuta*).

C 40. Detrivorous Amphipods - Those amphipods that feed primarily on detrital material: *Ampelisca* spp., *Gammarus mucronatus*, *Elasmopus* sp. and members of the family Melitidae.

C 41. Herbivorous Amphipods - Those amphipods feeding primarily upon plant material: *Acunmindeutopus naglei*, *Ampithoe longimana*, *Caprella penantis*, *Cymadusa compta* and *Lembos rectangularis*.

C 42. Isopods - Includes such species as: *Paracereis caudata*, *Edotea triloba* and members of the families Anthuridae (*Amakusanthura magnifica*) and Spaeromatidae.

C 43. Herbivorous Shrimp - Represented by the following common species: *Hippolyte zostericola*, *Latruetes fucorum*, *Tozeuma carolinense*, *Alpheus heterochaelis*, *A. normannii* and *A. angulatus*.

C 44. Predaceous Shrimp - Includes: *Palaemon floridanus*, *Perclimnes americana*, *P. longicaudus*, *Leander tenucornis*, *L. paulensis* and *Ambidexter symetricus*.

C 45. Pink Shrimp - *Penaus duoarum.*

C 46. *Thor floridanus* - A very abundant species of grass shrimp.

C 47. Spiny Lobster - *Panulirus argus*.

C 48. Detritivorous Crabs - Crabs whose primary food is detritus, including the following representative species: hermit crabs (*Pagarus mcglaughlinae*, *Paguristes tortugae*) and *Mithrax forceps*.

C 49. Omnivorous Crabs - Contains generalist crab species such as: mud crabs (*Neopanope packardii*, *Panopeus occidentalis*, *Dyspanopeus texanus* and *Rithropanopeus harrisii*), spider crabs (*Libinia dubia*), *Eucratopsis* spp. and members of the family Xanthidae.

C 50. Predatory Crabs - Primarily Portunid crabs, excluding those in the Callinectes compartment: *Portunus depresifrons*, *P. gibbesii*, *P. ordwayi*, Gulf Weed Crab (*P. sayi*), *P. sebae* and *P. spinimanus*.

C 51. *Callinectes* spp. - Contains the two most abundant Portunid crabs in Florida Bay, blue crab (*Callinectes sapidus*) and ornate crab (*Callinectes ornatus*).

C 52. Stone Crab - *Menippe mercenaria*.

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3.3 Fishes

Its possible to separate the fishes of Florida Bay in a number of different ways: demersal versus pelagic, game- versus non-gamefish and temporary versus permanent residents (Thayer et al 1989; Hoss et al. 1996). The distinction we made was primarily demersal versus pelagic, although other differentiations were used to add color and depth to the entire picture of the fish compartments. Fish compartments generally are resolved more precisely than were most of the macroinvertebrates (Tabb and Manning 1961; Hudson and Allen 1970; Thayer et al 1987; Cantillo et al 1995). In most cases, each compartment consists of only a small number of closely related species, while species of particular interest are highlighted with their own compartments (e.g., spotted seatrout, red snapper, etc.). Compartment names are follow by a list of species representative of that specific unit, although none of the lists are exhaustive, unless otherwise specified.

C 53. Sharks - requiem sharks, such as Atlantic sharpnose shark *(Rhizoprionodon terraenovae)* and sandbar shark (*Carcharhinus plumbeus*), nurse shark (*Ginglymostoma cirratum*), lemon shark (*Negaprion brevirostris*) and bonnethead shark (*Sphyrna tiburo*).

C 54. Rays -Representative species: southern stingray (*Dasyatis americana*), spotted eagle ray (*Aetobatis narinari*) and cownose ray (*Rhinoptera bonasus*).

C 55. Tarpon - All fishes of the Family Elopidae, primarily tarpon (*Megalops atlanticus*) and ladyfish (*Elops saurus*).

C 56. Bonefish - *Albula vulpes*.

C 57. Sardines -yellowfin menhaden (*Brevoortia smithi*), red-ear sardine (*Harengula humeralis*), scaled sardine (*H. jaguana*), dwarf herring (*Jenkensia lamprotema*), Atlantic thread herring (*Opisthonema oglinum*) and spanish sardine (*Sardinella aurita*)

C 58. Anchovies - striped anchovy (*Anchoa hepsetus*), Cuban anchovy (*Anchoa cubana*), and flat anchovy (*Anchoviella perfasciata*).

C 59. Bay Anchovy - *Anchoa mitchilli*.

C 60. Lizardfish - *Synodus foetens*.

C 61. Catfish - Hardhead catfish (*Arius felis*) and gafftopsail catfish (*Bagre marinus*).

C 62. Eels -Contains: moray eels (Spotted Moray [*Gymnothorax moringa*] and blackedge moray [*G. nigromarginatus*]), Ophicthid eels (Key Worm Eel [*Ahilia egmontis*] and speckled worm eel [*Myrophis punctatus*]) and whip eel (*Bascanichthys scuticaris*).

C 63. Toadfish - *Opsanus beta*.

C 64. Brotulas and Batfishes - Bottom fishes exclusively: Brotulas (For example: *Gunterichthys longipenis*) and batfish (*Ogcocephalus radiatus*).

C 65. Halfbeaks - Hardhead halfbeak (*Chriodorus atherinoides*), ballyhoo (*Hemiramphus brasiliensis*), balao (*H. balao*) and halfbeak (*Hyporamphus unifasciatus*)

C 66. Needlefishes - Redfin needlefish (*Strongylura notata*), Atlantic needlefish (*S. marina*) and timucu (*S. timucu*).

C 67. Killifishes - All killifishes [excluding *Floridythes carpio* and *Lucania parva*]: Sheepshead minnow (*FBayrinodon variegatus*), marsh killifish (*Fundulus confluentus*), diamond killifish (*Adinia xenica*), golden top-minnow (*F. chrysotus*), gulf killifish (*F. grandis*) and Seminole killifish (*F. seminolis*).

C 68. Goldspotted killifish- *Floridythes carpio*.

C 69. Rainwater killifish- *Lucania parva*.

C 70. Snooks -Members of the Family Centropomidae. The most abundant member is

common snook (*Centropomus undecimalis*), with lesser numbers of fat snook (*C. parallelus*), swordspine snook (*C. ensiferus*) and tarpon snook (*C. pectinatus*).

C 71. Mollies - All Poecilids: Sailfin molly (*Poecila latipina*).

C 72. Silversides - Members of the Family Atherinidae: Hardhead silversides (*Atherinomorus stipes*), reef silversides (*Hypoatherina harringtonensis*), rough silversides (*Membras martinica*) and Atlantic silversides (*Menidia menidia*).

C 73. Seahorses - Seahorses and Pipfishes: Lined seahorse (*Hippocampus erectus*), pugnose pipefish (*Sygnathus dunkeri*) and dusky pipefish (*S. floridae*).

C 74. Gulf pipefish - *Sygnathus scovelli*.

C 75. Dwarf seahorse - *Hippocampus zosterae*.

C 76. Groupers - Contains all the groupers and sea basses of the Family Serranidae: Black sea bass (*Centropristis striata*), black grouper (*Mycteroperca bonaci*), gag (*M. microlepis*) and red grouper (*Epinephelus morio*).

C 77. Jacks and Runners - Contains the runners and jacks of the Carangidae Family: Banded rudderfish (*Seriola zonata*), blue runner (*Caranx crysos*), crevalle jack (*C. hippos*) and lesser amberjack (*S. fasciata*).

C 78. Pompano and Permits - The remaining Carangids: *Trachinotus carolinus* and *T. falcatus*, respectively.

C 79. Snappers - All members of Family Lutjanidae [excluding gray snapper]: Cubera snapper (*Lutjanus cyanopterus*), lane snapper (*L. Synagris*) schoolmaster (*L. apodus*) and mutton snapper (*L. analis*).

C 80. Gray Snapper - *Lutjanus griseus*.

C 81. Mojarras - Spotfin mojarra (*Eucinostomus argentus*), silver jenny (*E. gula*), yellowfin mojarra (*Geres cinereus*) and striped mojarra (*Diapterus plumieri*).

C 82. Grunts - White grunt (*Haemulon plumieri*), tomate (*H. aurolineatum*), sailor's choice (*H. parrai*) and pigfish (*Orthopristis chrysoptera*).

C 83. Porgies - sheepshead (*Archosargus probatocephalus*), grass porgy *(Calamus arctifrons*) and whitebone porgy (*C. leucosteus*).

C 84. Pinfish - *Lagodon rhomboideus*.

C 85. Sciaenids - Those members of Family Sciaenidae [excluding spotted seatrout and red drum]: Blue croaker (*Bairdella batabana*), silver perch (*B. chrysoura*), southern kingfish (*Menticirrhus americanus*) and black drum (*Pogonias cromis*).

C 86. Spotted Seatrout - *Cynoscion nebulosus*.

C 87. Red Drum - *Sciaenops ocellatus*.

C 88. Spadefish - *Chaetodipterus faber*.

C 89. Parrotfishes - Bluelip parrotfish (*Cryptotomus roseus*), emerald parrotfish (*Nicholsina usta*), redfin parrotfish (*Sparisoma rebripinne*) and redtail parrotfish (*S. chrysopterum*).

C 90. Mackerels - Spanish mackerel (*Scomberomorous maculatus*), king mackerel (*S. cavalla*) and cero mackerel (*S. regalis*).

C 91. Mullets - Striped mullet (*Mugil cephalus*), white mullet (*M. curema*) and fantail mullet (*M. gyrans*).

C 92. Barracudas - Great baracuda (*Sphyraena baracuda*) and guaguanche (*S. guachancho*).

C 93. Blennies - Comprised of members of Family Clinidae (bluethroat pikeblenny [*Chaenopsis ocellata*], banded blenny [*Paraclinus fasciatus*] and marbled blenny [*P. marmoratus*]) and Family Blennidae (Florida blenny [*Chasmodes saburrae*] and seaweed blenny [*Parablennius marmoreus*]).

C 94. Code Goby - *Gobiostoma robustum*.

C 95. Clown Goby - *Microgobius gulosus*.

C 96. Flatfishes - Fringed flounder (*Etropus crossotus*), ocellated flounder *(Ancylopsetta quadrocelata*), southern flounder (*Paralychthys lethostigma*), lined sole (*Achirus lineatus*) and scrawled sole (*Trinectes inscriptus*).

C 97. Filefishes/Triggerfishes - Orange filefish (*Aluterus schoepfi*), scrawled filefish (*A. scriptus*) and fringed filefish (*Monacanthus ciliatus*).

C 98. Pufferfishes/Burrfishes - Southern puffer (*Sphoeroides nephelus*), bandtail puffer (*S. splengleri*), striped burrfish (*Chilomycterus schoepfi*) and web burrfish (*C. antillarum*).

C 99. Other Pelagics Fishes -Any isolated temporary residents of a pelagic nature are in this compartment: Bluefish (*Pomatomus saltatrix*), Atlantic threadfin (*Polydactylus octonemus*) and cobia (*Rachycentron canadum*). Additionally, pelagic squids are also here. There is little information about the abundance of squids in Florida Bay, but they occupy a functional niche similar to that of the pelagic / open water residents of Florida Bay.

C 100. Other Demersals Fishes - This compartment contains all the canopy and benthic fishes that do not fit in any of the above compartments: Other Gobies (Frillfin Goby (*Bathygobius soporator*), Emerald Goby (*Gobiostoma smaragdus*), Naked Goby (*G. bosci*) and Dash Goby (*Gobionellus saepepallens*), Sargassumfish (*Histrio histrio*) and Boxfishes (*Lactophrys quadricornis* and *L. trigonus*).

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3.6 Birds

Taxonomy, feeding habits and available information played the main role in establishing the final list of birds compartments. The species list after each unit provides a representative sample:

C 101. Loon - Common loon (*Gavia immer*) and red-throated loon (*G. stellata*)

C 102. Greeb - Horned grebe (*Podiceps aurotus*) and pied-billed grebe (*Podilymbus podiceps*).

C 103. Pelican - White pelican (*Phaethon lepturus*), brown pelican (*Pelecanus occidentalis*) and magnificent frigatebird (*Fregata magnificens*).

C 104. Comorant - Double-crested cormorant (*Phalacrocorax aurotus*) and anhinga (*Anhinga anhinga*).

C 105. Big Herons & Egrets - Great blue heron (*Ardea herodias*), great white heron (*A. occidentalis*) and great egret (*Casmerodius albus*).

C 106. Small Herons & Egrets - Little blue heron (*Florida caerulea*), Louisiana heron (*Hydranassa tricolor*), and snowy egret (*Egretta thula*).

C 107. Ibis - White ibis (*Eudocimus albus*) and glossy ibis (*Plegadis falcinellus*).

C 108. Roseate Spoonbill - (*Ajaia ajaia*).

C 109. Herbivorous Ducks - Those species feeding primarily upon plant material: Blue-winged teal (*Anas discors*), green-winged teal (*Anas carolinensis*), shoveler (*Spatula clypeata*), American wigeon (*Mareca americana*) and pintail (*Anas acuta*).

C 110. Omnivorous Ducks - Contains generalist species such as lesser scaup (*Aythya affinis*), ring-necked duck (*Aythya collaris*), ruddy duck (*Oxyura jamaicensis*) and canvasback (*Aythya valisineria*).

C 111. Predatory Ducks - Species who prey primarily upon living animals: Red-breasted merganser (*Mergus merganser*) and hooded merganser (*Lophodytes cucullatus*).

C 112. Raptors - Bald eagle (*Haliaeetus leucocephalus*) and osprey (*Pandion haliaetus*).

C 113. Gruiformes - American coot (*Fulica americana*) and clapper rail (*Rallus longirostris*).

C 114. Small Shorebirds - Least sandpiper (*Erolia minutilla*), semipalmated sandpiper (*Ereunetes pusillus*), western sandpiper (*Ereunetes mauri*), short-billed dowitcher (*Limnodromus griseus*), Dunlin (*Erolia alpina*), willet (*Catoptrophorus semipalmatus*) and black-bellied plover (*Squatarola squatarola*).

C 115. Gulls & Terns - Black skimmer (*Rynchops nigra*), laughing gull (*Larus atricilla*) and ring-billed gull (*Larus delawarensis*).

C 116. Kingfisher - *Megaceryle alcyon.*

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3.4 Reptiles

In the Bay there are only four significative reptile species, each occupying their own compartment:

C 117. Crocodiles - *Crocodylus acutus.*

C 118. Loggerhead Turtle - *Caretta caretta.*

C 119. Green Turtle - *Chelonia mydas.*

C 120. Hawksbill Turtle - *Eretmochelys imbricata.*

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3.7 Mammals

Mammals are represented by two charismatic animals:

C 121. Dolphin - *Tursiops truncatus.*

C 122. Manatee - *Trichechus manatus.*

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3.8 Detrital Compartments

Detritus has been divided in three separate compartments:

C 123. Water POC - This compartment represents all the particulate non-living carbon floating in the water column, plus the attached bacterial community.

C 124. Benthic POC - Includes all the non-living organic carbon available in the first 10 centimeters of sediment, including seagrass litter.

C 125. DOC - This unit contains all the dissolved organic carbon present in the water column.

The stocks and activities of all 125 compartments vary during the course of the year. Seasonality at this latitude, however, is marked more by variations in freshwater input than by changing temperature. Thus, seasonality is depicted in the form of two separate networks -- one for the wet season (from June to November) when freshwater inputs are high and another for the dry season (December to May), when inputs are relatively low and the salinity is markedly higher.

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4. METHODS

After the "lexical" phase of model building, the next step involves connecting the selected compartments to one another via feeding and detrital pathways. This topology is determined from information about the diets of each taxon. But the purpose here is not merely to formulate a qualitative "foodweb". We wish to *quantify* the connections as well. Toward this end, it is useful to concentrate first on assessing the densities, or stocks of the particpating taxa. Knowing the concentration of biomass is the key to scaling all the activities of a particular population.

4.1 Estimation Techniques

The biomasses of some species are known with reasonable precision. For example, the number of animals per cubic meter or liter is available for many of the compartments. As the standard units used in NA are grams of carbon per square meter, the available data had to be transformed to maintain dimensional consistency. Towards this end, information on the average weight (grams) of animals was gathered from technical manuals. The percentage of carbon per gram of dry weight was then combined with wet weight/dry weight ratio to obtain gC/m^3 (in the case of number of animals per liter we just need a simple equation to transform gC/l in gC/m^3). By assuming an average water depth (Philips et al., 1995), the carbon biomasses in the required units, g/m^2, could be calculated. In the case of primary producers, most sources report data on biomass in grams per hectare or square meter. In this case only the wet weight/dry weight ratio and the percentage of carbon per gram of dry weight (Jorgensen et al., 1991) were necessary to convert the biomasses into the correct units. For water POC and DOC, concentration was reported in gC/l, and the above procedure was followed.

The conversions for benthic microalgae proceeded slightly differently. Data from Florida Bay were given in micrograms of chlorophyl-a per square meter. To convert these figures into carbon, a C/chl-a ratio of 50/1 was assumed as representative of living microalgae (Strickland, 1965).

The biomasses of several fish compartments (most of the popular game species) were also calculated differently than most of the others. Recreational catch and harvest data (1995 and 1996) from National Park Service angler surveys were used to calculate values for both biomass and harvest rates (Schmidt unpublished). Harvest rate was calculated by multiplying the mass of an average harvested fish by the total number harvested. This value was then scaled down to an amount per square meter. Biomass was estimated similarly, but also incorporated assumptions about how much of the total population was represented by the catch and harvest numbers (Baird and Ulanowicz 1989). The assumed ratio varied from species to species, with values depending upon the size of the harvest and an estimation of the effort expended. For example, spotted seatrout harvest was considered to represent a higher proportion of its population than did the tarpon catch. Thus, spotted seatrout was assigned a higher scaling parameter than tarpon, catches of which were considered to comprise a substantially lower fraction of the actual population size. Once the total population sizes were estimated, the same scaling was used to determine harvest rates, with the exception that the mass of an average fish for the biomass estimate was significantly lower than that used to scale the harvest rate. This reflected both the presence of juveniles in the populations and the length restrictions that regulate harvest efforts.

Once the biomass had been approximated, information was sought on the consumption rate (or primary production rate) per unit biomass of each species. Multiplying a biomass density by this factor establishes the total input to the compartment in question. At this point, if one has solid data on the dietary proportions of heterotrophs, the total input can be apportioned among the various prey, and the magnitudes of those transfers can be set. Unfortunately, the dietary components of some taxa are available only as a list of species. In such cases we had no other option but to apportion the total input to

the several prey in proportion to the standing stocks of those prey.

The two networks were assumed to balance over each season. While this is not entirely realistic, balance is required for the critical input/output phase of NA (described below.) Furthermore, assuming balance facilitates the estimation of many rates. For example, when a component is balanced, its total output can be equated to its total input (as just described.) It remains to apportion this compartmental "throughput" among the output processes respiration, excretion, natural mortality and losses to predation. Fortunately, respiration and excretion rates per unit biomass are available from the literature for most species, so that these outputs can be established immediately. Most of the losses to predation are reckoned from the predator (input) side, as described above.

At this point, the balance is almost complete. It remains to estimate the exchanges of carbon with the outside world. Exogenous imports occur in three different ways: (1) Carbon from the atmosphere may be fixed as biomass through the process of photosynthesis. The magnitude of this import is assessed by multiplying the standing stock of the autotroph by its primary productivity per unit carbon, as mentioned above. (2) Biomass may enter or leave the system advected by water flow into and out of the study area. These exchanges can be estimated from the overall water budget for the bay, which includes figures for gross advective water exchange with the surrounding areas (Lutz, 1997). Multiplying these water exchanges by the concentrations of carbon suspended in the water column will provide an approximation for these exogenous transfers. (3) Biomass may enter and leave the system as animal populations migrate across the boundaries of the study area.

Migration applies to many animals species in the model, including invertebrates, fishes and birds. Florida Bay serves as a nursery ground for a variety of species of fish and invertebrates, including approximately 22 taxa (Davis et al., 1994). At various lifestages, some species move in or out the bay. For example, species such as red drum and gray snapper utilize the bay as juveniles and move offshore as they mature (Florida DEP 1997). This migration of post-juvenile fishes accounts for the net export of fish biomass from the system. The opposite situation represents inputs to the system, as in the case of stone crab. Emigrations, i.e., flows of carbon leaving the system, are considered like any other export, but immigration flows are treated differently. Migratory imports were considered separately during the trophic analysis section of NA so as to avoid compartments like snook and meroplankton from mistakenly being perceived as primary producers. Exactly how this was done will be explained more in detail in the next section.

Movements by avifauna worked a little differently than with fish. Some birds might nest in the bay, but then leave temporarily to feed elsewhere. Such feeding should be classified as an import to the system. Furthermore, different types of birds exhibit different feeding techniques. For example, some need high water levels and others, low. It also may happen that birds nest on the mainland and come to feed in the bay. This activity would constitute an export from the system. Due to the lack of detailed information on these aspects of feeding, we have assumed that such imports and outputs balance. That is, all the birds in the model are assumed to feed inside the bay, and none enter from outside simply to feed.

Another important export is related to fishing pressure. Most commercial harvests had been suspended by the early 1950's and the remainder were phased out by 1985. Nowadays, recreational fishing accounts for the entire harvest in Florida Bay, and it represent a net output of carbon. The data on harvested fish and shellfish come from the NPS harvest monitoring program for south Florida (Schmidt, unpublished data).

The estimation of all the flows entering and leaving each compartment now have been described. Of course, uncertainties inherent in these partially independent estimations will keep many of the compartments from balancing exactly. The degree of imbalance can be computed by entering the

existing flow estimates into a spreadsheet format (EXCEL[TM] was used for this purpose.) One may then compare the marginal sums of inputs to and outputs from each compartment to identify those that are most out-of-balance. The investigator has several options for treating an imbalanced compartment. If the imbalance is severe, it is probably best to recheck the sources and the arithmetic. Failing the discovery of an error, one might search for other references to cross-check the data being used.

If no amendments to a compartmental budget can be made on the basis of new data, some investigators prefer to bring the system nearly into balance by adjusting the least-well known flows. Others would rather maintain the flow proportions for each compartment as they appear in the literature and to rebalance the whole system under the covering assumption of linear, donor-control, which always maintains flows positive (Ulanowicz 1989). In this study all compartments could be balanced to within a few percent using literature values, and final balance was achieved using the program DATBAL, which assumes linear, donor control.

The resulting networks are too large and complicated to display easily as illustrations. Even a matrix representation of one such network spans several pages and is extremely cumbersome to use. For these reasons, we elected to follow the precedent we set last year and present our detailed results in hypertext format. The user is strongly urged to access the results over the World Wide Web at <http://www.cbl.cees.edu/~bonda/ATLSS.html>. There one may follow simple instructions to locate the estimated value of any stock or flow in either the wet or dry season. Furthermore, the entire rationale and associated references pertaining to the estimation of any particular value have been documented in hypertext. By pointing and clicking one may examine a trophic flow network in minute detail never before available for a network of such size and complexity.

The authors feel that this format for disseminating the network results should have important benefits for ecosystem science in general and for the visibility of the ATLSS endeavor in particular. We are aware of no other single source where the structural elements of entire ecosystems can be examined and scrutinized so readily. Even if a user has no idea of the benefits of NA, he/she can begin with the species that interests them most and trace the sources and fates of material in that compartment -- simply by pointing and clicking. The presentation also makes it easier to critique the networks, and online suggestions for improvements and amendments are welcomed.

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4.2 Network Analysis

4.2.1 Background

Sometime during the mid-1970's it became apparent that ecological modeling in the form of a set of coupled, deterministic differential equations was a problematical undertaking that required support from other, independent methods for systems analysis. In the search for parallel methods of describing the behavior of total ecosystems, various computations performed on the underlying network of trophic flows have figured prominently (SCOR, 1981).

The original impetus for diverting attention from dynamics and concentrating analysis on flow structure came from the field of economics, where success in elucidating indirect economic effects had been achieved by manipulations on matrices of economic flows (Leontief, 1951; Hannon, 1973). Thereafter followed a number of other topological treatments of the underlying flow graph (e.g., Finn, 1976;

Levine, 1980; Patten et al., 1976; Ulanowicz and Kemp, 1979). Eventually, Ulanowicz collected most of the methods for analyzing flow networks into a single executable package, called NETWRK (Ulanowicz and Kay 1991.) NETWRK 4.2 is the version used in this analysis.

Four types of analyses are performed by NETWRK. First, so- called input- output structure matrices are calculated. These allow the user to look in detail at the effects, both direct and indirect, that any particular flow or transformation might have on any other given species or flow. Next, the graph is mapped into a concatenated trophic chain (after Lindeman 1942). Then global variables describing the state of development of the network are presented. Finally, all the simple, directed biogeochemical cycles are identified and separated from their supporting dissipative flows. NETWRK 4.2 and its accompanying documentation may be downloaded from the WorldWide Web at <http://www.cbl.cees.edu/~ulan/ntwk/network.html>.

In addition to NETWRK, a package called IMPACTS was used to gauge both the positive and negative, direct and indirect impacts that heterotrophic predation may cause. The method was described in Ulanowicz and Puccia (1990). Of particular interest is how negative impacts at one level can ramify to become positive indirect effects.

The data required to run either of these programs have already been discussed. Above it was detailled how, for each compartment, it is necessary to know: (1) all the inputs from outside the system, (2) all the various inputs flowing from other compartments of the system, (3) all the outputs which flow as inputs to other compartments, (4) all exports of useful medium outside the system, and (5) all rates of dissipation of medium. Each of these flows can be represented by a positive scalar element of a matrix or a vector; the absence of a flow can be represented by a zero.

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4.2.2 Input/Output Analysis

The initial section of the NETWRK package is founded upon an ecological variation of input-output analysis. So- called "total contribution coefficients" (Szyrmer and Ulanowicz 1987) are calculated that describe exactly what fraction of the total amount leaving compartment i (prey or row designation) eventually enters compartment j (predator or column designation) over all pathways, both direct and indirect. Alternatively, the "total dependency coefficients" portray the fraction of the total ingestion by j which passed through compartment i along its way to j. The columns of this matrix are particularly useful in that they portray the "extended diet" of the species in question (or, correspondingly, the trophic "pyramid" that underlies each heterotroph.) As we demonstrated last year with the cypress wetland ecosystem, such indirect ratios can provide valuable information about how a system is functioning.

As an example of indirect diet coefficients, we consider the predatory gastropods (#34). They depend on the prey items bivalves (#31), detritivorous gastropods (#32) and catfish (#61) for about 90% of their sustenance. These prey items in their turn depend upon primary producers, such as Synedococcus (#2), benthic phytoplankton (#8), Thalassia (#9), and drift algae (#13), so that ca. 76% of the consumption by predatory gastropods originates from these compartments. In addition, detritus suspended in the water column (#123) and settled in the benthos (#124) also sustain the prey of the predatory gastropods by contributing indirectly some 47% of the intake by this predator. That is, carbon is counted more than once as it passes up the foodchain, and the fact that all of the above dependencies sum to over 200% is entirely consistent with the fact that predatory gastropods feed, on the average, at about trophic level 3.4.

Hannon (1973), Finn (1976), Levine (1980) and Patten et al. (1976) give various examples of how one may employ input-output analysis. One highly useful such application is the decomposition of the graph according to each input. That is, the eventual fate of each of the nonzero inputs to the system is traced independently of the other inputs to the system. Not only does this decomposition portray the isolated effects of the various inputs, but these sub-networks can be linearly recombined to recreate what the effects of any other combination of inputs would be, if the flow structure were kept the same.

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4.2.3 Trophic Aggregation

The second section of output from NETWRK interprets the given network according to the trophic concepts of Lindeman (1942). Of course, it is impossible to relegate omnivorous heterotrophs entirely to a single trophic level, but Ulanowicz and Kemp (1979) indicated how input-output techniques could be used to apportion the activities of omnivores among a series of integer trophic levels. This method has been expanded to include the effects of biogeochemical cycles by Ulanowicz (1995a).

In order for trophic aggregation to be meaningful, it is necessary that trophic pathways among living compartments remain finite in length, otherwise one is forced to interpret an infinite regress of trophic levels. Fortunately, Pimm (1982) states that cycles among living taxa are rare in ecosystem networks (although we shall encounter some interesting exceptions in the cypress networks.) The absence of such feeding cycles avoids trophic pathways of infinite length. As a preliminary to trophic aggregation, therefore, all cycles flowing only through active feeding links are first removed from the network. So long as the Finn cycling index for such heterotrophic cycling (see below) remains sufficiently small (say, below two percent or so), no appreciable distortion of results should ensue. The 2% requirement is more than satisfied by the Florida Bay networks.

When the fractions by which each component feeds at a particular trophic level are weighted by the value of that trophic level and the results are summed, one arrives at the effective trophic level for the given species (Levine 1980.) For example, if a species or compartment is receiving 15 units of medium along a pathway of length 2 and 5 units along a pathway of length 3, then it is acting 75% as a herbivore (trophic level=2) and 25% as a carnivore (level=3). The effective trophic position becomes (.75 x 2)+ (.25 x 3)=1.75. It is often interesting to compare the average trophic position of species under different circumstances (as is done below for the wet and dry seasons.)

The section on trophic aggregation culminates with the partitioning of activity into a trophic "chain" of transfers along aggregations of heterotrophs. Each such integer aggregation feeds back into detrital return loops. Such a depiction of the underlying trophic dynamics has been termed "canonical" by Ulanowicz (1995a), because any ecosystem can be mapped into this equivalent and simple form to allow the relative magnitudes of corresponding flows to be compared directly.

One change made recently as part of NETWRK, version 4.2 was to treat migratory inputs of heterotrophs differently than inputs to autotrophs (primary production.) NETWRK now treats inputs to heterotrophs as coming into the system at exactly the same trophic level as the receiving compartment occupies within the system. (Previously such inputs were automatically treated as primary production, and this unrealistic assumption artificially deflated many of the reported trophic levels.)

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4.2.4 System-Level Indices

The next section of output from NETWRK provides values for global attributes of the network that were defined by several information theorists to gauge the pattern of development in ecosystems (Ulanowicz, 1980,1986; Hirata and Ulanowicz, 1984; Ulanowicz and Norden, 1990). One begins by calculating the "total system throughput", or the gross sum of *all* transfers, to act as a measure of the size of the system. Multiplying the total throughput by the system indeterminacy (according to the Shannon Wiener formula) of the individual flows yields what has been termed the "development capacity" of the system. This quantity serves as an upper bound on the ascendency, which is a measure of the network's potential for competitive advantage over other real or putative network configurations. Ascendency is the product of a factor of size (total system throughput) times a factor representing the coherence of the flows (the average mutual information of the flow structure.)

The difference between the realized structure and its upper bound is the overhead (Ulanowicz, 1986). Overhead has conflicting interpretations. On one hand, it is a catchall for the system's inefficiencies in processing material and energy. What is a disadvantage under benign conditions can turn in the system's favor when it is perturbed in some novel way. Then, the overhead represents a "strength-in-reserve" of degrees of freedom which the system can utilize to adapt to the new threat. Overhead is generated in any of four ways: there is overhead due to indeterminacy of imports, exports, dissipations (respirations), and about which of several parallel pathways flow will proceed between any two nodes (redundancy.) The fractions of the development capacity encumbered by the ascendency and by each of the overhead components provide a profile of the structural composition of the system that often is useful for assessing the organizational status of a system.

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4.2.5 Cycles

Most networks of ecosystem flows contain cycles of material or energy, and the magnitude and structure of these cycles is fully described by NETWRK. The program enumerates all of the simple cycles in the given matrix of exchanges (an overwhelming task, as we shall see in the case of the Florida Bay networks.) Furthermore, the simple cycles are grouped into "nexuses" of cycles all of which share the same "weak arc." A weak arc is defined here as the smallest flow in a given directed cycle. The assumption is that the weak arc is the limiting or controlling link in a cycle, and that by grouping according to critical links, one identifies the domain of influence for each weak arc. Presumably, any change in a weak arc will propagate throughout its associated nexus. The nexuses are listed roughly according to ascending order of the magnitude of their defining weak arcs.

The cycles are then subtracted from the network in a fashion described in detail by Ulanowicz (1983). Briefly, the magnitude of flow in the smallest weak arc is distributed over the flows in that particular nexus and the resulting amounts are subtracted from each arc in that nexus. This process zeroes the weak arc, thereby eliminating all the cycles in that nexus, but it does not disturb the balance around any compartment, nor does it change any exogenous input, export or respiration. None of the remaining arcs of the nexus are driven negative. After that nexus has been removed, the next smallest weak arc is located; and nexuses are subtracted iteratively until all cycles have been removed from the network.

As each cycle is removed, the flow associated with that cycle is added to the magnitudes of other cycles of the same trophic length. The end result is a distribution of the magnitude of cycling according to the trophic length of cycles. This profile could be useful in assessing system response to perturbation. For example, cycling via the larger loops is often more sensitive to disturbance. The cycle distribution is then normalized by the total system throughput. Summing this normalized distribution yields the Finn cycling index, which is the fraction of total activity that is devoted to cycling (Finn 1976).

Finally, the separation of cycled from transient flow is reported in the form of separate matrices for each type of flow. The row sums and column sums of the matrix of aggregated cycles will always balance; no further reference to exogenous exchanges is necessary. The visual structure of the aggregated cycles existing in more complicated networks very often reveals separate domains of control in the network (e.g, Baird & Ulanowicz 1989). Finally, it should be remarked that the starting network has been neatly decomposed into an acyclic "tree" of dissipative flows and a wholly conservative nexus of cycled flows.

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4.2.6 Trophic Impacts

NETWRK treats only positive mass flows and does not consider the propagation of the negative effects that accompany predation. Ulanowicz and Puccia (1990) outlined how to treat the propagation of both positive and negative trophic effects, and their technique has been implemented in the algorithm, IMPACTS. For any particular component (designated as the "focal taxon"), IMPACTS provides a ranked listing of all the positive and negative impacts (both direct and indirect) upon that focal species. Also a ranked listing of all the direct and indirect trophic effects that focal species has upon all the other taxa is likewise presented. Of special interest are those predators that exert a direct negative impact upon a prey, but whose combined indirect positive influences more than compensate the prey for its direct losses. Such "beneficial predators" are more common than might be supposed and often highlight particular ecological roles that otherwise might have gone unnoticed. IMPACTS can be downloaded from <http://www.cbl.cees.edu/~ulan/ntwk/network.html>.

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5. RESULTS

5.1 Input/Output Analysis

Perhaps the most useful indices to result from the Input/Output section of NETWRK are the "total dependency coefficients" (Szyrmer and Ulanowicz 1987) or, more appropriately, the "indirect diets" of each taxon. By reading down the column of these dependency coefficients one notes the quantitative trophic history of material reaching that given compartment.

Last year, significant insights into the workings of the cypress ecosystem were revealed by observing how the various heterotrophs depended upon the suite of primary producers. Looking at the total dependency coefficients (TDC's) of the heterptrophs in Florida Bay reveals that a major fraction of the carbon reaching many of the predators originates in the seagrasses and epiphytes. The Florida Bay network includes 14 primary producer compartments. Phytoplankton has been separated into seven different compartments and seagrasses into three distinct units. In order to achieve a better understanding of the contributions of the various groups of primary producers to the higher trophic levels, we summed the dependency coefficients on all the seagrasses (9, 10, 11) and those on the phytoplankton compartments (1, 2, 3, 4, 5, 6, 7) and compared these two groups with the dependencies on other primary producers: Benthic phytoplankton (8), Roots (12), drift algae (13) and Epiphytes (14).

During the wet season, about 50% of the compartments were most dependent on seagrasses (Table 1), and the value of the TDC's varied from 25 to 60%. The manatee and green turtle diets are anchored on seagrasses, primarily Thalassia, and these two compartments had the highest dependencies coefficients (61% and 59% respectively) of all. The second most important group during the wet season is "Epiphytes" -- 30% of all compartments depend mostly on them. Invertebrates, such as pink shrimp and some species of gastropods, feed almost entirely on epiphytes. During the dry season seagrasses and epiphytes also dominate most indirect diets, with the seagrasses being the lesser in importance. 47% of all compartments depend more on epiphytes than on any other primary producer (for seagrasses the percentage was 32.) Hence, analysis of the total dependency coefficients yields interesting contrasts between the two study periods: Epiphytes are more important during the dry season, while seagrasses are dominant during the wet. Such dominance follows the trend in their respective biomasses, (Epiphytes have higher biomass during the dry season, while seagrasses prevail during the wet.) Together these two compartments provide by far the largest sources of carbon to the system.

Despite the importance of these two groups of producers, not many compartments feed *directly* on epiphytes and seagrasses, i.e., only a minor fraction of their production is grazed by herbivores. This observation is buttressed by the low ecotrophic efficiencies calculated for epiphytes and the even lower value for the seagrass species (Fig. 2 and Fig. 3). The overall dependency on these primary producers is manly via indirect pathways that involve the detrital compartments 123, 124 and 125.

Summing the dependency coefficients on all primary producers for each compartment reveals that, in most instances, the result is close to 100%. This shows that the system depends mainly on internal carbon fixation and receives only a very small subsidy from outside the system. There is one significant exception that occurs during the wet seasons. The stone crabs (#52) depend on internal carbon for only 65% of their sustenance, deriving a significant percentage of their support from outside the bay via massive migrations during the wet period.

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5.2 Trophic Impacts

Impact analysis is used to study indirect effects between compartments. In high- dimensional networks such as the one studied here, every pair of compartments is connected, at least indirectly. Coefficients in the impact matrix represent the *aggregated* (positive and negative) indirect effects between two species.

Of special interest are those compartments that function as "beneficial predators". The direct impact of a predator upon its prey is obviously negative; however, the overall effect can become positive, due to the potential for compensation via multiple indirect pathways. In such cases we speak of "beneficial predators". In last year's cypress networks, beneficial predation was quite abundant. The American alligator, for example was a net benefactor to 11 of its prey items.

In Florida Bay network the number of beneficial indirect links is exceedingly high. During the wet season there were 282 such interactions, and and the number during the dry period is slightly higher, with 294 links. The number of predators that exert a positive action on their prey are 71 and 74 for the wet and dry season, respectively, so that at least some predators are beneficial to more than one prey type. In table 2 and table 3 are listed all the beneficent predators during either season, together with the number of prey that each positively impact.

The "Other demersal fishes" compartment benefits the largest number of prey: During the wet season, it exerts positive effect upon 12 of its prey. During the same time period we note six other compartments that benefit 10 or more prey items: Sharks (10), Scianids (11), Flatfish (10), Greeb (10), Ibis (10) and Predatory ducks (10). In the dry season, those compartments that benefit the largest number of prey are: Scianids (11), Other demersal fishes (11), Big herons & egrets (10), Ibis (11) and Predatory ducks (10).

Although the number of beneficial links is high, the magnitude of the action is, in many cases, not very strong. In tables 2 and 3, we report the most significant positive impacts. (A significant impact is one in which more than 1% of the throughput of the prey compartment is affected. During the dry season only seven links from among 294 exceed the threshold, and none does so by more than 2%. The strongest beneficial action (1.96%) is exerted by the predator Echinoderma (#30) on their Isopod prey (#42). During the wet season the proportion of significant positive effects is slightly higher: ten out of 282. The strongest effect is by Dwarf seahorses (#75), which benefit the throughput of Herbivorous shrimp (#43) by 6.1%.

Although only a small minority of the number of beneficial predator interactions are of significant magnitude, in some cases more than a single predator affects the same prey in a net positive manner. Adding together all the positive effects by multiple predators, one obtains the total positive impact by the several predators (Table 4). In addition to those links cited above, six other prey receive significant benefit from a combination of predators during the wet season: Benthic ciliates (#25), Detritivorous gastropods (#32), Macrobenthos (#38), Herbivorous amphipods (#40), Predatory shrimp (#44) and Detritivorous crabs (#48). During the dry season, the number the number receiving significant combined benefits more than doubles (to 16.) Most of these prey are invertebrates or lower trophic level compartments with the exception of two fish populations: Clown goby (#95) and Other demersal fishes (#100.)

Having considered and identified instances of beneficial predation, one should also consider whether the reverse relationship might be possible, i.e., that the overall effect of a host on its predator over all pathways, direct and indirect, is negative. In such case we talk of a "malefic prey". A search of the

Florida Bay network uncovers 278 cases of "malefic" links during the wet season and 283 for the dry. A total of 70 prey affect their predators negatively in the wet period and 68 in the dry (Tab. 5). Predatory shrimps (#44), produce the highest number of negative indirect effects on its predators during both seasons, adversely affecting some 29 prey during the dry period. Other compartments exerting a substantial number of adverse indirect impacts upon its predators are: Paracalanus (#20), Predatory gastropods (#34), Predatory polychaetes (#36) and Callinectes sapidus (#51) (Table 5).

In comparing the "beneficial predator" links with the "malefic prey" interactions it was discovered that many pairings involved the same compartments. In fact, when a predator is beneficial to its prey, in 30% of those cases the prey is also malefic to that predator. This result is most interesting because it implies that the overall effect of the prey-predator relationship is completely the opposite of the direct effects. In the Florida bay network this circumstance occurs 89 times during the wet season and 107 during the dry.

Indirect interactions are very complicated in the context of a 125 component food web. Nevertheless, we consider this analysis a very important component of our study and intend to press the analysis further. A first step in this direction has already been taken. A program, PATHS has been written to identify all possible (direct and indirect) simple pathways connecting any two components. The output also provides the magnitude flowing over each route. Pathways playing strong roles in propagating indirect effect will be singled out and studied in detail.

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5.3 Trophic Levels

The average trophic rank of the species in Florida Bay ranged from the usual 1.0 for primary producers to a high of 4.6 for raptors during the wet season. In fact, 20 compartments during the wet season fed at average trophic levels greater than 4.0 (and 17 during the dry.)

In agreement with conventional wisdom, these average trophic levels were well below the limit of 5.0 postulated by (Pimm and Lawton, 1977) All of which is not to say that food chains longer than 5 links do not exist in the Florida Bay ecosystem. There were an enormous number of feeding pathways that exceeded five links. In fact, there even exist at least 4 pathways of transfers among living compartments 16 units long! One such long concatenation is from the benthic phytoplankton (#8) to the anchovy (#58) along 15 intermediaries:

Benthic phytoplankton Benthic flagellates --> Benthic ciliates --> Meiofauna --> Macrobenthos --> Pink Shrimp --> Blennies --> Toadfish --> Flatfish --> Other Dermersal Fishes --> Lizardfish --> Eels --> Brotalus --> Catfish --> Predatory Gastropods --> Anchovy

The probability of traversing this pathway is extremely small, but there is nothing to prohibit it outright.

On balance, trophic levels tended to be higher during the dry season. Seventy- five of the 125 components fed higher on the ladder during the dry season vs. only 24 during the wet. Those that gained most during the dry season were the sharks (#53) and other pelagic fishes (#99), both of which feed about 1/2 trophic level higher during the dry season. Grouper (#76), Detritivorous Crabs (#48) and Puffers (#98) rose by about half as much. Gains during the wet season were nowhere near as marked. Other demersal fishes (#100) increased by less than 1/5 a trophic level, and Dwarf Seahorse (#75) by half that amount. It appears that the pelagic chain is augmented somewhat during the dry season over

how it performs during the rainy period.

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5.4 System Level Indices

The whole- system indices for Florida Bay show remarkably little change between wet and dry seasons (Table 6). On first glance this may hardly seem to be the case, as the values during the wet season are mostly about 37% greater that their counterparts during the dry period. Further study reveals, however, that this difference in magnitude is caused almost exclusively by the change in the activity levels (total system throughputs) between the two seasons (2534 $mgC/m^2/y$ during the wet season vs. 1841 in the dry.) Otherwise, the fractions of ascendency vs. Redundancy and the distributions of the components of the overhead are almost identical during both seasons, indicating a remarkably stable ecosystem structure.

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5.5 Cycling

Never before has an ecosystem been parsed quantitatively to the level of resolution accomplished in this study of Florida Bay. With 125 compartments in the trophic flow network the number of *potential* pathways for recycling carbon is proportional to 125-factorial -- an immense number. Of course, the network is not fully connected, which reduces the number of potential cycles considerably. Nonetheless, the number of simple cycles in the Florida Bay network remains enormous. Counting them using the standard algorithm in NETWRK 4.2 was broken off after registering ca. 10 billion cycles! All is not lost, however, so long as one's purpose is simply to separate the cycled flow from the supporting straight throughput. Most of the overwhelming number of simple cycles involve more than one detrital component. As an approximation, one may choose to ignore those cycles that contain more than one nonliving compartment. The identification of such "single-detritus" cycles can be achieved first by removing the cycles that contain no detrital links, and then by successively adding the detrital compartments into the search, one at a time. The number of cycles counted in this manner will be a radical underestimate of the total number of cycles present, but once they have been extracted from the network, the residual graph will contain no cycles.

Even this simplification took considerable computing power to execute. The wet season apparently contains fewer routes for recycle, and the abbreviated algorithm took over two weeks to execute on a SPARC-Ultra. As of the time of this report, the analysis of the dry season is still underway after more than 3 weeks of runtime. Fortunately, the results from the wet season analysis probably give us a reasonable picture of what is going on in the Bay as concerns the recycling of carbon.

The first stage in the cycle analysis was the removal of the cycles that contain no nonliving compartments. These are generally rare in most ecosystems (Pimm 1982). There were 66 such cycles

during the wet season in Florida Bay. The cycle of greatest magnitude, Predatory Shrimp (#44) --> Other Cnidaridae (#29) --> Echinoderma (#30) --> Predatory polychaetes (#36) --> Predatory Shrimp (#44) is traversed by only 0.01 $MgC/m^2/y$.

By far the greatest number of cycles (5,846,035 to be exact) were associated with the pelagic POC (#123). Again, most nexuses (groupings according to smallest link) were created by transfers that were relatively small in magnitude, however, those nexuses behind the bulk of the carbon cycling through the pelagic POC were rather simple in structure. The key player in cycling of carbon through the pelagic POC are the pelagic flagellates (#16). Approximately 152 $mgC/m^2/y$ of carbon is ingested by the flagellates and recycled, either directly, via the aggregated zooplankton (#'s 18, 19, 21, and 23) or via the pelagic ciliates (Fig 4). The fuel for this recycling is provided to the flagellates for the most part by the Synedoccocus phytoplankton (#2) and the Free Bacteria (#15).

A relatively smaller number of cycles (82,950) was responsible for recycle through the benthic POC (#124). (The relative numbers associated with pelagic and benthic POC pools are probably an artifact of the order in which these components were added into the search. Had the benthic pool been invoked first, the relative numbers would likely have been reversed.) Interestingly, the trophic structure by which most of the carbon is recycled in the benthos proved strikingly parallel to that just described in the water column. The benthic flagellates (#24) consumed 92.2 $mgC/m^2/y$ of sediment POC that they subsequently recycled, either via the Meiofauna (#26) or via the Benthic ciliates (#25). The topology of this recycle subnetwork (Fig 5) is almost identical to that by which recycling is effected in the water column. In the benthos the meiofauna play the part of the zooplankton in the water column. In addition, they also directly recycle a considerable amount of POC.

Summing all the cycled flows in the ecosystem, one estimates that some 670 $mgC/m^2/y$ of carbon are being cycled in the ecosystem. This implies the Finn Cycling index for carbon is at exceeds 26% -- a very high figure for this non-conservative element. By way of comparison, the corresponding index in Chesapeake Bay is 21% and in the Big Cypress ecosystem it was a low 9%. Only coral reef ecosystems exhibit higher Finn indices. It is evident that much of the higher trophic production in the Florida Bay ecosystem owes to the activities of the flagellate community, as abetted by the zooplankton, meiofauna and ciliates.

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6. CONCLUDING REMARKS

It should come as no surprise that production by seagrasses provides the primary fuel for higher trophic level processes during the wet season. It is interesting, however, that during the dry period, the dominant source of carbon for system comes from the epiphytic periphyton that grows on the seagrasses. Epiphytic growth has been much-neglected as a source of primary production in aquatic ecosystems (Kitting et al. 1984, Ulanowicz 1995b), and the results on Florida Bay only underscore the priority that should be accorded this important ecosystem process.

The possibility that certain predator-prey relationships might actually be "inverted" opens up a potentially fertile field for further study. Exactly why such feeding relationships should persist in the face of their ostensibly "counterproductive" nature is an intriguing academic question that we intend to pursue further. From a quantitative standpoint, however, the magnitudes of the counterintuitive relationships are not so overwhelming as to seriously affect the ATLSS modeling exercise and so will not be pursued further here.

It is not yet clear exactly why organisms should tend to feed higher on the foodchain during the dry season, but this question will be clarified and illustrated with detailed examples before these results are prepared for publication in the peer- reviewed literature.

It is intriguing that the Finn cycling index should be so high in the Florida Bay ecosystem. At >26% it is significantly greater than the amount recycled in Chesapeake Bay -- the archtype for estuaries. This imposing rate of recycle is mediated, for the most part, by organisms that heretofore have received little attention in Florida Bay -- the flagellate community. We urge that our results concerning the pathways for significant cycling be tested through further field studies.

7. ACKNOWLEDGMENTS

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Network Analysis of Trophic Dynamics in South Florida Ecosystem, FY 98: The Mangrove Ecosystem

Robert E. Ulanowicz, Cristina Bondavalli, Johanna J. Heymans, Michael S. Egnotovich

University of Maryland System, Chesapeake Biological Laboratory, Solomons, MD 20688-0038

E-mail: ulan@cbl.umces.edu
Tel: (410) 326-7266
FAX: (410) 326-7378

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EXECUTIVE SUMMARY

A 94- component budget of the carbon exchanges occurring during the wet and dry seasons in the mangrove ecosystem of South Florida has been assembled. These trophic networks will serve as independent benchmarks against which the performance of the ATLSS multi-model, now under construction, will be assessed. As is the case with such detailed, quantitative descriptions of ecosystems, the overall configuration of trophic transfers yields numerous clues as to how the ecosystem is functioning:

Study of the indirect dependencies within the system reveals that the mangrove ecosystem for the most part is functioning like a detrital- based ecosystem. (This was not the case with the cypress ecosystem.) Most of the predator compartments depended ultimately upon detrital carbon for their sustenance. Exceptions to this pattern were the mammals, which depended more upon herbivorous rather than detritivorous prey. The mangrove ecosystem was observed to depend mainly upon internal fixation of carbon and receives only a small subsidy from elsewhere. Most of this subsidy is imported by the birds, which obtain 20% of their sustenance outside the mangroves. There were over 200 instances of "beneficial predation", i.e., instances where the positive indirect trophic benefits of a predator more than outweighed their direct negative impacts. In a full 30% of these instances, the prey had a net overall negative (malefic) effect upon its predator. That is, with at least 60 of the trophic processes in the mangrove ecosystem, the net overall effects of predation are exactly opposite to the direct effects. Like with the Florida Bay ecosystem, the birds fed at the highest trophic levels and on average feed a full trophic level higher than they do in the cypress swamps. This accords with the underlying trophic efficiencies, which ran only slightly lower than their counterparts in Florida Bay, but some 15% higher than in the swamps. No significant differences between wet and dry seasons were observed in the trophic statuses of the various mangrove compartments.

There were an enormous number of pathways for recycle of carbon in the mangrove ecosystem (more than could be easily handled by the computing machinery available), but fully 97.5% of all recycle activity occurred along only 15 cycles. Like with other estuaries, these cycles occurred among the benthic compartments. The main route for recycle was mediated by the sediment bacteria and the meiofauna, with auxiliary routes passing through the benthic flagellates and ciliates. The proportion of activity devoted to recycle (Finn Index) was 17.2%, which is comparable to other estuaries, comparable to Florida Bay, but much higher than in the cypress swamps.

From a whole- system perspective, the mangrove ecosystem shows virtually the same rate of trophic activity as is found in Florida Bay. The trophic network is not quite as rigidly organized as that in the Bay, however, because the system ascendency of Bay community exceeds that of the mangrove ecosystem by about 25%. As with the cypress system, the rare feline predators contributed the most to the community ascendency per unit of their aggregate activity. Whole- system information indices painted a picture of the mangrove ecosystem as being subjected to heavy natural stressors (presumeably osmotic in nature.) By comparison, the cypress swamp exhibited depressed activity, probably due to nutrient limitation. A surprising result was that Florida Bay, despite its recent erratic changes in biota, seemed to be the least stressed of the three ecosystems. Of all the three systems studied to date, the mangrove community showed least change between seasons.

PAST WORK

This report covers work done during the third year of a four year task under ATLSS to quantify the trophic processes in South Florida ecosystems. During the first year, 1996-7, a 69-compartment network of trophic exchanges in the cypress wetlands was constructed and analyzed. The analysis revealed that the higher trophic populations in the ecosystem were not as dependent on cypress litterfall, as had been assumed. Rather, most of the litterfall was being buried in the sediments of this peat- building system. Many of the upper trophic components were being supported instead by the production of the understory vegetation. Relatively little recycling occurs in this ecosystem. Despite the lack of physical advection in the horizontal dimension, most system activity resembles a pass- thru system in the vertical direction, i.e., litter falling and being buried in the sediments. An attempt was made for the first time to assess the "intrinsic value" of each ecosystem component in terms of the amount it contributes per unit of activity to the overall performance of the system at processing mass and energy (the ascendency.) This evaluation revealed that rare and endangered species, such as the Florida panther, were contributing more per unit of activity than some taxa that feed at higher trophic levels. Finally, the key role of the American Alligator in maintaining the species diversity of this ecosystem was highlighted and quantified through a method called "impact analysis." Eleven items in the diet of the alligator derived overall (indirect) benefit from the alligator's eating habits.

During the 1997-8 reporting period a 125- compartment network of the trophic flows through the ecosystem of Florida Bay was estimated for both wet and dry seasons. These networks stand as the most highly- resolved and complete foodwebs ever to be assembled. Analysis of the network revealed that seagrasses are the ultimate source of reduced carbon for most of the rest of the system during the wet season, but that epiphytic periphyton supports most ecological activity during the dry period. Although 37% more activity transpires in the Bay during the wet season, most species feed higher on the food chain during the dry months. Concatonations as long as 15 exchanges can be identified among the network of trophic exchanges in the Bay. The recycling of carbon in the Bay ecosystem is representative of most estuaries. Over 14% of total system activity is devoted to recycling, and most of these processes involve the pelagic and benthic flagellates.

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1. RATIONALE

A primary goal of coordinated research on South Florida's environmental resources is to understand those communities as whole ecosystems. Toward that end, the Across Trophic Levels System Simulation (ATLSS) project is an attempt to simulate the interactions of the various elements of wetland biotic communities within the framework of a single, encompassing computational scheme.

The resulting ATLSS model is one of the most complex and sophisticated models ever attempted. It will consist of simulation modules of varying and often very high complexity that represent the important components of the ecosystems of South Florida. It follows that the output from ATLSS will be exceedingly complicated, and it may not be a straightforward task to elucidate the causal origins of any particular model behavior. Such uncertainty could become problematical, especially if the initial trials of ATLSS should behave "pathologically" (as is highly probable during the initial runs of such a complex model). Even should outputs not appear unrealistic, the difficulty remains that there exist no precedents for evaluating how well such a "multi-model" performs as an analog of the real system. I.e., there are no set protocols for "calibrating" such complex simulations. ATLSS, therefore, requires a partially independent benchmark against which one may gauge the plausibility of its outputs; and, towards that end, ATLSS investigators have chosen to create a suite of trophic flow networks that estimate material exchanges in the ecosystems being modeled. These will serve as calibration standards. In addition, these networks will be analyzed by a set of quantitative methods called Network Analysis (NA) that will provide useful information for calibrating the model and important clues for debugging the initial modeling trials.

Trophic flow networks are graphical and mathematical depictions of the answers to the questions, "Who eats whom, and by how much?" Typically, diagrams of flow networks are comprised of boxes that represent the major components of the ecosystem. The boxes are connected by arrows, which indicate the transfers of material or energy between the components. Usually, each arrow is labeled with the magnitude of its transfer as averaged over a prescribed period of time.

Accordingly, the University of Maryland contingent of ATLSS investigators is assembling very detailed networks of carbon exchanges as they normally occur in the ecosystems of South Florida. Networks consisting of more than 60 important compartments are being estimated for each of four habitats, using existing data and ongoing field work. Separate networks for wet and dry seasons are being created for the ecosystems of the forested wetlands, the gramminoid marshes, the mangrove estuaries, and the shallows of Florida Bay. Each network will be a snapshot of the trophic flows and biomasses as averaged both over the hydroperiod in question and over the spatial domain of that particular biotope.

Analyses are to be performed on the resulting networks at several scales. The key questions that can be answered for any fully- quantified trophic network include: (1) To what extent does each taxon depend upon (or contribute to) all other taxa over all trophic pathways, both direct and indirect? (2) What are the efficiencies with which material is being transferred up the trophic ladder? (3) What are the pathways by which material is being recycled within the system? and (4) What is the current organizational status of the ecosystem? Any or all of these answers can be used to debug an ATLSS model that is not performing realistically.

During the 1996 Calendar Year we reported our findings on the cypress wetland ecosystems, as summarized in the introductory material. The 1997 Calendar Year was devoted to elucidating the flows in the ecosystem of Florida Bay (also summarized above), and the elucidation and analysis of the third of these four habitats - the Mangrove Ecosystem- are presented below. In the next annual report (May, 2000) we will present the corresponding results for the networks of the gramminoid wetlands (or Everglades proper).

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2. STUDY AREA

The huge mangrove belt along the seaward edge of the Everglades forms part of the most significant wilderness in this area of the United States. There are approximately 190,000 ha of mangroves remaining in Florida (Coastal Coordinating Council, 1974), and about 90 percent of this area lies in the four southern counties of Lee, Collier, Monroe and Dade.

Mangrove ecosystems lie at the interface of land and sea, representing a crucial link in tropical and subtropical regions. Mangroves are important as a food source and habitat for fish and wildlife, as well as to estuarine nutrient-cycling processes and have an important role in stabilizing the sediments deposited by physical processes (Odum and McIvor, 1990). In regions such as Cuba and south Florida, which have frequent and severe hurricanes, mangrove forests tend to be periodically damaged or destroyed before they reach their maximum height and development; these forests act as an important buffer, protecting coastal uplands from flooding (Surface water improvement and management plan for the Everglades,1992).

Mangrove species dominate these ecotones because they have evolved several mechanisms that allow them to be successful under highly variable salinity regimes (Chapman, 1976; Clough, 1984). Mangroves are facultative halophytes, *i.e.* they are able to utilize either fresh water or salt, water depending upon prevailing conditions. Salt water plays a key role in mangrove ecosystem development by excluding potential competing species (Kuenzler, 1974).

There are three key species of mangroves in Florida's mangrove forests: the red mangrove (*Rhizophora mangle L.*), the black mangrove (*Avicennia germinans L.*), and the white mangrove (*Laguncularia racemosa L.*) (Tomlinson, 1986). Generally, red and black mangroves are distributed along the intertidal zone. The red mangrove dominates the middle and lower portions of the intertidal and the upper sub-tidal zone, while the black mangrove predominates in the upper part of the intertidal zone and into irregularly flooded higher elevation (Davis, 1940). White mangrove is typically found in patches, often patches that have been created by lightning, storm or human disturbance. It occurs throughout the intertidal zone, but more in the irregularly flooded higher elevations than in areas of sand/strand vegetation (Tomlinson, 1986). There are many variations and exceptions to this generalized description of the distribution of the mangrove species in Florida. The classical pattern can be altered by the interplay of chemical and physical factors with interspecific competition and possibly seed predation (Odum and McIvor, 1990).

There is also significant variability in structural appearance that affects how mangrove communities are identified. The three major types are: riverine forest, fringing forest and basin forests (Cintron *et al.*, 1985; Lugo *et al.*, 1989). The riverine forest occurs along tidal rivers and creeks and receive the greatest amount of tidal flushing and freshwater runoff of nutrients from terrestrial ecosystems. The trees in this community may be higher than 20 m and have high primary production rates. The fringing forest forms a relatively thin fringe along waterways and embayments. (Mangrove islands are included in this category.) They are flushed by tidal water and do not receive as much terrestrial nutrient runoff as riverine forests. Trees rarely exceed 10m, and primary production is lower than in riverine forests. The basin forests occur further inland and take on a variety of forms, such as forests in depressions channeling terrestrial runoff, hammock forests, or dwarf scrub forests. Each of the basin subtypes can have its own characteristic primary production, tidal flushing rate, etc. (Odum and McIvor, 1990).

A very peculiar characteristic of these mangrove forests is their root systems. Mangroves have adapted to life in highly anaerobic soils by developing shallow root systems, and unlike most trees, they also lack a deep taproot. The red mangrove has developed drop roots from branches and upper parts of stems, but these roots extend only a few centimeters into the soil. The above-ground portions of these roots

have many lenticles that allow oxygen to diffuse into the plant and down to the underground roots. A different strategy has been evolved by certain other species, such as the black mangrove: they have system of cable roots, a few centimeters deep, which radiate outward for many meters from the stem base. Extending upward from the cable roots one may find erect aerial roots called pneumatophores (Odum and McIvor, 1990). The aerial root systems of mangroves provide a convenient substrate for attachment of algae. These root algal communities are particularly noticeable on red mangrove prop roots, but also occur to a lesser extent on intertidal black mangrove pneumatophores (Odum *et al.*, 1982).

Other primary producers occur on bay and creek bottoms adjacent to mangrove forests. These include primarily aquatic grasses such as turtle grass (*Thalassia testudinum*), manatee grass (*Syringodium filliforme*), shoal grass (*Halodule wrightii*) and widgeon grass (*Ruppia maritima*) (Odum *et al.*, 1982).

In Florida mangrove forests and their associated waters provide valuable habitat for a wide range of invertebrates, fishes, amphibians, reptiles, birds and mammals. Odum *et al.*, (1982) reviewed the scattered literature dealing with mangrove habitat utilization and found the following numbers of species reported from the Florida mangrove ecosystems: 220 species of fishes; 24 species of reptiles and amphibians, including turtles, snakes, lizards and frogs; 18 species of mammals; and 181 bird species (guilds include 18 wading birds, 25 probing shore birds, 29 floating and diving water birds, 14 aerially searching birds, 20 birds of prey and 71 arboreal birds).

Even though the mangroves are primarily a wetland habitat, the aquatic macro-invertebrates and fishes still contribute a great deal to the overall trophic structure and function of the system. With its tree canopies, masses of aerial roots and muddy substrates, this ecosystem offers many habitats for a wide variety of invertebrates. The mangroves also provide a good habitat for sessile organisms that have a difficult time establishing themselves on the soft substrates of Florida Bay. The prop roots *of Rhizophora mangle* serve as the anchor for these animals, permitting organisms like sponges (*Hymeniacidon heliophila*), oysters (*Crassostrea virginica*) and ascidians (*Ascidia niger*) to be present in high densities (Bingham 1992, Farnsworth and Ellison 1996).

One of most abundant groups of animals in the mangrove community are the crabs, which appear to utilize virtually every square inch of this habitat (Warner 1969, Wilson 1989). The host of marine species that are present in Florida Bay are accompanied by other crabs that live exclusively in the trees and intertidal mud flats of the mangroves. One of these, the mangrove tree crab, *Aratus pisoni*, is a key element of the above-water food web (Beever *et al.*, 1979). It is a resident of the mangrove canopy, and feeds mostly on red mangrove leaves (Wilson 1989). The other non-predatory crabs utilize the litterfall detritus as their primary food sources, creating the link for energy flow from the lower trophic levels to the fishes and other large predators of the mangroves.

The species of fish found in the mangroves are generally the same species that are found in Florida Bay (Thayer *et al.*, 1987a), but also include freshwater species as well. During the wet season there is a strong influence by freshwater, so that the presence and importance of freshwater fishes increase. The majority of dry season fishes cannot tolerate the reduced salinity, and depart for the more marine conditions found in Florida Bay (Odum *et al.*, 1982). Certain species, like snook, prefer the low salinity conditions, and remain in the mangroves throughout the year, interacting with the freshwater invaders (Thue *et al.*, 1982).

Mangroves can also be important nursery areas for invertebrates, sport and commercial fishes (Odum *et al.*, 1982, Robertson and Duke 1987, Thayer *et al.*, 1987b). For example, the spiny lobster (*Panulirus argus*) spend only early juvenile stages in the mangrove area, and as they mature, they migrate to the nearshore waters of Florida Bay (Herrnkind and Butler 1986). Snappers (*Lutjanus* spp.), spotted sea

trout (*Cynoscion nebulosus*) and red drum (*Sciaenops ocellatus*) also utilize the mangroves primarily as a juvenile nursery (Rutherford *et al.*, 1989, Tilmant *et al.*, 1989). The young use the shallows and prop roots as shelter until they are of sufficient size to avoid most predators. These three species represent the cornerstone of the recreational fishery in South Florida, and are the fish most sought by anglers (Tilmant 1989, Schmidt and Alvarado, *in review*). The necessity of mangrove systems as nursery habitats for fishes and invertebrates is well established (Lewis *et al.*, 1985). Both sport and commercial fisheries decline when mangrove ecosystems are destroyed.

Ten species of turtles have been identified in the mangrove area: four are typical of freshwater (striped mud turtle, *Kinosternon bauri*; chicken turtle, *Deirochelys reticularia*; Florida red-bellied turtle, *Chrysemys nelsoni*; Florida softshell, *Trionyx ferox*), two are found in brackish water (mud turtle, *Kinosternon subrubrum*; ornate diamondback terrapin, *Malaclemys terrapin macrospilota* and *M. t. rhizophorarum*), and the remainder are found in marine waters (hawksbill, *Eretmochelys imbricata*; green turtle, *Chelonia mydas*; loggerhead, *Caretta caretta*; Atlantic ridley, *Lepidochelys kempii*) (Odum *et al.,* 1982). Freshwater species usually occur in the headwater regions of mangrove-lined river systems. All four freshwater species are found in habitats other than mangrove swamps, including streams, ponds, and freshwater marshes. The brackish water species are found in salt marshes in addition to mangrove swamps. All four of the marine turtles are associated with mangrove vegetation at some stage of their lives, although loggerhead and green turtles are much less dependent on mangroves than hawksbills and the Atlantic ridley (Odum *et al,* 1982).

Three species in the genus Anolis have been reported from Florida mangroves: the green anole (*Anolis carolinensis*), Cuban brown anole (*Anolis sagrei*) and Bahaman bank anole (*Anolis distichus*). All three species are arboreal lizards that feed on insects (Odum *et al,* 1982).

Of the six species of snakes listed, the mangrove water snake (*Nerodia fasciata compressicauda*) is most dependent upon mangrove habitat.

Two important reptiles found in mangrove swamps are the American alligator (*Alligator mississippiensis*) and the American crocodile (*Crocodylus acutus*). The alligator is found only in low salinity sections of Florida mangrove areas, while mangroves appear to be a critical habitat for the American crocodile. Mangroves play an important role in the breeding of this endangered species (Odum *et al.*, 1982).

Only three species of amphibians have been recorded in Florida mangrove swamps: giant toad (*Bufo marinus*), squirrel treefrog (*Hyla squirella*) and Cuban treefrog (*Hyla septentrionalis*) (Odum *et al.*, 1982).

Because mangroves present a more diverse structural habitat than most coastal ecosystems, they tend to harbor a greater variety of bird life than areas such as salt marshes, mud flats or beaches (MacArthur and MacArthur, 1961). Herons, egrets, ibises, bitterns and spoonbills are the most conspicuous groups of birds found among the mangroves. The shallow water and exposed sediments below the mangroves also are home to probing shorebirds. Plovers and sand pipers are opportunistic feeders, taking the most abundant invertebrates present in whatever habitat the birds happen to occupy. Longer-legged wading birds utilize these shallow areas as well as deeper waters along mangrove-lined pools and waterways. Surface-feeding and diving birds would also be expected to share the habitats of the wading birds. Twenty nine species of ducks, grebes, loons, cormorants, and gallinules were identified as populating mangrove areas in South Florida. Eight species are year round residents and usually breed in mangrove swamps. The remainder are present only during migration or as winter visitors. The major difference between mangrove swamps and other coastal ecosystems is the availability of the trunks, limbs and foliage comprising the tree canopy. These can shelter a variety of passerine and non-passerine birds

commonly not found in other wetland areas. The canopy also allows extensive breeding activity by a number of tree-nesting birds. Among the birds of prey, the bald eagle, osprey and peregrine falcon are dependent on mangrove ecosystem, they feed extensively on the wealth of fishes found associated with mangroves; additionally mangroves are used as roosts and support structures for nests. In all, the composition of the avifauna community in mangrove ecosystems is highly diverse (Odum *et al.*, 1982).

A number of medium-sized and large carnivores, including Florida panther (*Felis concolor*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), mink (*Mustela vison*), river otter (*Luntra canadensis*), and black bear (*Ursus amaricanus*), utilize south Florida mangrove areas. Only three of these species (the bobcat, striped skunk and raccoon) are common in mangroves, but several of the other species seem to be highly dependent on mangrove swamps. Hamilton and Whittaker (1979) state that it is the coastal hammocks of south Florida, including mangrove areas, which serve as the ultimate refuge for the Florida panther (Odum *et al.*, 1982).

Two marine mammals, the bottle-nosed dolphin (*Tursiops truncatus*) and the West Indian manatee (*Trichechus manatus*) frequent mangrove-lined waterways. The dolphin feeds on mangrove associated fishes and, although the manatee feed primarily on sea grasses and other submerged aquatic plants found outside the mangroves, it commonly appears in canals, coastal rivers and embayments close to mangrove swamps (Odum *et al.*, 1982).

Mangrove ecosystems provide valuable habitat for a wide range of animals, including seven species and four subspecies listed by the U.S. Fish and Wildlife Service as endangered, threatened or of concern. These are the American crocodile (*Crocodylus acutus*), hawksbill sea turtle (*Eretmochelys imbricata*), Atlantic ridley sea turtle (*Lepidochelys kempi*), Florida manatee (*Trichechus manatus*), bald eagle (*Haliaeetus leucocephalus*), American peregrine (*Falco peregrinus*), brown pelican (*Pelecanus occidentalis*), Key deer (*Odocoileus virginianus clavium*), Florida panther (*Felis concolor coryi*), Atlantic salt marsh snake (*Nerodia fasciata taeniata*) and the eastern indigo snake (*Drymarchon corais couperi*) (Odum and McIvor, 1990).

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3. PARSING THE NETWORK

As with most methodologies, some of the most important assumptions in Network Analysis are made at the outset. They concern decisions as to what to choose as the primary elements of the network and how these taxa are to be connected. In this project, these decisions are simplified somewhat by the requirement that the network be comparable to the ATLSS simulation. That is, each state variable of the ATLSS model must have its counterpart in the accompanying network.

Network analysis, however, can treat far more complicated webs of interaction than are possible using simulation modeling. Keeping the simulation dynamics of many coupled processes from becoming pathological is a difficult balancing act. Because NA does not deal explicitly with dynamics, far greater taxonomic resolution becomes possible with this form of analysis. As a result, some taxa in the ATLSS model will be represented by several compartments in the mangrove network. In addition, compartments can be added to the network with relative ease. For example, the creation of an individual- based model for one of the lesser-known fishes would entail significant effort. As will be described below, it requires nowhere near as much work to include this compartment in the quantified trophic web.

Although the primary reason for creating these networks is to serve as a calibration benchmark for ATLSS, it should be mentioned that each single network and its ensuing analysis can also serve independent purposes. For example, some biologists will be curious to know how their particular species of interest, which might not appear in ATLSS, will fare under the proposed hydrological scenarios. With regard to trophic interactions at least, the results of NA should allow those investigators and managers to make some educated guesses about how the excluded population might change. For example, NA quantifies the direct and indirect trophic interactions of each compartment with all other compartments in the web. In particular, the stocks and activities of each compartment not appearing in ATLSS can be compared with all those that do participate through NA, and such coefficients and ratios as may result can be applied to the predicted outputs from ATLSS to estimate the accompanying trophic status of the non- included species. In other words, after calibration NA can serve to expand the scope of predictions from ATLSS.

From an ecological viewpoint, virtually all the important trophic components (*i.e.,* those comprising at least 5% of the standing biomass or activity) have been written into ATLSS. These include: detritus, microbes, aquatic/estuarine macrophytes, zooplankton, mesoinvertebrates, macroinvertebrates, piscivorous fish, planktivorous fish, wading birds, etc.

As for the previous two networks, the Cypress Wetland Ecosystem and the Florida Bay Ecosystem, it happened that data did exist to make at least crude estimates of the stocks and activities of a number of some other ecosystem members. Similarly, it was decided to include these "parallel" species in the NA of the mangrove network.

In addition, in order to wind up with more homogeneous and comparable networks, the choices that were made in the two previous network models have been taken into consideration in drawing up the list of components for the mangrove ecosystem. Because mangroves are a transition environment, both between salt and fresh water and between land and open water, it hosts species from all these habitats. For example, most of the fishes and invertebrates listed for Florida Bay are present as well in the mangrove. Ditto for some fresh-water species. Similarly, the marine mammals included in the bay network are also found in the mangroves. The same goes for many of the mammals that inhabit the cypress system. In deciding which are to be the elements of the network and how these taxa are to be connected, the same resolution was used as was employed with the previous two biotopes, so that the elements and structure of the three different network models will be comparable.

For some categories, such as shrimp, individual compartments for each of the more abundant and better-documented species have been reserved, while the remaining species were combined into a single "Other shrimps" compartment. Similarly, there are groupings for "Other primary producers" and "Other fishes".

In many networks the major lexical question involved how to treat the manifold species that comprise some functional groups for which data at the level of individual species were not available. To characterize these poorly-resolved parts of the ecosystem, it was decided to group the species into generalized compartments. Such was the case in the mangrove network for small benthic invertebrates, which were all included in the compartment called "Meiofauna". The same aggregation has been done for bacteria and protozoans in the water column, which were assign to a single compartment called the "Water microbial community".

The completed networks consist of 94 separate components. Only those species closely associated with the dominant patterns have been retained. Hence, only those primary producers, invertebrates, fishes, reptiles, birds and mammals commonly found in the mangrove system made the final list of species (although some additional species have been included following suggestions by experts.) Once completed, the list was aggregated somewhat according to certain criteria, such as species sharing the same diet, available data and the goals of ATLSS. For example, most species to be included in ATLSS as individual-base models have been maintained as separate compartments in the network.

Seasonality at this latitude is marked more by variations in freshwater input than by changing temperature. Thus, seasonality is depicted in the form of two separate networks, one for the wet season (from June to November) when freshwater inputs are high and the salinity is markedly lower and another for the dry season (December to May), when inputs are relatively low.

The following is the final list of components composing the mangrove ecosystem network, along with a very brief description of what each compartment entails:

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3.1 Primary Producers.

The initial elements of the network are the primary producers. A description of the dominant primary producers is reported in the "study area" section of this report. They have been divided as follows:

- 1. PHYTOPLANKTON. A single compartment has been used to represent the whole phytoplankton community, because available quantitative data relate only to aggregated chlorophyll-a concentration. Net plankton usually comprised of diatoms, but blooms of dinoflagellates may dominate seasonally (Odum *et al.* 1982).
- 2. OTHER PRIMARY PRODUCERS. Available data are mainly qualitative or significantly vague on other primary producers, including periphyton, the prop root community, benthic microalgae and macroalgae/ macrophyte communities in the mangroves. This entire group of species had been lumped in a single general compartment.
- 3. LEAVES. Even though mangroves are the most important players in the economy of this ecosystem, the three major species are grouped in a single compartment, because of the lack of specific information. Leaves from the three species of mangrove growing in south Florida: the red mangrove (*Rhizophora mangle L.*), the black mangrove (*Avicennia germinans L.*), and the white mangrove (*Laguncularia racemosa L.*) are included in this compartment.

- 4. WOOD. This compartment includes all the woody trunks and branches of the three species of mangrove growing in South Florida: the red mangrove (*Rhizophora mangle L.*), the black mangrove (*Avicennia germinans L.*), and the white mangrove (*Laguncularia racemosa L.*).
- ROOTS. We identify an aggregate compartment for the all the root systems, both aerial and in the sediment.

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3.2 Planktonic and Microbenthic Compartments.

The manifold species that comprise functional groups, such as the microorganisms and the benthic meiofauna, are grouped into general compartments, because data at the level of individual species are not available.

- 6. WATER MICROBIAL COMMUNITY. Bacteria and protozoans that occur in the water column are all represented in this compartment.
- 7. ZOOPLANKTON. This compartment includes all zooplankton.
- 8. BACTERIA IN SEDIMENT. Includes all bacteria and fungi living at the sediment level.
- 9. FLAGELLATES IN SEDIMENT. Includes all flagellates found in the sediment.
- 10. CILIATES IN SEDIMENT. Includes all ciliates inhabiting the sediment.
- 11. MEIOFAUNA. All meiofauna species have been grouped into this single compartment.
- 12. MEROPLANKTON. Includes all planktonic larval forms of both fishes and macroinvertebrates. Inputs into the system for many species are represented here (*e.g.*, *Callinectes* spp., *Penaeus duorarum*, many of the fish compartments, *etc.*).

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3.3. Macroinvertebrates

As might be expected, the macroinvertebrates of the Everglades mangroves are similar in species composition to those of Florida Bay, but there are a few notable differences. The seasonal influx of freshwater into the mangrove system permits upstream freshwater organisms to penetrate deeply into the mangroves. These invaders are contained in the Freshwater Macroinvertebrates compartment. While most of the marine organisms do not interact with members of these two compartments, the freshwater organisms do interact with the system enough to be considered a vital component of its dynamics. They interact with those components that remain in the system when the freshwater enters, such as euryhaline species (blue crabs, snooks, etc.) or permanent features of the system (detritus and primary producers). During the wet season they provide an avenue for the flow of energy from lower to upper trophic levels after the marine residents have moved to locations with higher salinity.

The mangroves also provide habitat for the juveniles of many macroinvertebrate species (Odum *et al.* 1982, Robertson and Duke 1987, Thayer *et al.* 1987b). Many of the compartments are comprised almost exclusively of juvenile individuals. For example, the lobster compartment in this network contains only early juvenile stages of the spiny lobster (*Panulirus argus*).

While the mangroves in the Everglades are rather expansive (covering approximately 500 square miles [Lodge 1994]), aquatic species utilize only a portion of it. Those areas that receive sufficient inundation to support aquatic life consist of small open water areas, the tidal streams and their fringing prop root

habitats. This area is estimated to be approximately 10% of the entire mangrove habitat (Lutz 1997, Yokel 1983).

Macroinvertebrates compartments are very similar to those used in the Florida Bay network. The differences reflect the presence of mangrove prop roots (Root Epifauna) and the terrestrial habitat (Terrestrial Crabs, Terrestrial Insects and Spiders). Macroinvertebrates contains all the invertebrates not found in the planktonic and microbenthic compartments. For an inclusive list of species, see Tabb and Manning 1961, Odum and Heald 1972, Courtney 1975, Bingham 1992, Abele 1973 and Farnsworth and Ellison 1996.

- 13. ROOT EPIFAUNA. This compartment contains those sessile organism found on the red mangrove prop roots, *excluding* sessile mollusks. It includes sponges (*e.g. Hymeniacidon heliophila*), ascidians (*e.g. Ascidia nigra*), bryozoans (*e.g. Bugula neritina*), and barnacles (*e.g. Balanus eberneus*).
- 14. POLYCHAETES. Contains all species of polychaetes, including *Nereis pelagica* and *Neanthes succinea*.
- 15. TERRESTRIAL GASTROPODS. Gastropods that spend the majority of their existence on the roots and stems of mangrove trees and on the exposed mudflats. The most abundant species are *Melampus coffeus*, *Cerithidea scalariformis* and *Littorina angulifera*.
- 16. AQUATIC GASTROPODS. Those found in Florida Bay include Squilaridae (*Caecum pulchellum* , *C. nitildum* , *C. floridanum* , and *C. imbricatum*), Olividae (*Olivella* spp., *Oliva* sp.), Nassariidae (*Nassarius albus*), Atydae (*Haminoea succinea*), Cerithidae (*Cerithrum* spp.), Crepidulidae (*Crepidula maculosa*), *Modulus modulus*, *Marginella eburneola* , *M. guttata* and *Thais deltoidea*.
- 17. BIVALVES. Includes all bivalves, both benthic species and those found on the prop roots, e.g, *Congeria leucophaeta* (False mussel), *Brachiodontes exustus* (scorched mussel), *Anomalocardia cunimeris* (pointed venus) and *Crassostrea virginica* (eastern oyster).
- 18. MACROBENTHOS. Includes all other invertebrates that spend most of their time among the benthos and are larger than the meiofauna or are not included in the other macroinvertebrate compartments. Representatives include Marine Oligochaetes, Sipunculids, Platyhelminthes, Nemerteans, Bryozoans, *etc.*
- 19. SMALL MACROCRUSTACEANS. Primarily Cumaceans, Tanaidaceans, Ostracods and Isopods (*i.e.,* crustacean species too large to be included in smaller-sized benthic organism compartments). Among them are the Cumacea (*Cyclaspis varians, Oxyurostylis sp.*), Tanaidacea (*Pseudoleptochelia* spp., *Leptochelia forresti* , *Kalliapseudes* spp. and *Pagurapseudes largoensis*), Ostracoda (*Eusariella* spp., *Parasterope muelleri*, *Eusarsiella paniculata* and *E. cornuta*) and Isopods (*Ligea exotica*, *Limnoria* sp. *Leptochelia* sp. and *Phycolimnoria clarkae*).
- 20. AMPHIPODS. Those amphipods that feed primarily on plant and detrital material: *Melita nitida, Grandidierella bonnieri, Corophium lacustrae, Cymadusa compta, Gammarus mucronatus, Elasmopus* sp. and *Gitanopsis* sp.
- 21. PENAEID SHRIMPS. Primarily juvenile *Penaeus duorarum* (pink shrimp).
- 22. CARIDEAN SHRIMPS. Marine grass shrimps: *Palaemonetes intermedius, Palaemonetes paludosus, Palaemonetes pugio, Periclimenes americanus, Periclimenes longicaudus, Thor floridanus* and *Palaemon floridanus*.
- 23. OTHER SHRIMPS. All the remaining shrimps not included in the previous two compartments, for example, *Synalpheus fritzmuelleri* and *Alpheus heterochaelis*.
- 24. JUVENILE LOBSTERS. The mangroves are used only by young lobsters, *Panulirus argus*, and leave the protection of the prop roots before maturity.
- 25. OMNIVOROUS CRABS. Contains generalist crab species, such as mud crabs (*Neopanope packardii* , *Panopeus occidentalis* , *Dyspanopeus texanus* and *Rithropanopeus harrisii*), spider crabs (*Libinia dubia*), *Eucratopsis* spp., fiddler crabs (*Uca* spp.) and crabs of the genus *Sesarma*.

- 26. TERRESTRIAL CRABS. Exclusively the mangrove tree crab (*Aratus pisoni*) that are limited primarily to terrestrial (arboreal) habitats.
- 27. DETRITIVOROUS CRABS. Crabs that feed primarily on detritus, including the hermit crabs (*Pagarus mcglaughlinae* , *Paguristes tortugae*).
- 28. PREDATORY CRABS. Mainly *Eurytium limosum* ,*Callinectes sapidus*, and other marine Portunids.
- 29. FRESH WATER MACROINVERTEBRATES. All the macroinvertebrates that require freshwater habitats. These organisms invade the mangroves during the wet season. *Palaemonetes paludosus* and *Procambarus alleni* are the species of primary importance.
- 30. AQUATIC INSECTS AND LARVAE. All insect larvae (*e.g. Chironomis* spp.) found in the mangroves, plus any other aquatic insects that tolerate the saline environment.
- 31. TERRESTRIAL INSECTS. Contains all non-aquatic insects (both terrestrial and arboreal) and other terrestrial organisms not found in other compartments (*e.g.*, terrestrial isopods)
- 32. SPIDERS. Includes all terrestrial arachnids in the mangroves.

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3.4. Fishes.

The fishes in the mangroves are generally the same species that are found in Florida Bay (Thayer *et al.* 1987a), with the addition of the freshwater species, which are all grouped together in the compartment, Freshwater Fishes. Obviously, during the wet season the presence and importance of freshwater fishes increases. The majority of dry season resident fishes cannot tolerate the reduced salinity, and depart for the more marine conditions found in Florida Bay (Odum *et al.* 1982). This is reflected in a lower biomass for most fishes during the wet season. Certain species, like snooks, prefer the low salinity conditions, and remain abundant in the mangroves throughout the year, interacting with the freshwater invaders (Thue *et al.* 1982).

The mangroves also provide a habitat for the juveniles of many fish species (Odum *et al.* 1982, Robertson and Duke 1987, Thayer *et al.* 1987b). Snappers (*Lutjanus* spp.), spotted sea trout (*Cynoscion nebulosus*) and red drum (*Sciaenops ocellatus*) utilize the mangroves primarily as a nursery (Rutherford *et al.* 1989, Tilmant *et al.* 1989). The young use the shallows and prop roots as shelter until they are of sufficient size to avoid most predators. These three species represent the cornerstone of the recreational fishery in south Florida; they are the fish most sought by anglers (Tilmant 1989, Schmidt and Alvarado, *in review*).

Although similar to the list of compartments used in the Florida Bay network, the resolution of the fishes in the mangroves isn't as detailed (e.g., all the sciaenids are placed into one compartment instead of three). The need for aggregation is due to the limitations placed on the available data by doubly difficult task of trying to sample highly mobile organisms in a habitat that is very difficult to sample (Thayer *et al.* 1987b), and by the extreme variability in habitat structure that induces differences in their associated fish committees (Odum *et al.* 1982). For lists of all species found in Florida mangrove systems, see Odum *et al.* 1982 and Thayer *et al.* 1987a.

- 33. SHARKS. Includes requiem sharks, such as Atlantic sharpnose shark *(Rhizoprionodon terraenovae*) and sandbar shark (*Carcharhinus plumbeus*), nurse shark (*Ginglymostoma cirratum*), lemon shark (*Negaprion brevirostris*) and bonnethead shark (*Sphyrna tiburo*). These sharks inhabit the open water areas of the mangrove system.
- 34. RAYS. Representative species are the Southern stingray (*Dasyatis americana*), spotted eagle

ray (*Aetobatis narinari*) and cownose ray (*Rhinoptera bonasus*).

- 35. TARPONS AND LADYFISHES. All fishes of the Family Elopidae, but primarily Tarpon (*Megalops atlanticus*) and Ladyfish (*Elops saurus*).
- 36. HERRINGS. Yellowfin menhaden (*Brevoortia smithi*), red-ear sardine *(Harengula humeralis*), scaled sardine (*H. jaguana*) dwarf herring (*Jenkensia lamprotema*), Atlantic thread herring (*Opisthonema oglinum*) and Spanish sardine (*Sardinella aurita*).
- 37. ANCHOVIES. Primarily consists of bay anchovy, *Anchoa mitchilli*, but also contains striped anchovy (*Anchoa hepsetus*), Cuban anchovy (*Anchoa cubana*), and flat anchovy (*Anchoviella perfasciata*).
- 38. NEEDLEFISHES. Redfin needlefish (*Strongylura notata*), Atlantic needlefish (*S. marina*) and timucu (*S. timucu*).
- 39. KILLIFISHES. All the marine and estuarine killifishes, especially *Floridychthes carpio* (goldspotted killifish) and *Lucania parva* (rainwater killifish). Also contains sheepshead minnow (*Cyprinodon variegatus*), marsh killifish (*Fundulus confluentus*), diamond killifish (*Adinia xenica*), golden top-minnow (*F. chrysotus*), gulf killifish (*F. grandis*) and seminole killifish (*F. seminolis*).
- 40. POECILIDS. All Poecilids, primarily Sailfin Molly (*Poecila latipina*) and mosquitofish (*Gambusia affinis*).
- 41. SEAHORSES AND PIPEFISHES. Lined seahorse (*Hippocampus erectus*), pugnose pipefish (*Bryx dunkeri*), dusky pipefish (*Sygnathus floridae*), Gulf pipefish (*Sygnathus scovelli*) and dwarf seahorse (*Hippocampus zosterae*).
- 42. SILVERSIDES. Members of the Family Atherinidae: Hardhead silversides (*Atherinomorus stipes*), reef silversides (*Hypoatherina harringtonensis*), rough silversides (*Membras martinica*) and Atlantic silversides (*Menidia menidia*).
- 43. SNOOKS. Members of the Family Centropomidae. The most abundant member is the common snook (*Centropomus undecimalis*), with lesser numbers of fat snook (*C. parallelus*), swordspine snook (*C. ensiferus*) and tarpon snook (*C. pectinatus*).
- 44. BARRACUDAS. Barracudas - the great baracuda (*Sphyraena baracuda*) and guaguanche (*S. guachancho*).
- 45. FRESH WATER FISHES. Contains any and all species of fish that primarily reside in the upstream cypress and sawgrass habitats.
- 46. BENTHIC FISHES. The remaining fish that are not contained in other compartments that reside and feed primarily on the benthos: Flatfishes (southern flounder [*Paralychthys lethostigma*], lined sole [*Achirus lineatus*]), Groupers, batfishes (*Ogcocephalus radiatus*), brotulas (*Gunterichthys longipenis*), and toadfishes (*Opsanus beta*).
- 47. EPIFAUNAL-FEEDING FISHES. Those fish that rely primarily on the sessile epifauna of the prop roots as a source of food in the mangrove systems: Filefishes and triggerfishes, such as orange filefish (*Aluterus schoepfi*), scrawled filefish (*A. scriptus*) and fringed filefish (*Monacanthus ciliatus*), the bluelip parrotfish (*Cryptotomus roseus*), emerald parrotfish (*Nicholsina usta*), redfin parrotfish (*Sparisoma rebripinne*), redtail parrotfish (*S. chrysopterum*) and Spadefish (*Chaetodipterus faber*).
- 48. SNAPPERS. All members of Family Lutjanidae, including the Gray Snapper (*Lutjanus griseus*), cubera snapper (*Lutjanus cyanopterus*), lane snapper (*L. synagris*) schoolmaster (*L. apodus*) and mutton snapper (*L. analis*).
- 49. MOJARRAS. Spotfin mojarra (*Eucinostomus argentus*), silver jenny (*E. gula*), yellowfin mojarra (*Geres cinereus*) and striped mojarra (*Diapterus plumieri*).
- 50. SCIAENIDS. Those members of Family Sciaenidae, including Spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), blue croaker (*Bairdella batabana*), silver perch (*B. chrysoura*), southern kingfish (*Menticirrhus americanus*) and black drum (*Pogonias cromis*).
- 51. PINFISHES. Sheepshead (*Archosargus probatocephalus*), grass porgy *(Calamus arctifrons*), whitebone porgy (*C. leucosteus*), and, most importantly, the pinfish (*Lagodon rhomboideus*).

- 52. MULLETS. Striped mullet (*Mugil cephalus*), white mullet (*M. curema*) fantail mullet and *M. gyrans*.
- 53. GOBIES. Code goby (*Gobiostoma robustum*), clown goby (*Microgobius gulosus*), frillfin goby (*Bathygobius soporator*), emerald goby (*Gobiostoma smaragdus*), naked goby (*G. bosci*) and dash goby (*Gobionellus saepepallens*).
- 54. OTHER FISHES. Any isolated temporary residents of a pelagic nature are grouped in this compartment, for example, bluefish (*Pomatomus saltatrix*), Atlantic threadfin (*Polydactylus octonemus*), cobia (*Rachycentron canadum*), jacks and runners (blue runner [*Caranx crysos*], crevalle jack [*C. hippos*]).

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3.5. Reptiles and Amphibians.

Although not exactly the same species composition, the list of reptile compartments resembles that of the Cypress ecosystem. Reptiles have been divided into four separate compartments, each consisting of several species. Unfortunately, no significant resolution was possible for amphibians, which were lumped into a single Amphibian compartment. For lists of all species found in the Florida mangrove systems, see Odum *et al.* 1982 and Martin *et al.* 1993.

- 55. TURTLES. Species found in the mangroves area are Mud turtle (*Kinosternon subrubrum*), Striped mud turtle (*Kinosternon bauri*), Ornate diamondback terrapin (*Malaclemys terrapin macrospilota* and *M. t. rhizophorarum*), Florida red-bellied turtle (*Chrysemys nelsoni*), Chicken turtle (*Deirochelys reticularia*), Florida softshell (*Trionyx ferox*), Atlantic ridley (*Lepidochelys kempii*), as well as those species cited in Florida Bay: Green turtle (*Chelonia mydas*), Hawksbill (*Eretmochelys imbricata*) and Loggerhead (*Caretta caretta*).
- 56. LIZARDS. Species found in the mangroves include the Green anole (*Anolis carolinensis*), Cuban brown anole (*Anolis sagrei*) and Bahaman bank anole (*Anolis distichus*).
- 57. SNAKES. Species found in the mangroves are the Green water snake (*Nerodia cyclopion*), Striped swamp snake (*Liodytes alleni*), Eastern indingo snake (*Drymarchon corais*), Rat snake (*Elaphe corais*), Eastern cottonmouth (*Agkistridin piscivorus*) and the characteristic Mangrove water snake (*Nerodia fasciata compressicauda*).
- 58. CROCODILES. Two charismatic species are grouped together in this compartment -- the American alligator (*Alligator mississippiensis*) and the American crocodile (*Crocodylus acutus*).
- 59. AMPHIBIANS. Species found in the mangroves are the Giant toad (*Bufo marinus*), Squirrel tree frog (*Hyla squirella*), and the Cuban tree frog (*Hyla septentrionalis*).

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3.6. Birds

Taxonomy, feeding habits and available information were of primary importance in establishing the final list of birds. Not unexpectedly, birds in the mangroves are found either in the Cypress swamp or Florida Bay networks. The species listed under each unit are meant to provide a representative sample. For lists of all species to be found in the Florida mangrove ecosystems, see Odum *et al.* 1982, Martin *et al.* 1993 and Lefebvre *et al.* 1992.

- 60. LOONS AND GREBES. Species found in the mangroves are the common loon (*Gavia immer*), horned grebe (*Podiceps aurotus*) and pied-billed grebe (*Podilymbus podiceps*).
- 61. PELICANS. Species found in the mangroves include the white pelican (*Phaethon lepturus*), brown pelican (*Pelecanus occidentalis*), and the magnificent frigatebird (*Fregata magnificens*).
- 62. CORMORANTS. Primarily the double-crested cormorant (*Phalacrocorax aurotus*) and the anhinga (*Anhinga anhinga*).
- 63. BIG HERONS AND EGRETS. Species found in the mangroves include the great blue heron (*Ardea herodias*), great white heron (*A. occidentalis*), great egret (*Casmerodius albus*) and woodstork (*Mycteria americana*).
- 64. SMALL HERONS AND EGRETS. Including the little blue heron (*Florida caerulea*), Louisiana heron (*Hydranassa tricolor*), snowy egret (*Egretta thula*) and the roseate spoonbill (*Ajaia ajaia*).
- 65. IBISES. Especially the white ibis (*Eudocimus albus*) and glossy ibis (*Plegadis falcinellus*).
- 66. HERBIVOROUS DUCKS. A few species of pigeons and doves were added to the duck species because of the similarities in diet and the very poor resolution among primary producer compartments. Some of the species found in the mangroves include the blue-winged teal (*Anas discors*), green-winged teal (*Anas carolinensis*), shoveler (*Spatula clypeata*), American wigeon (*Mareca americana*), pintail (*Anas acuta*), mourning dove (*Zenaidura macroura carolinensis*) and white-crowned pigeon (?).
- 67. OMNIVOROUS DUCKS. Some of the species visiting the mangroves include the lesser scaup (*Aythya affinis*), ring-necked duck (*Aythya collaris*), ruddy duck (*Oxyura jamaicensis*) and canvasback (*Aythya valisineria*).
- 68. PREDATORY DUCKS. Included in this compartment are the red-breasted merganser (*Mergus merganser*) and hooded merganser (*Lophodytes cucullatus*).
- 69. VULTURES. Species found in the mangrove area included in this compartment are the turkey vulture (*Cathartes aura*) and the black vulture (*Coragyps atratus*).
- 70. KITES AND HAWKS. Some of the species found in the mangroves area and included in this compartment are: swallow-tailed kite (*Elanoides forficatus*), red-tailed hawk (*Buteo jamaicensis*), red shouldered hawk (*Buteo lineatus*), short-tailed hawk (*Buteo brachyurus*), Cooper's hawk (*Accipiter cooperii*), sharp-shinned hawk (*Accipiter striatus*) and broad-winged hawk (*Buteo platypterus*).
- 71. EAGLES AND OSPREYS. Found in the mangroves and included in this compartment are the bald eagle (*Haliaeetus leucocephalus*) and the osprey (*Pandion haliaetus*).
- 72. GRUIFORMES. Including the American coot (*Fulica americana*), clapper rail (*Rallus longirostris*) and the limpkin (*Aramus guarauna*).
- 73. SMALL SHORE BIRDS. Include the least sandpiper (*Erolia minutilla*), semipalmated sandpiper (*Ereunetes pusillus*), western sandpiper (*Ereunetes mauri*), short-billed dowitcher (*Limnodromus griseus*), Dunlin (*Erolia alpina*), willet (*Catoptrophorus semipalmatus*) and black-bellied plover (*Squatarola squatarola*).
- 74. GULLS AND TERNS. The black skimmer (*Rynchops nigra*), laughing gull (*Larus atricilla*) and ring-billed gull (*Larus delawarensis*).
- 75. CUCULIFORMES AND CAPRIMULGIFORMES. Includes the yellow-billed cuckoo (*Coccyzus americanus americanus*), mangrove cuckoo (?), and Chuck-will's-widow (*Caprimulgus carolinensis*).
- 76. OWLS. The great horned owl (*Bufo virginianus*), barn owl (*Tyto alba*), and barred owl (*Strix varia*).
- 77. WOODPECKERS. The pileated woodpecker (*Dryocopus pileatus*), red-bellied woodpecker (*Centurus carolinus*) and yellow-bellied sapsucker (*Sphyrapicus varius*).
- 78. OMNIVOROUS PASSERINES. The mockingbird (*Mimus polyglottos*), brown thrasher (*Toxostoma rufum*), cardinal (*Richmondena cardinalis*), tufted titmouse (*Parus bicolor*), catbird (*Dumetella carolinensis*), robin (*Turdus migratorius*) and swamp sparrow (*Melospiza georgiana*).

- 79. PREDATORY PASSERINES. The eastern kingbird (*Tyrannus tyrannus*), gray kingbird (?), blue-gray gnatcatcher (*Polioptila caerulea*), black and white warbler (*Mniotilta varia*), yellow-rumped warbler (?) and palm warbler (*Dendroica palmarum*).

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3.7. Mammals

Mammals in the mangroves show considerable overlap with the species listed in the Cypress wetland network and includes as well the two marine mammals found in Florida Bay. For inclusive lists of all species found in the Florida mangrove ecosystem, see to Odum *et al.* 1982 and Martin *et al.* 1993.

80. OPOSSUMS. The Virginia opossum (*Didelphis virginiana*).

81. RABBITS. The Marsh rabbit (*Silvilagus paulstris*).

82. SQUIRRELS. The eastern gray squirrel (*Sciurus carolinensis*) and the fox squirrel (*Sciurus niger*).

83. MICE AND RATS. Species found in the mangroves include marsh rice rat (*Oryzomys palustris*), cudjoe key rice rat (*Oryzomys argentatus*), hispid cotton rats (*Sigmodon hispidus*) and black rats (*Rattus rattus*). The short-tailed shrew *(Balarina brevicauda)* was also included in this compartment.

- 84. FOXES. The gray fox (*Urocyon cinereoargenteus*).
- 85. BEARS. The black bear, *Ursus amaricanus*.
- 86. RACOONS. The racoon, *Procyon lotor*.
- 87. MINKS AND OTTERS. The mink (*Mustela vison*), striped skunk (*Mephitis mephitis*) and the river otter (*Luntra canadensis*).
- 88. PREDATORY FELINES. Both the Florida panther (*Felis concolor*) and the bobcat (*Lynx rufus*).
- 89. DEER The white-tailed deer (*Odocoileus virginianus*) and the Key deer (*O. v. clavium*).
- 90. DOLPHINS. The bottle-nosed dolphin (*Tursiops truncatus*).
- 91. MANATEES. The West Indian manatee (*Trichechus manatus*).

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3.8. Detritus Compartments

Detritus has been divided in three separate compartments:

- 92. CARBON IN SEDIMENT. Includes all the non-living organic carbon available in the first 10 centimeters of sediment, including mangrove litter.
- 93. POC. This compartment represents all the particulate non-living carbon floating in the water column.
- 94. DOC. This unit contains all the dissolved organic carbon present in the water column.

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4. METHODS

After the "lexical" phase of model building, the next step involves connecting the selected compartments to one another via feeding and detrital pathways. This topology is determined from information about the diets of each taxon. But the purpose here is not merely to formulate a qualitative "foodweb". We wish to *quantify* the connections as well. Toward this end, it is useful to concentrate first on assessing the densities, or stocks of the participating taxa. Knowing the concentration of biomass is the key to scaling all the activities of a particular population.

4.1 Estimation Techniques

The biomasses of some species are known to reasonable precision. For example, the number of animals per cubic meter or liter is available for many of the compartments. As the standard units used in NA are grams of carbon per square meter, the available data had to be transformed to maintain dimensional consistency. Towards this end, information on the average weight (grams) of animals was gathered from technical manuals. The percentage of carbon per gram of dry weight was then combined with wet weight/dry weight ratio to obtain gC/m^3 (in the case of number of animals per liter we just need a simple equation to transform gC/l in gC/m^3). By assuming an average water depth (Fell and Cefalu, 1976), the carbon biomasses in the required units (g/m^2) could be calculated. In the case of primary producers, most sources report data on biomass in grams per hectare or square meter. In this case only the wet weight/dry weight ratio and the percentage of carbon per gram of dry weight (Jorgensen *et al.*, 1991) were necessary to convert the biomasses into the correct units. For water POC and DOC, concentration was reported in gC/l, and the above procedure was followed.

The conversions of units for phytoplankton proceeded slightly differently. Data from the mangrove system were given in micrograms of chlorophyll-a per square meter. To convert these figures into carbon, a C/chl-a ratio of 50/1 was assumed to be representative of living microalgae (Strickland, 1965).

The biomass of the sharks compartment was calculated differently than most of the others. Recreational catch and harvest data (1995 and 1996) from The National Park Service angler surveys were used to calculate values for both biomass and harvest rates (Schmidt, *unpublished*). Catch rate was calculated by multiplying the mass of an average caught fish by the total number caught. This value was then scaled down to an amount per square meter. Biomass was estimated similarly, but also incorporated assumptions on how much of the total population was represented by the catch and harvest numbers (Baird and Ulanowicz 1989).

Once the biomass had been approximated, information was sought on the consumption rate (or primary production rate) per unit biomass of each species. Multiplying a biomass density by this factor establishes the total input to the compartment in question. At this point, if one has solid data on the dietary proportions of heterotrophs, the total input can be apportioned among the various prey, and the magnitudes of those transfers can be established. Unfortunately, the dietary components of some taxa were available only as a list of species. In such cases the total input was apportioned to the list of prey in proportion to the standing stocks of those populations.

The two seasonal networks were assumed to balance over each period. Although this assumption is not entirely realistic, balance is required for the critical input/output phase of NA (described below). Furthermore, assuming balance facilitates the estimation of many rates. For example, when a component is balanced, its total output can be equated to its total input as a quantity known as the compartmental throughput. It remains to apportion this throughflow among the output processes, namely, respiration, excretion, natural mortality and losses to predation. Fortunately, respiration and excretion rates per unit

biomass are available for most species from the literature, so that these outputs can be established immediately. Most of the losses to predation are reckoned from the predator (input) side, as described above.

At this point, the balance is almost complete. It remains to estimate the exchanges of carbon with the outside world. Exogenous imports occur in three different ways: (1) Carbon from the atmosphere may be fixed as biomass through the process of photosynthesis. The magnitude of this import is assessed by multiplying the standing stock of the autotroph by its primary productivity per unit carbon, as mentioned above. (2) Biomass may enter or leave the system advected by water flow into and out of the study area. These exchanges can be estimated from the overall water budget for the mangrove area, which includes figures for gross advective water exchange with the surrounding areas (Robertson and Alongi, 1992; Lutz, 1997). Multiplying these water exchanges by the concentrations of carbon suspended in the water column will provide an approximation for these exogenous transfers. (3) Biomass may enter and leave the system as animal populations migrate across the boundaries of the study area.

Migration applies to many animals species in the model, including invertebrates, fishes and birds. Mangroves water serve as a nursery ground for a variety of species of fish and invertebrates, (Odum *et al.* 1982, Robertson and Duke 1987, Thayer *et al.* 1987b). Among the invertebrates, spiny lobster (*Panulirus argus*) have early juvenile stages in the mangrove area. As these juveniles mature, they migrate to the nearshore waters of Florida Bay, and ultimately enter the deeper waters of offshore habitats (Herrnkind and Butler 1986). This is the case also for some fishes, such as snappers (*Lutjanus* spp.), spotted sea trout (*Cynoscion nebulosus*) and red drum (*Sciaenops ocellatus*) (Rutherford *et al.* 1989, Tilmant *et al.* 1989). This migration of post-juvenile organisms accounts for the net export of biomass from the system. Flowing in the opposite direction are the inputs to the system, *e.g.* meroplankton. Emigrations of populatons, *i.e.,* flows of carbon leaving the system, are considered like any other export, but immigrations are treated differently. The network analysis routine, NETWRK, was amended so that migratory imports would be considered separately so as to avoid compartments like meroplankton from mistakenly being perceived as primary producers. Exactly how this was done will be explained more in detail in the next section.

Movements by avifauna are different from those of fish. Some birds may nest for awhile on the mangroves, but then leave temporarily to feed elsewhere. Such feeding should be classified as an import to the system. Furthermore, different types of birds exhibit different feeding techniques. For example, some need high water levels and others, low. It could also happen that some birds nest on the mainland and come to feed in the bay. This activity would constitute an export from the system. These activities are all built into the estimates of imports to, and exports from, the mangrove ecosystem and lent the system the role of an "interface" between the cypress biome and Florida Bay. All told, we estimated that approximately 20% of birds counted in the entire mangrove habitat fed there and exported material out of the system (Odum *et al.*, 1982; Martin *et al.*, 1993).

The estimations of all the flows entering and leaving each compartment now have been described. Of course, uncertainties inherent in these partially independent estimations will mean that many of the compartments will not balance exactly. The degree of imbalance can be computed by entering the estimated flows into a spreadsheet format (EXCEL[TM] was used for this purpose.) Doing this allows one to compare the marginal sums of inputs to and outputs from each compartment in order to identify those that are most out-of-balance. The investigator has several options for treating an imbalanced compartment. If the imbalance is severe, it is probably best to recheck the sources and the arithmetic. Failing the discovery of an error, one might search for other references to cross-check the data being used.

If no amendments to a compartmental budget can be made on the basis of new data, some investigators

prefer to bring the system nearly into balance by adjusting the least-well known flows. Others would rather maintain the flow proportions for each compartment as they appear in the literature and then re-balance the whole system under the covering assumption of linear, donor-control, which always maintains flows positive (Ulanowicz 1989). In this study all compartments could be balanced to within a few percent using literature values, and a final balance was achieved using the program DATBAL, which assumes linear, donor control.

The resulting networks are too large and complicated for easy illustration. Even a matrix representation of one such network spans several pages and is extremely cumbersome to use. For these reasons, detailed results are probably best presented in hypertext format, which can be accessed over the World Wide Web at http://www.cbl.umces.edu/~atlss . Using hypertext, one follows simple instructions to locate the estimated value of any stock or flow in either the wet or dry season. Furthermore, the entire rationale and associated references pertaining to the estimation of any particular value have also been documented in hypertext. Thus, by pointing and clicking one may examine a trophic flow network in minute detail.

This format for disseminating the details of the network should have important benefits for ecosystem science in general and for the visibility of the ATLSS endeavor in particular. We are aware of no other single source where the structural elements of entire ecosystems can be examined and scrutinized so readily. Even if a user has no idea of the benefits of NA, he/she can begin with the species that interests them most and trace the sources and fates of material into and out of that compartment -- simply by pointing and clicking. The presentation also makes it easier to critique the networks, and online suggestions for improvements and amendments are welcomed.

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4.2. Network Analysis

4.2.1. Background

Sometime during the mid-1970's it became apparent that ecological modeling in the form of a set of coupled, deterministic differential equations was a problematical undertaking that required support from other, independent methods of systems analysis. In the search for parallel methods of describing the behavior of total ecosystems, various computations performed on the network of trophic flows have figured prominently (SCOR, 1981).

The original impetus for diverting attention from dynamics and concentrating analysis on flow structure came from the field of economics, where success in elucidating indirect economic effects had been achieved by manipulations on matrices of economic flows (Leontief, 1951; Hannon, 1973). Thereafter followed a number of other topological treatments of the underlying flow graph (e.g., Finn, 1976; Levine, 1980; Patten *et al.*, 1976; Ulanowicz and Kemp, 1979). Eventually, Ulanowicz collected most of the methods for analyzing flow networks into a single executable package, called NETWRK (Ulanowicz and Kay 1991.) NETWRK 4.2a is the version used in this analysis.

Four types of analyses are performed by NETWRK. First, so- called input- output structure matrices are calculated. These allow the user to look in detail at the effects, both direct and indirect, that any particular flow or transformation might have on any other given species or flow. Next, the graph is mapped into a concatenated trophic chain (after Lindeman 1942). Then global variables describing the

state of development of the network are presented. Finally, all the simple, directed biogeochemical cycles are identified and separated from their supporting dissipative flows. NETWRK 4.2a and its accompanying documentation may be downloaded from the World Wide Web at http://www.cbl.umces.edu/~ulan/ntwk/network.html .

In addition to NETWRK, a package called IMPACTS was used to gauge both the positive and negative, direct and indirect impacts that heterotrophic predation may cause. The method was described in Ulanowicz and Puccia (1990). Of particular interest is how negative impacts at one level can ramify to become positive indirect effects.

The data required to run either of these programs have already been discussed. Above it was detailed how, for each compartment, it is necessary to know: (1) all the inputs from outside the system, (2) all the various inputs flowing from other compartments of the system, (3) all the outputs which flow as inputs to other compartments, (4) all exports of useful medium outside the system, and (5) all rates of dissipation of medium. Each of these flows can be represented by a positive scalar element of a matrix or a vector; the absence of a flow can be represented by a zero.

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4.2.2. Input/Output Analysis

The initial section of the NETWRK package is founded upon an ecological variation of economic input-output analysis. So- called "total contribution coefficients" (Szyrmer and Ulanowicz 1987) describe exactly what fraction of the total amount leaving compartment i (prey or row designation) eventually enters compartment j (predator or column designation) over all pathways, both direct and indirect. Alternatively, the "total dependency coefficients" portray the fraction of the total ingestion by j which passed through compartment i along its way to j. The columns of this matrix are particularly useful in that they portray the "extended diet" of the species in question (or, correspondingly, the trophic "pyramid" that underlies each heterotroph). As was demonstrated with the cypress wetland ecosystem, such indirect ratios can provide valuable information about how a system is functioning.

As an example of indirect diet coefficients, consider the spiders (#32). They depend on the prey item insects (#31) for 100% of their sustenance. These prey items in their turn depend upon primary producers, such as mangrove leaves and wood (#3 and 4), and other primary producers (#2), so that ca. 93% of the consumption by spiders originates from these compartments. That is, carbon is counted more than once as it passes up the food chain, and the fact that all of the above dependencies sum to over 270% is entirely consistent with the fact that spiders feed, on the average, at about trophic level 3.

Hannon (1973), Finn (1976), Levine (1980) and Patten *et al.* (1976) give various examples of how one may employ input-output analysis. One highly useful application is the decomposition of the graph according to each input. That is, the eventual fate of each of the nonzero inputs to the system is traced independently of the other inputs to the system. Not only does this decomposition portray the isolated effects of the various inputs but these sub-networks can be linearly recombined to recreate what the effects of any other linear combination of inputs would be, if the flow structure were kept the same.

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4.2.3. Trophic Aggregation

The second section of output from NETWRK interprets the given network according to the trophic concepts of Lindeman (1942). Of course, it is impossible to relegate omnivorous heterotrophs entirely to a single trophic level, but Ulanowicz and Kemp (1979) indicated how input-output techniques could be used to apportion the activities of omnivores among a series of integer trophic levels. This method has been expanded to include the effects of biogeochemical cycles by Ulanowicz (1995a).

In order for trophic aggregation to be meaningful, it is necessary that trophic pathways among living compartments remain finite in length, otherwise one is forced to interpret an infinite regress of trophic levels. Fortunately, Pimm (1982) states that cycles among living taxa are rare in ecosystem networks (although we encountered some interesting exceptions in the two previous networks). The absence of such feeding cycles avoids trophic pathways of infinite length. As a preliminary to trophic aggregation, therefore, all cycles flowing through only living compartments are first removed from the network. So long as the Finn cycling index for such heterotrophic cycling (see below) remains sufficiently small (say, below two percent or so), no appreciable distortion of results should ensue. The 2% requirement is more than satisfied by the mangrove networks.

When the fractions by which each component feeds at a particular trophic level are weighted by the value of that trophic level and the results are summed, one arrives at the effective trophic level for the given species (Levine 1980). For example, if a species or compartment is receiving 15 units of medium along a pathway of length 2 and 5 units along a pathway of length 3, then it is acting 75% as a herbivore (trophic level=2) and 25% as a carnivore (level=3). The effective trophic position becomes (.75 x 2)+ (.25 x 3)=1.75. It is often interesting to compare the average trophic position of species under different circumstances (as, for example, between wet and dry seasons.)

The section of NETWRK dealing with trophic aggregation culminates with the partitioning of system activity into a trophic "chain" of transfers along linear aggregations of heterotrophs. Each such aggregation feeds back into detrital return loops. Such a depiction of the underlying trophic dynamics has been termed "canonical" by Ulanowicz (1995a), because any ecosystem can be mapped into this equivalent and simple form to allow the relative magnitudes of corresponding flows to be compared directly.

One change made recently as part of NETWRK, version 4.2a was to treat migratory inputs of heterotrophs differently than inputs to autotrophs (primary production.) NETWRK now treats inputs to heterotrophs as coming into the system at exactly the same trophic level as the receiving compartment would otherwise occupy within the system. (Previously such inputs were treated as primary production by default, and this unrealistic assumption artificially deflated many of the reported trophic levels.)

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4.2.4. System-Level Indices

The next section of output from NETWRK yields estimates for global attributes of the network that have been defined with the help of information theory to assess the pattern of development in ecosystems (Ulanowicz, 1980,1986; Hirata and Ulanowicz, 1984; Ulanowicz and Norden, 1990). The first such property is the "total system throughput", or the gross sum of *all* transfers, which provides a measure of

the size of the system. Multiplying the total throughput by the system indeterminacy (according to the Shannon Wiener formula) of the individual flows yields what has been termed the "development capacity" of the system. This quantity serves as an upper bound on the ascendency, which is a measure of the network's potential for competitive advantage over other real or putative network configurations. Ascendency is the product of a factor of size (total system throughput) times a factor representing the coherence of the flows (the average mutual information of the flow structure.)

The difference between the realized structure and its upper bound is the overhead (Ulanowicz, 1986). Overhead has conflicting interpretations. On one hand, it is a catchall for the system's inefficiencies in processing material and energy. What is a disadvantage under benign conditions can turn in the system's favor when it is perturbed in some novel way. Then, the overhead represents a "strength-in-reserve" of degrees of freedom, which the system can utilize to adapt to the new threat. Overhead is generated in any of four ways: three components of overhead are due to indeterminacies in imports, exports, dissipations (respirations), and a fourth is related to the indeterminacy over which of several parallel pathways flow will proceed between any two nodes (flow redundancy). The fractions of the development capacity encumbered by the ascendency and by each of the overhead components provide a profile of the structural composition of the system that often is useful for assessing the organizational status of an ecosystem.

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4.2.5. Cycles

Most networks of ecosystem flows contain cycles of material or energy, and the magnitudes and structure of these cycles are fully assessed by NETWRK. The program enumerates all of the simple cycles in the given matrix of exchanges (a hurculean task, as we shall see below.) Furthermore, the simple cycles are grouped into "nexuses" of cycles all of which share the same "weak arc." A weak arc is defined here as the smallest flow in a given directed cycle. The assumption is that the weak arc is the limiting or controlling link in a cycle, and that by grouping according to critical links, one identifies the domain of influence for each weak arc. Presumably, any change in a weak arc will propagate throughout its associated nexus. The nexuses are listed roughly according to ascending order of the magnitude of their defining weak arcs.

The cycles are then subtracted from the network in a fashion described in detail by Ulanowicz (1983). Briefly, the magnitude of flow in the smallest weak arc is distributed over the flows in that particular nexus and the resulting amounts are subtracted from each arc in that nexus. This process zeroes the weak arc, thereby eliminating all the cycles in that nexus, but it does not disturb the balance around any compartment, nor does it change any exogenous input, export or respiration. None of the remaining arcs of the nexus are driven negative. After that nexus has been removed, the next smallest weak arc is located; and nexuses are subtracted iteratively until all cycles have been removed from the network.

As each cycle is removed, the flow associated with that cycle is added to the magnitudes of other cycles of the same trophic length. The end result is a distribution of the magnitude of cycling according to the trophic length of cycles. This profile could be useful in assessing system response to perturbation. For example, cycling via the larger loops is often more sensitive to disturbance. The cycle distribution is then normalized by the total system throughput. Summing this normalized distribution yields the Finn cycling index, which is the fraction of total activity that is devoted to cycling (Finn 1976).

Finally, the separation of cycled from transient flow is reported in the form of separate matrices for each type of flow. The row sums and column sums of the matrix of aggregated cycles will always balance; no further reference to exogenous exchanges is necessary. The visual structure of the aggregated cycles existing in more complicated networks very often reveals separate domains of control in the network (*e.g.* Baird & Ulanowicz 1989). Finally, it should be remarked that the starting network has been neatly decomposed into an acyclic "tree" of dissipative flows and a wholly conservative nexus of cycled flows.

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4.2.6. Trophic Impacts

NETWRK treats only positive mass flows and does not consider the propagation of the negative effects that accompany predation. Ulanowicz and Puccia (1990) outlined how to treat the propagation of both positive and negative trophic effects, and their technique has been implemented in the algorithm, IMPACTS. For any particular component (designated as the "focal taxon"), IMPACTS provides a ranked listing of all the positive and negative impacts (both direct and indirect) upon that focal species. Also a ranked listing of all the direct and indirect trophic effects that focal species has upon all the other taxa is likewise provided. Of special interest are those predators that exert a direct negative impact upon a prey, but whose combined indirect positive influences more than compensate the prey for its direct losses. Such "beneficial predators" are more common than might be supposed and often highlight particular ecological roles that otherwise might have gone unnoticed. IMPACTS can be downloaded from http://www.cbl.umces.edu/~ulan/ntwk/network.html .

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5. RESULTS

5.1. Input/Output Analysis

Perhaps the most useful indices to result from the Input/Output section of NETWRK are the "total dependency coefficients" (Szyrmer and Ulanowicz 1987) or, more appropriately, the "indirect diets" of each taxon. By reading down the column of these dependency coefficients one notes the quantitative trophic history of material reaching that given compartment.

The total dependency coefficients (TDC's) of the heterotrophs in the mangrove ecosystem reveal that a significant fraction of the carbon reaching many of the predators originates in the detrital compartments (Fig. 1). Macroinvertebrates such as bivalves (17) and shrimps (23) depend on the detritus compartments (92, 93 and 94) for about 95%, and on aquatic gastropods (16) and polychaetes (14) for about 90% of their sustenance. Detritus contributes a significant amount of carbon to the diets of many fishes. The dependency of mullets (52) and needlefishes (38) on detritus is more than 87%. Conversely, only very small flows link detritus with mammals that mainly feed upon herbivorous species. Such is the case for Florida panthers and bobcats (88), which get a mere 10% of their carbon via detrital pathways. Mammals such as rabbits (81) and deer (89), which feed only on primary producers, utilize no carbon whatsoever from detritus.

One may employ the total dependency matrix to test how dependent each single compartment is on the other major groups. For example, looking at how much various groups are dependent on invertebrates (compartments 12 to 32) reveals that the fishes show the highest dependencies (Fig. 2). More than 100% of the carbon reaching snooks (43), tarpon and ladyfishes (35), rays (34) and needlefishes (38) passes through invertebrates. Sharks (33) are dependent on invertebrates to the tune of 133%. (These values greater than 100% simply mean that the same carbon is spending time in more than one invertebrate compartment.)

Birds, such as cormorants (61) and pelicans (62), are dependent to a significant degree on the carbon coming from fishes (82%), but the species that depend more on fishes than any others are the mammal compartment dolphins (#90, with a dependency of 107%), and the fish compartment, barracuda (#44, 108%). (See Fig. 3).

Dependencies on the remaining three big groups (herptofauna, birds and mammals) do not exceed 20% in most cases. Among the herptofauna, the two compartments with the highest dependencies on herptofauna are owls (76) and kites and hawks (70), with dependencies of 80% and 70%, respectively (Fig. 4.) These are followed by snakes (57) with a TDC of 32%, and then minks and otters (87) and racoons (86), each showing a dependency around 15%.

Foxes receive the most carbon leaving the bird compartments (Fig. 5). Forty percent of the carbon reaching the foxes once passed through birds. The second- largest dependency coefficient on the list, eagle and osprey (71) weighs in at only 11%.

Foxes also show a high dependency upon mammal compartments (40 %), but predatory felines (88) top the list (Fig. 6). Cats depend upon other mammal species by as much as 95 %. All the other compartments depend upon mammals for less than 10% of their sustenance. (Dependency coefficients generally decline as one proceeds from invertebrates up to mammals, as expected.)

Summing the dependencies on all primary producers for each compartment, one sees that, in most instances, the result is close to 100% (Fig. 7). This indicates that the system depends mainly on internal

carbon fixation and receives only a small subsidy from outside the system. The one exception is birds (#'s 60 to 79), which depend on internal carbon for less than 80% of their sustenance and import the remaining percentage of their support from outside the system.

No significant differences in indirect diets were found between wet and dry seasons.

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5.2. Trophic Impacts

Impact analysis is used to study both positive and negative indirect effects between compartments. In high- dimensional networks, such as this mangrove ecosystem, every pair of compartments is connected in this way, at least indirectly. Coefficients in the impact matrix represent the *aggregated net* (positive and negative) indirect effects between two species.

Of special interest are those compartments that function as "beneficial predators". The direct impact of a predator on its prey is obviously negative; however, the overall effect can become positive, due to the potential for compensation via multiple indirect pathways. In such cases one speaks of "beneficial predators". In the two previous networks, beneficial predation was quite abundant. In the cypress swamp, for example, the American alligator was a net benefactor to 11 of its prey items.

In the mangrove system network the number of beneficial indirect links is also quite high. During the dry season there were 208 such interactions, and the number during the wet period is slightly higher, with 218 links. The number of predators that exert a positive action on their prey are 48 and 49 for the dry and wet season respectively. Hence, at least some predators are beneficial to more than one prey type. Table 1 and table 2 list all the beneficent predators during either season, together with the number of prey that each positively impacts.

The "Snakes" compartment benefits the largest number of prey. During both dry and wet season, it exerts a net positive effect upon 14 of its prey. Other compartments that benefit large numbers of prey (nine or more) are: crocodiles (58), loons and grebes (60), pelicans (61), cormorants (62), big herons and egrets (63), small herons and egrets (64) and predatory ducks (68).

Although the number of beneficial links is high, the magnitude of the action is, in many cases, not very strong. The most significant positive impacts are given in table 3. (A significant impact is one in which more than 1% of the throughput of the prey compartment is affected. During both seasons, only nine links from among more than 200 exceed this threshold.) The strongest beneficial action (8.1%) is exerted during the wet season by the Snakes (#57) on their Lizard prey (#56). This particular interaction also imparts the greatest such benefit to the prey during the dry season, however the magnitude of the effect has dropped to 6.7%.

As mentioned above, a high number of positive actions exerted by a compartment does not necessarily indicate a strong net positive effect. For example, snakes are beneficial to 14 of their prey, but none of these effects are significant (greater than 1%). On the other hand, there is a fish compartment, sciaenids (#50), that benefits only 7 prey, but five of them are significant in the dry season and four during the wet. The compartments that benefit from the sciaenids are the aquatic gastropods (#16), bivalves (17), macrobenthos (#18), small crustaceans (#19) and amphipods (#20). (During the wet season aquatic

gastropods do not benefit).

Although only a small number of beneficial predator interactions achieve significant magnitude, in a few cases more than one predator affects the same prey in a net positive manner. Adding together all the positive effects by multiple predators, one obtains an aggregate positive impact by the several predators (Table 3). In addition to those links cited above, three other prey receive significant benefit from a combination of predators during the wet season: Caridean shrimps (#22), other shrimps (#23) and predatory crabs (#28). During the dry season, the prey receiving significant combined benefits from multiple predators are four in number: polychaetes (#14), freshwater mavroinvertebrates (#29), Caridean shrimps (#22) and other shrimps (#23).

Having considered and identified instances of beneficial predation, one should also consider whether the reverse relationship might be possible, *i.e.,* that the overall effect of a host on its predator over all pathways, direct and indirect, can be negative. In such case we talk of a "malefic prey". A search of the mangrove network uncovers 186 cases of "malefic" links during the wet season and 185 for the dry. A total of 47 prey affect their predators negatively in the wet period and 48 in the dry (Table 4). The compartment predatory crabs (#28), produces the highest number of negative indirect effects on its predators during both seasons, adversely affecting some 19 prey during the dry period.

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5.3. Trophic Levels

As with most ecosystems studied by Network Analysis thus far, none of the compartments of the mangrove ecosystem feed, on the average, at or above trophic level 5. Owls feed highest on average (level 4.53 during the wet season), which is close to where the raptors in Florida Bay are feeding (level 4.59, also in the wet season.) Both of these systems stand in marked contrast to the birds in the cypress swamps, most of which feed a full trophic level lower. (Those highest in trophic rankings in the swamp were the alligators and snakes, which feed at level 3.79.) The average trophic levels during both seasons are listed in Table 5. There were almost no changes in trophic levels between seasons; the greatest difference was in the foxes, which fell from 3.93 in the wet season to 3.72 in the dry.

A quick perusal of the Lindeman transformation matrix, which apportions compartments among trophic levels, reveals that there are 19 trophic levels in the overall network. (Meaning that at least one non-redundant trophic pathway with 19 links can be found in the network.) As usual, however, not much carbon reaches beyond the fifth trophic stage, and the amounts calculated to reach the 19th level are absolutely infinetesimal (of the order 10^{-38} grams.) The first six trophic levels during each season are depicted on Fig. 8. One notices immediately that the trophic chains in the two seasons are virtually identical. The efficiencies of the trophic levels are just slightly lower than those observed in Florida Bay, but significantly greater (ca. 15%) than those in the cypress swamp ecosystem.

The ratio of detritivory:herbivory is a little greater than 7:1 in the mangrove. This is somewhat lower than the 10:1 ratio for temperate estuaries, but only slightly less than the 8:1 calculated for Florida Bay and higher than the 5:1 ratio in the cypress swamp.

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5.4. System Level Indices

In many areas, the mangrove ecotope lies physically between the freshwater cypress biome and the waters of Florida Bay. As both of these networks have been estimated in the previous two years of this contract, it is useful to compare the system level indices calculated for the mangrove ecosystem with those of its neighbors. It is useful to keep in mind here that in some ways the mangrove is intemediate to its neighbors, and might be expected to exhibit system indices intermediate to the other two. A word of caution is in order, however, as transition regions can be regions of greater stress than the endpoints they join. For example, estuaries, such as the mangroves, are known to subject resident populations to much higher osmotic stresses than are encountered in either fresh or seawater.

With respect to total activity, the mangrove system is almost identical to the Florida Bay community (Table 6). Its total system throughput is 3,342 gCarbon/m^2/y, while that of Florida Bay is 3,459 of the same units. (The cypress ecotope exhibits only 2,585 units, which might be the effect of nutrient limitation within the swamps.) Florida Bay, however, has a significantly higher developmental capacity (18,540 gCarbon-bits/m^2/y vs. 15,744 for the mangroves.) Almost all of this difference can be accounted for by the higher ascendency of the Florida Bay marine system (7,003 gCarbon-bits/m^2/y against only 5,608 units in the mangrove.)

The story in words that these numbers are revealing is that Florida Bay appears to be the least stressed of the three communities studied thus far. (This despite the fact that some species displacements have occurred in the Bay in recent years.) The mangrove system is more stressed than the Bay community due to the (natural) variations in osmolarity common to estuaries. The cypress swamps appear to be limited in comparison to both other systems by a dearth of nutrients (probably phosphorus), which are abundant in the marine and estuarine waters and sediments. Some will point out that it may seem incongruous to say that Florida Bay is the least stressed of the three systems, given the serious species displacements that have occurred there in recent years. The other two systems seem almost pristine by comparison. But one must keep in mind the order of magnitude of the disturbances. Whatever stresses are afflicting Florida Bay have affected only the mix of species in that marine community. Its fundamental system processes remain largely intact. The natural stressors affecting the mangroves and the swamp are apparently much greater in magnitude, for they modulate the very rates of material and energy processing. (One should not conclude from this that humans have done little detriment to Florida Bay. Rather, it should be sobering to contemplate how future damage to the ecosystem could be even more catastrophic by comparison with what has already transpired.)

Information indices are usually applied only to whole systems. Evidence is accumulating, however, that the various sub-components of the ascendency-like variables can serve to gauge the contributions of individual system elements to the performance of the whole system (Ulanowicz and Baird 1999). For example, the ascendency is comprised of terms that are generated by each transfer in the system. If, for example, one sums up all the terms generated by the inputs to a given taxon (say, the jth one), the result is a measure of the contribution of that compartment to the full system ascendency (call it A_j). Because ascendency may be viewed as an indicator of efficient system performance (Ulanowicz 1997), the same partial-sum, A_j, represents the contribution of taxon j to overall system performance. Furthermore, if one then divides A_j by the corresponding throughput for taxon j (call it T_j), the ratio A_j/T_j will represent the contribution per unit of activity of j to the total system ascendency.

Calculating and ranking these "relative contribution coefficients" proves to be a most interesting exercise. When the average trophic levels of the 68 compartments of the cypress wetland ecosystem were calculated, for example, the alligators, snakes and wading birds were seen to feed at trophic levels higher than some other "charismatic megafauna", such as the Florida panther, Bobcat, or Grey Fox. The relative contributions to ascendency by the latter, however, actually outweighed those of the former (Ulanowicz *et al.* 1998). The relative values of these coefficients seem to accord well with most people's normative judgments of the specific "value" of the various taxa to the organization of the system as a whole (Table 7).

The relative contributions of the taxa of the mangrove ecosystem closely mirrored the results obtained from the cypress ecosystem (Ulanowicz *et al.* 1997) The feline predators (Florida panther and bobcats, #88) ranked only 25 and 27 in terms of trophic level (average levels 3.33 and 3.26, respectively.) Their relative contributions to the system ascendencies were highest of all taxa during both seasons, however. They were followed, as in the cypress glades, by the foxes. Barracuda and dolphins ranked in third and fourth places, just ahead of the snakes. (The snakes in the cypress ecosystem ranked 12th and 7th during the wet and dry seasons, respectively.)

The system indices in the mangrove ecosystem show remarkable little change between wet and dry seasons -- even less than what was observed in the other two biomes.

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5.5. Cycling

With 94 compartments in the trophic flow network the number of *potential* pathways for recycling carbon is roughly proportional to 94-factorial -- an immense number! The fact that the network is not fully connected reduces the number of potential cycles considerably. Nonetheless, the number of simple cycles in the mangrove network remains enormous. Counting them using the standard algorithm in NETWRK 4.2a was broken off after registering ca. 3.3 billion cycles. The situation is similar to what happened last year with the Florida Bay network, and the same approach taken then was followed with the mangrove systems: Most of the overwhelming number of simple cycles counted above involve more than one detrital component. We make the approximation, then, that one may choose to ignore those cycles that contain more than one nonliving compartment. The identification of such "single-detritus" cycles can be achieved first by removing the cycles that contain no detrital links, and then by successively adding the detrital compartments into the search, one at a time. The number of cycles counted in this manner will be a radical underestimate of the total number of cycles present, but once they have been extracted from the network, the residual graph will contain no cycles. Even this simplification takes considerable computing power to execute. The dry season apparently contains fewer routes for recycle (unlike with Florida Bay, where the wet season showed a greater number of cycles), and the abbreviated algorithm took approximately 10 days to execute on a SPARC-Ultra. As of the time of this report, the analysis of the wet season is still underway after more than 2 weeks of runtime. Fortunately, the results from the dry season analysis probably give us a reasonable picture of what is going on in the mangrove ecosystem as concerns the recycling of carbon. The first stage in the cycle analysis was the removal of the cycles that contain no nonliving compartments. These are generally rare in most ecosystems (Pimm 1982). There were only 12 such cycles during the dry season in the mangroves. The cycle of greatest magnitude was the mutual predation of turtles and crocodiles (Large turtles can eat juvenile crocodiles, but the amount cycled over this route is a miniscule 211 micrograms

carbon/ m^2/ y.

By far and away the greatest number of single- detrital cycles was generated by compartment #92, carbon in the sediment (9,482,523 to be exact.) Of this huge number of cycles, only 15 accounted for 97.5% of all recycling by the system. The major route for recycle was from carbon in the sediment (#92) to sediment bacteria (#8) to meiofauna (#11) and back to the carbon sediment. Secondary routes involved detours through the flagellae (#9) and ciliates (#11) in the sediment, as shown in Figure 9. In this regard, the mangrove estuary is behaving much like conventional estuaries, such as the Chesapeake, where the bulk of recycling activity occurs among the small bodied denizens of the sediment (Baird and Ulanowicz 1989).

Only 59,819 simple cycles were generated by the water column POC alone. The largest of these involved immediate exchange between POC (#93) and free microbes in the water column (#6). This route cycled a mere 5.66 $gC/m^2/y$. Similarly, only one cycle was generated by the dissolved organic carbon in the water column (#94). Along with the POC and free microbes, the DOC cycled 7.96 $gC/m^2/y$.

The aggregate activity devoted to cycling in the mangrove ecosystem during the dry season is 575.5 $gC/m^2/y$, which puts the Finn Cycling Index at 17.2%. This value is intermediate to an FCI of 21% for Chesapeake Bay and 14.4% for Florida Bay, but significantly greater than the relatively sparse cycling (8 - 9%) occurring inland in the cypress swamps.

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6. CLOSING REMARKS

The first two reports emphasized the individual characteristics of the cypress and Florida Bay ecosystems. With the mangrove community being the third network to be estimated, intersystem comparison is becoming feasible. The fact that the series cypress - mangrove- bay form a gradient from terrestrial to marine habitats make this comparison even more interesting. The ways in which the mangrove is intermediate to its neighbors (and especially how it is not!) yield interesting insights. It did not occur to us beforehand that the mangrove might be more stressed than Florida Bay, but the quantitative evidence for this circumstance is strong. What it forces the reader to do is differentiate between natural and anthropogenic stressors, and it becomes apparent that smaller magnitudes of the latter can have disproportionately visible effects.

We now look forward to the specification of the fourth, final and most well known of the biomes -- the gramminoid wetlands. The mangrove is also intermediate geographically to the gramminoid wetlands and Florida Bay. It will be exciting to see how its relationships with the gramminoid marshes compares with those it has with the cypress swamps to see if, in turn, that tells us anything about how the gramminoids compare directly with the cypress domain. With all four networks at our disposal, we should have enough dimensions to perform the most interesting whole-system comparison ever to be made. Certainly, the insights gained from the comparative exercise should serve the ATLSS modellers well as they begin their task of running this most complex of all ecosystem simulations.

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7. ACKNOWLEDGMENTS

During the past year several individuals have been most generous in devoting their time and data to the construction of the mangrove ecosystem networks. These include Andrew Baldwin, Sarah Belmund, Brian Bingham, Joan Browder, Edward Matheson, and Gordon Thayer. We sincerely appreciate their help with this daunting task.

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Network Analysis of Trophic Dynamics in South Florida Ecosystems, FY 99: The Graminoid Ecosystem

Robert E. Ulanowicz, Johanna J. Heymans, Michael S. Egnotovich

University of Maryland System, Chesapeake Biological Laboratory, Solomons, MD 20688-0038

E-mail: ulan@cbl.umces.edu
Tel: (410) 326-7266
FAX: (410) 326-7378

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EXECUTIVE SUMMARY

A 66 component budget of the carbon exchanges occurring during the wet and dry seasons in the graminoid ecosystem of South Florida has been assembled. These trophic networks will serve as independent benchmarks against which the performance of the ATLSS multi-model, now under construction, will be assessed. As is the case with such detailed, quantitative descriptions of ecosystems, the overall configuration of trophic transfers yields numerous clues as to how the ecosystem is functioning:

In the graminoid system, the breakdown of carbon into detritus is very important, but the recycling of detritus seems not to be as important as one might expect of wetland ecosystems. Most of the carbon sinks out of the system. In contrast, periphyton seems to be very important to the higher trophic levels.

An analysis of beneficial predators and malefic prey in the graminoids indicates that the living POC (microbiota attached to labile and refractory detritus) and living sediment (microbiota attached to sediment carbon) compartments actually receive indirect benefits from a large number of their predators. On the other hand, living POC appears to impact many of its predators negatively via indirect routes.

Thus, it seems that the bacterial component of the graminoid system affects the rest of the system in a negative way, even though it is affected positively by most of its predators. One thereby infers that the sediment is a natural sink for carbon in this system.

The ratio of detritivory to herbivory is very high in the graminoid system. However, a low value for the Finn Cycling Index reveals a relative unimportance of cycling in this system. This seeming paradox is explained by the fact that much of what is produced by the primary producers seems to make its way into the detritus (sediment carbon, labile and refractory detritus), which is then consumed by the bacteria in the living POC and living sediment. The total dependency analysis shows, however, that the carbon in the detrital and bacterial compartments is not recycled to the higher trophic levels, but seems to be deposited as peat.

The cycle analysis also supports the theory that cycling in the graminoid ecosystem is confined primarily to the sediment and water column detritus. The link between the detrital cycles and the higher trophic levels is very weak, which is to say there is little interaction between the microbial loop and upper trophic levels in the graminoid system.

The fact that the graminoid ecosystem is a source of food to many of the migratory species that reside in the cypress and mangrove systems has influenced the systems properties of the graminoid model. The analysis of beneficial predation is a good example of this interaction. In the graminoid system there are 13 beneficial predators in the wet season and 17 in the dry season. These numbers are much fewer than the instances of beneficial predation that occur in the cypress, mangrove and bay systems, where beneficial predation was more prolific. It may be that excluding the wading birds and other birds that do not roost in the graminoids, but still feed in the system reduces the number of beneficial predators.

Even though the graminoid system has the fewest compartments, it is far more active than the cypress, mangrove and Florida Bay communities. Its total system throughput is an order of magnitude larger than that of any of the other systems, and consequently, the development capacity of the graminoid system is significantly higher than its counterparts in the other systems.

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PAST WORK

This report covers work done during the last year of a four year task under ATLSS to quantify the trophic processes in South Florida ecosystems. During the first year, 1996-7, a 69-compartment network of the cypress wetlands was constructed and analyzed. The analysis revealed that the higher trophic populations in the ecosystem were not as dependent on cypress litterfall as had been assumed. Rather, most of the litterfall was being buried in the sediments of this peat-building system. Many of the upper trophic components were being supported instead by the production of the understory vegetation. Relatively little recycling occurs in this ecosystem. Despite the lack of physical advection in the horizontal dimension, most system activity resembles a pass-through system in the vertical direction, i.e., litter falling and being buried in the sediments. An attempt was made for the first time to assess the "intrinsic value" of each ecosystem component in terms of the amount it contributes per unit of activity to the overall performance of the system at processing mass and energy - the ascendency. This evaluation revealed that rare and endangered species, such as the Florida panther, were contributing more per unit of activity than some taxa that feed at higher trophic levels. Finally, the key role of the American alligator in maintaining the species diversity of this ecosystem was highlighted and quantified

through "impact analysis". Eleven items in the diet of the alligator derived overall (indirect) benefit from the alligator's eating habits.

During 1997-8 a 125-compartment network of the trophic flows through the ecosystem of Florida Bay was estimated for both wet and dry seasons. These networks stand as the most highly resolved and complete food webs ever to be assembled. Analysis of the network revealed that seagrasses are the ultimate source of reduced carbon for most of the rest of the system during the wet season, but that epiphytic periphyton supports most ecological activity during the dry period. Although 37% more activity transpires in the Bay during the wet season, most species feed higher on the food chain during the dry months. Concatenations as long as 15 exchanges can be identified among the network of trophic exchanges in the Bay. The recycling of carbon in the Bay ecosystem is representative of most estuaries. Over 14% of the total system activity is devoted to recycling, and most of these processes involve pelagic and benthic flagellates.

During 1998-9, an 87-compartment network of the mangrove ecosystem was estimated for both wet and dry seasons. The study showed that the mangrove ecosystem mostly functions like a detrital-based ecosystem. Most of the predator compartments depended ultimately upon detrital carbon for their sustenance, while mammals depended more upon herbivorous rather than detritivorous prey. The system depends mainly on internal fixation of carbon and receives only a small subsidy from elsewhere, mostly imported by the birds, which obtain 20% of their sustenance outside the mangroves. There were an enormous number of pathways for recycle of carbon in the mangrove ecosystem, but 97.5% of all recycle activity occurred along only 15 cycles - among the benthic compartments. The main route for recycling was mediated by the sediment bacteria and the meiofauna, with auxiliary routes passing through the benthic flagellates and ciliates. The rare feline predators contributed the most to the community ascendency per unit of their aggregate activity. Whole-system information indices paint a picture of the mangrove ecosystem as being subjected to heavy natural stressors. Of all the three systems studied previously, the mangrove community showed least seasonal change.

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1. RATIONALE

A primary goal of coordinated research on South Florida's environmental resources is to understand those communities as whole ecosystems. Toward that end, the Across Trophic Levels System Simulation (ATLSS) project is an attempt to simulate the interactions of the various elements of wetland biotic communities within the framework of a single, encompassing computational scheme.

The resulting ATLSS model is one of the most complex and sophisticated models ever attempted. It will consist of simulation modules of varying and often very high complexity that represent the important components of the ecosystems of South Florida. It follows that the output from ATLSS will be exceedingly complicated, and it may not be a straightforward task to elucidate the causal origins of any particular model behavior. Such uncertainty could become problematical, especially if the initial trials of ATLSS should behave "pathologically" (as is highly probable during the initial runs of such a complex model). Even should outputs not appear unrealistic, the difficulty remains that there exist no precedents for evaluating how well such a "multi-model" performs as an analog of the real system, i.e., there are no set protocols for "calibrating" such complex simulations. ATLSS, therefore, requires a partially independent benchmark against which one may gauge the plausibility of its outputs; and, towards that end, ATLSS investigators have chosen to create a suite of trophic flow networks that estimate material exchanges in the ecosystems being modeled. These will serve as calibration standards. In addition, these networks will be analyzed by a set of quantitative methods called Network Analysis (NA) that will provide useful information for calibrating the model and important clues for debugging the initial modeling trials.

Trophic flow networks are graphical and mathematical depictions of the answers to the questions, "Who eats whom, and by how much?" Typically, diagrams of flow networks are comprised of boxes that represent the major components of the ecosystem. The boxes are connected by arrows, which indicate the transfers of material or energy between the components. Usually, each arrow is labeled with the magnitude of its transfer as averaged over a prescribed period of time.

Accordingly, the University of Maryland contingent of ATLSS investigators is assembling very detailed networks of carbon exchanges as they normally occur in the ecosystems of South Florida. Networks consisting of more than 60 important compartments are being estimated for each of four habitats, using existing data and ongoing field work. Separate networks for wet and dry seasons are being created for the ecosystems of the forested wetlands, the graminoid marshes, the mangrove estuaries, and the shallows of Florida Bay. Each network will be a snapshot of the trophic flows and biomasses as averaged both over the hydroperiod in question and over the spatial domain of that particular biotope.

Analyses are to be performed on the resulting networks at several scales. The key questions that can be answered for any fully quantified trophic network include (1) To what extent does each taxon depend upon (or contribute to) all other taxa over all trophic pathways, both direct and indirect? (2) What are the efficiencies with which material is being transferred up the trophic ladder? (3) What are the pathways by which material is being recycled within the system? and (4) What is the current organizational status of the ecosystem? Any or all of these answers can be used to debug an ATLSS model that is not performing realistically.

During the 1996 Calendar Year we reported our findings on the cypress wetland ecosystems, as summarized in the introductory material. The 1997 Calendar Year was devoted to elucidating the flows in the ecosystem of Florida Bay (also summarized above), and the elucidation and analysis of the third of these four habitats - the mangrove ecosystem- was presented during the 1998 Calendar Year. In this, the final annual report we present the corresponding results for the networks of the graminoid wetlands (or Everglades proper).

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2. STUDY AREA

The historical Everglades system occupied a 9,300 km^2 basin that extended from the southern shore of Lake Okeechobee south and southwest to the Gulf of Mexico (Hoffman, *et al.* 1990). The basin can now be divided into three sections: Everglades Agricultural Area, Water Conservation Areas, and the Southern Everglades, which includes the marshes south of Tamiami Trail, including Shark River Slough. The Southern Everglades is still relatively natural and includes much of Everglades National Park. The Everglades National Park occupies an area of 214,000 ha (Gunderson & Loftus, 1993), and is the area used in this study.

Freshwater marsh and wet prairies comprise 33% of all Florida wetlands and 13% of all natural vegetation types (Kautz, *et al.* 1993). Freshwater marshes are defined as herbaceous plant communities occurring on sites where the soil is usually saturated or covered with surface water for one or more months during the growing season. Wet prairies are characterized by shallower water and more abundant grasses, and usually fewer of the tall emergents, such as bulrushes, than marshes (Moler, 1992). This category also includes the wet and dry marshes and prairies found on marl areas in south Florida (Moler, 1992).

Water enters the Everglades National Park from rainfall or as flow from water conservation areas to the north and from numerous canals east of the park boundary (Roman, *et al.* 1994). Oligotrophic, nutrient poor waters are characteristic of the interior portions of Everglades National Park (Roman, *et al.* 1994). In a study on the general limnology of an alligator hole in the Everglades, Kushlan & Hunt (1979) found that the physico-chemical characteristics varied seasonally.

DeAngelis *et al.* (1998) states that freshwater marshes of the Everglades are relatively oligotrophic and not highly productive, averaging only about 150 $g.m^{-2}.y^{-1}$ in wet prairie areas. However, because of the flood and drought cycle, with rapid decomposition during the dry period, much of the primary production is transferred into the detrital food chain, to fish and aquatic macroinvertebrates, and to higher trophic levels, such as wading birds (DeAngelis, *et al.* 1998). During flooding populations of small fish, crayfish, etc. are nourished by detritus and seasonal algal growth. They reach large numbers because they are relatively protected from large predatory fish, in the shallow marshes. During the dry period, the fish are concentrated into pools and depressions by receding waters (DeAngelis, *et al.* 1998). There are differences in the fauna of short and long hydroperiod areas: in the short hydroperiod areas, fish and prawn densities are generally lower, whereas the crayfish density is higher (Roman, *et al.* 1994).

Two distinct communities are evident in this system, and have been modeled separately. These two communities inhabit the short and long hydroperiod areas (Lodge, 1994) that are divided approximately 75:25 in area.

- Short Hydroperiod: Marl (mixed) prairie that occurs on thin, calcitic soil over limestone bedrock, which may be exposed as jagged, foot-tall projections called pinnacle rock or dissolved below the surface into pockets or solution holes. Short hydroperiod areas flank both sides of the southern Everglades, and contain low sawgrass, with high plant diversity (100 species) (Lodge, 1994). Most of the marl prairies are dominated by two species: muhly grass and sawgrass, but other species include blackrush, arrowfeather, Florida bluestem, and Elliot's lovegrass (Gunderson, 1994). Typically, the vegetation is less than 1m tall (Herndorn & Taylor, 1986).
- Long Hydroperiod: Deeper marsh community that are developed on peat soil, characteristically with lower plant diversity (Goodrick, 1984), and dominated by maidencane, Tracy's beak rush or spike rush (Lodge, 1994). This community occurs more commonly in the central Everglades

where they lie between sawgrass marshes and sloughs, and is important for fish and aquatic invertebrates, such as prawns. Long hydroperiod areas provide abundant prey for wading birds towards the end of the dry season (March-April). Goodrick (1984) found that beak rush, maidencane, and spike rush comprises 74% of the wet weight biomass at a typical wet prairie.

General categories of marsh vegetation include sawgrass marsh, wetland prairies, sloughs, ponds and creeks (Lodge, 1994). Busch *et al.* (1998) grouped marsh vegetation into associations dominated by:

1. Sawgrass (*Cladium jamaicense*) (Short hydroperiod — Daoust & Childers, 1999),
2. A group of emergents including *Eleocharis cellulosa, Sagittaria lancifolia*, and *Rhyncospora tracyi* (Long hydroperiod — Daoust & Childers, 1999),
3. Taxa associated with algal mats (*Utricularia* spp. and *Bacopa caroliniana*), and
4. The grasses *Panicum hemitomon* and *Paspalidium geminatum* (Long hydroperiod — Daoust & Childers, 1999).

Sawgrass covers 65 — 70% of the Everglades marsh, in nearly mono-specific stands or in association with a variety of other macrophyte species (Loveless, 1959). The sawgrass marsh community consists almost exclusively of *Cladium jamaicense*, which comprised on average 96.8% of the total plot aboveground biomass (Daoust & Childers, 1999). Only two other species were found to coexist with *C. jamaicense* — *Peltandra virginica* and *Pontederia cordata*. *Eleocharis* spp. was most abundant within the wet prairie community, comprising on average 61.2% of the total aboveground biomass throughout the year. Three other species, *Hymenocallis palmeri, Panicum hemitomon*, and *Sagittaria lancifolia*, were also found to co-occur within the wet prairie — long hydroperiod community (Daoust & Childers, 1999).

Caprio & Taylor (1984) and Olmsted *et al.* (1980) report that *Muhlenbergia* prairies are found in areas with the shortest hydroperiod (2-4 months). The dominant plant species in these prairies are the graminoids, *Cladium jamaicense, Rhychospora tracyi, Muhlenbergia filipens,* and *Schizachyrium rhizomatum*. A periphyton mat also covers the soil of these prairies. This relatively short hydroperiod results in a dry soil surface during most of the dry season (Caprio & Taylor, 1984).

According to Trexler (FIU, *pers. comm.*) the floating mat includes all non-rooted plants (and a few that may or may not be rooted) and algae. It also includes algal mats (periphyton) that float up from the bottom surface and may be suspended at mid water, or near the bottom, depending on the time of year and time of day (as the algae photosynthesize they accumulate bubbles which make them float, and at night they sink). The vascular plants included in the floating mat consist of two species: *Utricularia chara* and *Utricularia bacopa* (not common). *Utricularia* is a carnivorous plant that generally occur in nutrient-poor habitats that are sunny and moist (at least in the growing season), where they are often dominant (Givnish, 1989).

Periphyton is defined as an assemblage of attached microorganisms (primarily algae) which form living biofilms on the free surface of submerged substrates (Swift & Nicholas, 1987). Both plant stems and the surface of the marsh are covered with a complex association of numerous types of algae. Where it grows on the soil surface, it is commonly called an "algal mat" (Lodge, 1994). Gaiser *et al.* (1998) found that floating mat communities contained a matrix of *Utricularia purpurea*, cyanobacterial filaments (mostly *Schizothrix hofmanni* and *Scytonema calcicola*), and other associated algae, bacteria, fungi, and invertebrate animals. They found that the organic portion of the periphyton mat (excluding the *Utricularia* and invertebrates) comprise on average ~41% of dry biomass and consisted of mostly senescent and a lesser quantity of living material (Gaiser, *et al.* 1998).

Gunderson & Loftus (1993) found that rotifers, oligochaetes, snails, chironomids, and microcrustacea are the most numerous primary consumers in the graminoids. Several cyprinodontoids, tadpoles, moorhens and coots and some mammals are also primary consumers. Various fishes, herpetofauna and wading birds prey on the invertebrates and smaller vertebrates. Top level predators include the wading birds, alligator, otter, mink, and raptors. Scavengers include vultures, fishes and many invertebrates. The few specialists and their prey include the limpkin and snail kite — feeding on apple snails; redear sunfish feeding on gastropods; and lepidopterans feeding on specific larval food plants (Gunderson & Loftus, 1993).

Lodge (1994) suggests that the Everglades does not have a great diversity of freshwater invertebrates due to its limited type of habitat and its nearly tropical climate, which many temperate species cannot tolerate. Gunderson & Loftus (1993) also found that aquatic invertebrates are generally depauperate in the Everglades: there are no stoneflies and only two mayflies (Berner & Pescador, 1988), a few snails (Thompson, 1984), and one amphipod, while chydorid cladocerans, odonates, and dipterans are diverse.

The Florida applesnail (*Pomacea paludosa*) is an important freshwater mollusk in the Everglades. It is found in Florida's wetlands, lakes, and rivers. The Florida applesnail is important, due to its predation by a variety of wildlife including young alligators and numerous birds (Kushlan, 1978). The most publicized example is the snail kite, a hawk-like bird that feeds exclusively on the applesnail and is thus completely dependent upon water levels that maintain the snail's habitat. The limpkin, a wading bird, which is related to cranes, is also heavily dependent on the applesnail (Lodge, 1994).

There is only one species of crayfish that lives in the Everglades, *Procambarus alleni*. *P. alleni* is endemic to the Florida peninsula and is adapted to the motionless waters of marshes and to the alternating wet and dry seasons of the region. It lives in underground burrows during the dry season and browses on algae and small invertebrates over the marsh bottom during the wet season. Crayfish are important prey for largemouth bass, pig frogs, young alligators, and wading birds, particularly the white ibis (Kale, 1978). Because of its reproductive timing, *P. alleni* is one of the first abundant prey species in the Everglades early in the wet season (Franz & Franz, 1990). Crayfish make up a substantial proportion of the diets of great egrets, tricolored herons, and little blue herons, especially during the early part of the nesting season (Frederick & Callopy, 1988).

Another important decapod crustacean in the Everglades is the freshwater prawn, *Palaemonetes paludosus*. Much smaller than the crayfish, these shrimps can reach very high densities during the wet season (Kushlan & Kushlan, 1980). Unlike the crayfish, it appears that the population numbers and biomass swells in the later stages of the wet season, as the current year's larvae enter the adult shrimp-population (Beck & Colwell, 1976). The shrimps feed primarily on algae, vascular plants, detritus and small aquatic insects, with algae being the largest diet component (Beck & Colwell, 1976). These organisms are prey items of larger fish, and many of the birds that also feed on crayfish.

Aquatic insects are important in the food chain of the Everglades, as they are in all freshwater habitats (Rader, 1994). Numerous insects (*e.g.* water scavenger beetles, water boatmen, and giant water bugs) are totally aquatic but have retained the ability to fly and will attempt to relocate if their environments dry up. Most species that inhabit aquatic habitats, however, live in the water only as larvae and emerge to live in the air as adults. Prominent examples are mosquitoes, mayflies, damselflies, and dragonflies. Their dual lifestyles represent a significant transfer of energy from aquatic to terrestrial environments, where flying insects are important in the diets of many birds (Pennak, 1978).

Loftus & Kushlan (1987) found an assemblage of 30 species of fish in the freshwater marshes, all of which occurred in the spikerush or wet prairie habitat. Of these 30 species only 16 species are found in the sawgrass marshes (Loftus & Kushlan, 1987). Small species of killifishes (Cyprinodontidae),

livebearers (Poeciliidae), and juvenile sunfishes (Centrarchidae) were the common inhabitants of spikerush and sawgrass habitats. The killifishes and livebearers are short-lived, rapidly growing species (Haake & Dean, 1983), which respond to favorable conditions with rapid increases in population. The deeper, open-water alligator holes were used by larger fishes such as Florida gar, yellow bullhead, and adult sunfishes, although smaller species including mosquitofish and sailfin molly are also common (Loftus & Eklund, 1994). Loftus *et al.* (1998) found that the majority of common species in the marsh were omnivorous, while a smaller number were mainly herbivorous, detritivorous or predators on fishes and decapods. Most species of Everglades fishes acted as predators on aquatic insects and crustaceans which are major trophic links between primary and secondary production in this system. The sailfin molly was the only strict herbivore in the piscifauna but the flagfish, sheepshead minnow, least killifish, and large mosquitofish also took high proportions of algae, in addition to animal prey (Loftus *et al.* 1998).

Freshwater fish are a mainstay of the Everglades food chains. They provide the diet for alligators, otters, wading birds, and other predators (Dineen, 1984; Loftus & Eklund, 1994; Loftus & Kuslan, 1987). Herbivorous species include the golden shiner, sailfin molly, least killifish, and flagfish. Other fishes, such as golden topminnows, marsh killifish, mosquitofish, bullheads, redear sunfish, and bluegills, feed on invertebrates, many of which grazes on plants. Adult Florida gar, warmouth and largemouth bass feed principally on other fishes, and in turn, all of these fishes are the vital food supply for other predators (Hunt, 1952).

The Everglades assemblage of herpetofauna include 56 species of reptiles and amphibians, excluding the American alligator (Dalrymple, 1988) and Diffendorfer *et al.* (1999) classified them into nine functional groups. The herpetofauna include the alligators (*Alligator mississippiensis*), snakes, turtles, salamanders, salamander larvae, large frogs, medium frogs, small frogs, tadpoles and lizards. The species composition of the herpetological assemblage varies across the different habitat types (Diffendorfer, *et al.* 1999). Marshes contain four turtle species absent in the wet prairie and drier upland areas, while upland areas contain four frogs and lizards adapted for the drier conditions that do not occur in the marsh (Diffendorfer, *et al.* 1999). Wet prairie has the highest species richness, because many species found in both the marsh and upland also use prairies. During wet periods, marsh species move into the wet prairie, while upland species utilize the wet prairie when it is dry (Dalrymple, 1988).

Raccoons (*Procyon lotor*) and marsh rabbits (*Sylvilagus palustris*) are probably the most commonly seen mammals in Everglades National Park (Humphrey, 1992, Layne, 1984). Otters (*Lutra canadensis*), which are more at home in water than on land, are reasonably common but are usually seen only in the dry season (Lodge, 1994). Gunderson & Loftus (1993) found that carnivores compose nearly 50% of the 17 mammals known from true Everglades habitats and rodents are the most abundant mammals. Sowder & Woodall (1985) found no cotton mice (*Peromyscus gossypinus*) or cotton rats (*Sigmodon hispidus*) in the melaleuca strands they studied, but they do occur in the other parts of the graminoids. Gaines *et al.* (1995) found that rice rats (*Oryzomys*) move between hammock islands — indicating that they would also occur in the graminoids — even if they are only in transit. Other rodents include the exotic house mouse (*Mus musculus*) and the muskrat (*Neofiber alleni*) or Florida water rat (Burt & Grossenheider, 1961). Species that do not occur in the graminoids, but do occur in the Cypress, are the bats, feral pigs, squirrels, skunks and foxes.

Opossums (*Didelphis virginiana*) are the only marsupials in the graminoids, and North America (Burt & Grossenheider, 1976). Opossums are about the size of a house cat and prefer farming areas, but they also occur in woodlands and along streams. They are usually active only at night (Burt & Grossenheider, 1976).

Everglades mink (*Mustela vison evergladensis*) is a rare animal, but they are found in the true

Everglades region of South Florida (Layne, 1978). Most mink collected by Smith (1980) were obtained during the wet season, with very few data gathered during the dry season. Smith (1980) speculates that the population density of mink could have been enhanced due to the presence of canals and levees. Smith & Cary (1982) found that runways of mink were generally in sawgrass habitat within 3 m of the edge of the levee and appeared to be used frequently. Humprey (1982) suggests that mink retreat from marshland as it dries, and most move to permanent ponds in the late dry season, which concentrates them during this time, making for higher densities during the dry season. The swim very well and can remain under water in search of prey for several minutes (Layne, 1978).

The rarest mammal in the Everglades is the Florida panther (*Felis concolor*), whose preferred prey is white-tailed deer (*Odocoileus virginianus*) (Lodge, 1994). Smith & Bass (1994) report that whereas sub-adults and non-breeding female panthers feed almost exclusively on small prey, such as raccoon, marsh rabbit and alligator, breeding females prey primarily on white-tailed deer. In the Everglades, female white tailed deer make greater use of prairie habitat, than do males, who prefer to stay in the hummocks (Miller 1993). Labisky *et al.* (1995) report that bobcat (*Lynx rufus*) predation on adult deer is common in the Everglades (MacDonald, 1997).

Approximately 350 species of birds have been recorded within the Everglades National Park, and just under 300 species are considered to occur regularly (Robertson & Kushlan, 1984). Sixty percent of these birds are winter residents, migrating into South Florida from the north, or are hurried visitors, stopping only briefly in the spring or fall. The remaining 40% of the species of birds breed in the area. Approximately 116 species of birds breed in southern Florida (Lodge, 1994). According to Gunderson & Loftus (1993) only 70 species are know to breed in the Everglades - mostly on the tree islands and in thickets. Thus, they do not truly reside in the graminoid marshes, but only feed there.

Water birds that breed or roost in the graminoids are the pied-billed grebe (*Podilymbus podiceps*), least bittern (*Ixobrychus exilis*), fulvous whistling duck (*Dendrocygna bicolor*), green-winged teal (*Anas crecca*), mottled duck (*Anas fulvigula*), mallard (*Anas platyrhynchos*), blue winged teal (*Anas discors*), northern shoveler (*Anas clypeata*), ring necked ducks (*Aythya collaris*) and the ruddy duck (*Oxyura jamaicensis*) (Stevenson & Anderson, 1994).

Just over 70 species of land birds breed in southern Florida, but relatively few of them breed in the marshes. Land birds are those types of birds that normally live in terrestrial habitats and have no obligate dependence on aquatic or marine habitats, e.g. hawks, vultures, kites, doves, owls, woodpeckers, and songbirds (passerine birds). Some misfits within the land bird category include the osprey and the bald eagle, both of which are seen regularly in the Everglades, but neither breeds in the graminoids themselves (Lodge, 1994).

The terrestrial birds include the two Accipitridae: the snail kite (*Rostrhamus sociabilis*) and the northern harrier (*Circus cyaneus*) (Stevenson & Anderson, 1994) and the Caprimulgiformes: the common nighthawk (*Chordeiles minor*) (Werner & Woolfenden, 1983). The Gruiformes are a heterogeneous assemblage of birds often living in marshy places and are characterized by their long legs and lack of a crop (Stevenson and Anderson, 1994). There are various species in the graminoids: king rails (*Rallus elegans*), common moorhens (*Gallinula chloropus*), American coots (*Fulica americana*), limpkins (*Aramus pictus*) and Sandhill cranes (*Grus canadensis pratensis*) (Stevenson & Anderson, 1994).

The endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) breeds in marl prairies on either side of the Shark River Slough, that are typified by dense mixed stands of graminoid species, naturally inundated by freshwater for two to four months annually (ANON, 1997). They share their range with some of the passerines, such as marsh wrens, common yellowthroats, red winged blackbirds and clapper rails (Stevenson & Anderson 1994). Almost the entire range of the Cape Sable seaside

sparrow (an endemic subspecies of the seaside sparrow) is the southern Everglades and Big Cypress Swamp areas in the Everglades National Park.

The omnivorous passerines that breed and roost in the graminoids include the red winged blackbirds *(Agelaius phoeniceus)*, common yellowthroat (*Geothlypis trichas*), swamp sparrow (*Melospiza georgiana*), bobolink (*Dolichonyx oryzivorus*), eastern meadowlark (*Sturnella magna*), boat-tailed grackle (*Quiscalus major*), common grackle (*Quiscalus quiscula*), western kingbird (*Tyrannus verticalis*), tree swallow (*Tachycineta bicolor*), blue jay (*Cyanocitta cristata*), fish crow (*Corvus ossifragus*), blue-gray gnatcatcher (*Polioptila caerulea*), northern mockingbird (*Mimus polyglottos*), white-eyed vireo (*Vireo griseus*), yellow rumped warbler (*Dendroica coronata*) and the cardinal (*Cardinalis cardinalis*) (Stevenson & Anderson 1994). The predatory passerines include the eastern phoebe (*Sayornis phoebe*), loggerhead shrike (*Lanius ludovicianus*) and the palm warbler (*Dendroica palmarum*) (Stevenson & Anderson 1994).

Graminoid ecosystems provide valuable habitat for a wide range of animals, including species listed by the U.S. Fish and Wildlife Service as endangered, threatened or of concern. Examples of federally listed species are the Florida panther (*Felis concolor coryi*) and the eastern indigo snake (*Drymarchon corais couperi*) (Odum and McIvor, 1990). The Everglades mink (*Mustela vison evergladensis*) (Layne, 1978), snail kites (*Rostrahamus sociabilis*), the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), the sandhill crane (*Grus canadensis*) and the wood stork (*Mycteria americana*) are also species of concern that are listed as rare or endangered (Kushlan, 1990).

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3. PARSING THE NETWORK

As with most methodologies, some of the most important assumptions in Network Analysis are made at the outset. They concern decisions as to what to choose as the primary elements of the network and how these taxa are to be connected. In this project, these decisions are simplified somewhat by the requirement that the network be comparable to the ATLSS simulation. That is, each state variable of the ATLSS model must have its counterpart in the accompanying network.

Network analysis, however, can treat far more complicated webs of interaction than are possible using simulation modeling. Keeping the simulation dynamics of many coupled processes from becoming pathological is a difficult balancing act. Because NA does not deal explicitly with dynamics, far greater taxonomic resolution becomes possible with this form of analysis. As a result, some taxa in the ATLSS model will be represented by several compartments in the graminoid network. In addition, compartments can be added to the network with relative ease. For example, the creation of an individual-based model for one of the lesser-known bird species (e.g. the swamp sparrow) would entail significant effort. As will be described below, it requires nowhere near as much work to include this compartment in the quantified trophic web.

Although the primary reason for creating these networks is to serve as a calibration benchmark for ATLSS, it should be mentioned that each single network and its ensuing analysis could also serve independent purposes. For example, some biologists will be curious to know how the particular species that they are interested in, which might not appear in ATLSS, will fare under the proposed hydrological scenarios. With regard to trophic interactions at least, the results of NA should allow those investigators and managers to make some educated guesses about how the excluded population might change. For example, NA quantifies the direct and indirect trophic interactions of each compartment with all other compartments in the web. In particular, the stocks and activities of each compartment that do not appear in ATLSS can be compared with all those that do participate through NA. Any coefficients and ratios as may result can be applied to the predicted outputs from ATLSS to estimate the accompanying trophic status of the non-included species. In other words, after calibration NA can serve to expand the scope of predictions from ATLSS.

From an ecological viewpoint, virtually all the important trophic components (i.e., those comprising at least 5% of the standing biomass or activity) have been written into ATLSS. These include detritus, microbes, aquatic macrophytes, mesoinvertebrates, macroinvertebrates, piscivorous fish, planktivorous fish, etc.

As for the previous three networks, the cypress wetland ecosystem, the Florida Bay ecosystem and the mangrove ecosystem, it happened that data did exist to make at least crude estimates of the stocks and activities of a number of some other ecosystems members. Similarly, it was decided to include these "parallel" species in the NA of the graminoid network.

In addition, in order to wind up with more homogeneous and comparable networks, the choices that were made in the three previous network models have been taken into consideration in drawing up the list of components for the graminoid ecosystem. Because many of the species that are resident in the mangroves and cypress systems feed in the graminoid marshes, there will be interactions between these systems, and some redundancies among their species. For example, most of the fishes and invertebrates listed for cypress system are present as well in the graminoids. The same goes for many of the mammals and birds in the cypress and the birds in the mangroves. Conversely, the estuarine and marine species of the mangrove and Florida Bay systems are not seen in the freshwater graminoid marshes. This results in a lower number of compartments in the graminoid ecosystem than comprised any of the preceding three systems. In deciding which elements to include in the network and how these taxa are to be connected,

the same resolution was used as was employed with the previous three biotopes, in order that the elements and structure of the four different network models will remain comparable.

For some categories, such as invertebrates and fish, individual compartments for each of the more abundant and better-documented species have been reserved, while the remaining species were combined into single "other macroinvertebrates", "other small fish" and "other large fish" compartments.

In many networks the major lexical question involved how to treat the manifold species that comprise some functional groups for which data at the level of individual species were not available. To characterize these poorly resolved parts of the ecosystem, it was decided to group the species into generalized compartments. Such was the case in the graminoid network for mesoinvertebrates and passerine birds. The same aggregation has been done for bacteria and protozoans in the water column and sediments, which were assigned to a compartment called "living POC" and "living sediments", respectively.

The completed networks both consist of 66 separate components. Only those species closely associated with the dominant patterns have been retained. Hence, only those primary producers, invertebrates, fishes, reptiles, birds and mammals commonly found in the graminoid system made the final list of species. Once completed, the list was aggregated somewhat according to certain criteria, such as species sharing the same diet, available data and the goals of ATLSS. For example, most species to be included in ATLSS as individual-base models have been maintained as separate compartments in the network.

The following is the final list of components composing the graminoid ecosystem network, along with a very brief description of what each compartment entails:

3.A Living Microbial compartments

The initial elements of the network are the living compartments of the microbial loop. They have been divided as follows:

1. LIVING SEDIMENTS. Includes all bacteria and fungi living at the sediment level.
2. LIVING POC. Bacteria and protozoans that occur in the water column are all represented in this compartment.

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3.B Primary producers

A description of the dominant primary producers is reported in the "study area" section of this report. They have been divided as follows:

3. PERIPHYTON. Mostly diatomaceous forms of algae.
4. MACROPHYTES. The macrophyte assemblage includes sawgrass (*Cladium jamaicense*), two

species that coexist with sawgrass — *Peltandra virginica* and *Pontederia cordata*. *Eleocharis* spp. was most abundant within the wet prairie community, while *Hymenocallis palmeri, Panicum hemitomon*, and *Sagittaria lancifolia*, co-occur within the wet prairie community (Daoust & Childers, 1999).

5. UTRICULARIA. The vascular plants included in the floating mat consist of two species: *Utricularia chara* and *Utricularia bacopa* (not common). *Utricularia* is a carnivorous plant that generally occurs in nutrient-poor habitats that are sunny and moist (at least during the growing season), where they are often dominant (Givnish, 1989).
6. FLOATING VEGETATION. The floating vegetation includes all non-rooted plants, and a few that may or may not be rooted. Examples include as pond lilies and duckweed.

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3.C Invertebrates

As might be expected, the invertebrates of the Everglades graminoids are similar in species composition to those of the Cypress system. However, better data were available for the construction of the graminoid network, so that the invertebrate assemblage could be expanded in the newer graminoid model.

7. APPLE SNAIL. This compartment contains only *Pomacea paludosa*, the apple snail. Other snails are found in Aquatic Macroinvertebrates.
8. FRESHWATER PRAWN. Contains only the freshwater shrimp *Palaemonetes paludosus*.
9. CRAYFISH. The Everglades are populated almost exclusively by *Procambarus alleni*. There is some evidence, however, that another species, *Procambarus clarkii*, which has been introduced throughout Florida, may be present in some areas of the Everglades (Franz and Franz 1990).
10. MESOINVERTEBRATES. This is the first of four general invertebrate compartments. It contains small aquatic invertebrates, including animals from the following taxonomic groups: Oligochaeta, Bosminidae, Chydoridae, Daphniidae, Macrothricidae, Sididae, Calanoid and Harpacticoid copepods, Chironmidae. Fish larvae of comparable size are also included in this compartment.
11. OTHER MACROINVERTEBRATES. The second of the general invertebrate compartment contains all aquatic invertebrates larger than the mesoinvertebrates (just described) and smaller than the predatory aquatic insects. Representative animals from the following taxonomic groups: Trichoptera, Certaopogonidae, Tanypodinae, Gastropoda (excluding apple snails). Fish larvae of comparable size are also placed in this compartment because of their similar trophic stature.
12. LARGE AQUATIC INSECTS. All large predatory aquatic insects and larvae (e.g., dragonfly and damselfly nymphs) found in the graminoid marshes.
13. TERRESTRIAL INVERTEBRATES. This compartment contains all the invertebrates that are active in non-aquatic environments. There are very little quantitative data about these organisms, and the data here have been extrapolated from tropical grasslands outside the Everglades (Janzen and Schoener 1968). Organisms in this compartment will include adult forms of members of the aquatic invertebrates (Odonates, Ephemeroptera) and also any of the exclusively terrestrial insects (Lepidopterans, ants, wasps, etc.).
14. FISHING SPIDER. This compartment contains only the fishing spider, *Dolomedes triton*, because of its unique feeding habits (Jordan et al. 1994). The other spiders are found in the Terrestrial Invertebrates compartment.

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3.D Fishes

The fishes in the graminoids are generally the same species that were found in Cypress, however the fish assemblage in the Cypress was divided into only three compartments, small, herbivorous-omnivorous fish, small predatory fish and large, predatory fish. These assemblages could be separated in the graminoid marshes due to significantly more quantitative information available for this system.

15. GAR. A member of the family Lepisosteidae, *Lepisoseus platyrhinchus*, one of the top predatory fish species.
16. SHINERS AND MINNOWS. This compartment contains only the diminutive minnows of the family Cyprinidae, including such species as: golden shiner (*Notemigonus chrysoleucas*), tailight shiner (*Notropis maculatus*), coastal shiner (*Notropis petersoni*) and pugnose minnow (*Opsopoedus emiliae*)
17. CHUBSUCKERS. Lake chubsucker (*Erimyzon succetta*) is a member of the family Catastomidae.
18. CATFISH. Contains species from the family Ictaluridae and Clariidae. Typical species are: white catfish (*Ameiurus catus*), yellow bullhead (*A. natalis*), brown bullhead (*A. nebulosus*), channel catfish (*Ictalurus punctatus*) and tadpole madtom (*Noturus gyrinus*). The exotic walking catfish (*Clarias batrachus*) is the only representative from the family Clariidae.
19. FLAGFISH. One of the most abundant fishes in the Everglades, the flagfish (*Jordanella floridae*) is a member of the family Cyprinodontidae.
20. TOPMINNOWS. The topminnow species of the family Fundulidae. Included representatives are: Golden topminnow (*Fundulus chrysotus*), banded topminnow (*F. cingulatus*) and lined topminnow (*F. lineolatus*).
21. BLUEFIN KILLIFISH. One member of the family Fundulidae, the bluefin killifish (*Lucania goodei*), has been given its own compartment, because it is so abundant.
22. KILLIFISHES. This compartment contains the remaining species of family Fundulidae, such as the Seminole killifish (*Fundulus seminolis*) and the marsh killifish (*F. confluentus*).
23. MOSQUITOFISHES. Consists of only the Poecilid species, *Gambusia affinis*. The mosquitofish is another highly abundant small fish species.
24. POECILIDS. Contains the remaining Poecilds, including the very abundant species least killifish (*Heterandria formosa*) and sailfin molly (*Poecilla latipinna*). It also contains an introduced Poecilid species, the pike killifish (*Belonesox belizanus*).
25. PYGMY SUNFISH. The Centrarchids (sunfishes) have been split into as many single species compartments as possible, due both to their diverse feeding habits and to the large proportion of total fish biomass that they comprise. This compartment is devoted to the Everglades Pygmy Sunfish (*Elasoma evergladei*).
26. BLUESPOTTED SUNFISH. *Enneacanthus gloriosus* is one of the smaller Centrarchid species.
27. WARMOUTH. The warmouth (*Lepomis gulosus*) is one of the larger predatory species of sunfish in the Everglades.
28. DOLLAR SUNFISH. *Lepomis marginatus*.
29. REDEAR SUNFISH. The redear sunfish (*Lepomis microlophus*) consumes primarily gastropods.
30. SPOTTED SUNFISH. *Lepomis punctatus*.
31. OTHER CENTRARCHIDS. Contains any previously unmentioned Centrarchid, most notably the bluegill (*Lepomis macrochirus*) and the black crappie (*Pomoxis nigromaculatus*).
32. LARGEMOUTH BASS. *Micropterus salmoides* is one of the top predator fishes.
33. CICHLIDS. This compartment contains the assemblage of introduced Cichlids: Oscar (*Astronotus oscellatus*), peacock cichlid (*Cichla ocellaris*), black acaria (*Cichlasoma bimaculatum*) mayan cichlid (*Cichlasoma uropthalmus*), blue tilapia (*Tilapia aurea*), and spotted tilapia (*Tilapia*

mariae).

34. OTHER LARGE FISHES. This is the first of two generic fish compartments and contains the rarer large freshwater fish of the Everglades as well as those euryhaline species that sometimes invade the freshwaters. Included are: Bowfin (*Amia calva*), American eel (*Anguilla rostrata*), pickerels (*Esox* spp.) shads (*Dorosoma* spp.), mullets (*Mugil* spp.) and snooks (*Centropomis* spp.)
35. OTHER SMALL FISHES. This is the second of two generic fish compartments and contains the rarer small freshwater fish of the Everglades as well as those euryhaline species that are known to invade freshwaters at various times of the year. Included are Silversides (*Menidia* spp.), gobies (*Gobiosoma* spp. and *Microgobius* spp.) and swamp darter (*Etheostoma fusiforme*).

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3.E Reptiles and Amphibians

Although not composed of exactly the same species, the list of reptile compartments resembles that of the cypress ecosystem. Reptiles have been divided into four separate compartments: snakes, lizard, turtles and alligators, most consisting of several species, with the exception of one single- species taxon, devoted to the American alligator (*Alligator mississippiensis*). Amphibians were divided into six separate compartments: salamanders, salamander larvae, large frogs, medium frogs, small frogs and tadpoles (Diffendorfer, *et al.* 1999).

36. SALAMANDERS. The salamander compartment includes the dwarf and greater sirens (*Pseudobranchus striatus* and *Siren lacertina*), the two-toed amphiuma (*Amphiuma means*) and the pensinsula newt (*Notophthalmus viridescens*) (Diffendorfer, *et al.* 1999).
37. SALAMANDER LARVAE. The larvae of all salamander species present in the graminoids are lumped here.
38. LARGE FROGS. Only one species of large frog is found in the graminoids: the pig frog (*Rana grylio*) (Diffendorfer, *et al.* 1999).
39. MEDIUM FROGS. Medium frogs include the southern toad (*Bufo terrestris*), green treefrog (*Hyla cinerea*), Cuban treefrog (*Osteopilus septentrionalis*), Florida chorus frog (*Pseudacris nigrita*), southern cricket frog (*Acris gryllus*), squirrel treefrog (*Hyla squirella*) and southern leopard frog (*Rana sphenocephala*) (Diffendorfer, *et al.* 1999).
40. SMALL FROGS. Small frogs include the oak toad (*Bufo quercicus*), eastern narrowmouth toad (*Gastrophryne carolinensis*), greenhouse frog (*Eleutherodactylus planirostris*) and the little grass frog (*Limnaoedus ocularis*) (Diffendorfer, *et al.* 1999).
41. TADPOLES. The tadpoles of all the frogs in the graminoids are gathered into this compartment.
42. TURTLES. Turtles include the common musk turtle (*Sternotherus odoratus*), striped mud turtle (*Kinosternon baurii*), eastern mud turtle (*K. subrubrum subrubrum*), Florida box turtle (*Terrapene carolina bauri*), chicken turtle (*Deirochelys reticularia*), peninsula cooter (*Pseudemys floridana*), Florida redbelly turtle (*P. nelsoni*), red ear slider (*P.scripta*), Florida snapping turtle (*Chelydra serpentina*) and the Florida softshell turtle (*Apalone ferox*) (Diffendorfer, *et al.* 1999).
43. SNAKES. Snakes found in the graminoids include: the Florida water snake (*Nerodia fasciata*), Florida green water snake (*N. floridana*), brown water snake (*N. taxispilota*), striped crayfish snake (*Regina alleni*), Florida brown snake (*Storeria dekayi victa*), black swamp snake (*Seminatrix pygaea*), eastern garter snake (*Thamnophis sirtalis*), peninsula ribbon snake (*Thamnophis sauritus*), southern ringneck snake (*Diadophis punctatus*), rough green snake (*Opheodrys aetivus*), mud snake (*Farancia abacura*), black racer (*Coluber constrictor*), eastern indigo snake(*Drymarchon corais couperi*), red rat snake (*Elaphe guttata*), yellow rat snake (*E. obsoleta*), Florida kingsnake (*Lampropeltis getulus floridana*), scarlet kingsnake (*L. triangulum*

elapsoides), scarlet snake (*Cemophora coccinea*), cottonmouth (*Agkistrodon piscivorus*), dusky pygmy rattlesnake (*Sistrurus miliarius barbouri*) and eastern diamondback rattlesnake (*Crotalus adamenteus*) (Diffendorfer, *et al*, 1999).

44. LIZARDS. Lizards in the graminoid Everglades include the brown anole (*Anolis sagrei*), green anole (*A. carolinensis*), ground skink (*Scincella laterale*), island glass lizard (*Ophisaurus compressus*) and the five-lined skink (*Eumeces inexpectatus*) (Diffendorfer, *et al.* 1999).
45. ALLIGATORS. The American alligator (*Alligator mississippiensis*).

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3.F Mammals

Mammals in the graminoids show considerable overlap with those listed in the cypress wetland network.

46. MUSKRAT. Colonies of muskrat (*Neofiber alleni*) are abundant throughout the Shark River Slough and the open glades of the ENP (Tilmant, 1975).
47. MICE AND RATS. Species found in the graminoids include the cotton mice (*Peromyscus gossypinus*), cotton rats (*Sigmodon hispidus*), rice rats (*Oryzomys palustris*) and the exotic house mouse (*Mus musculus*).
48. RABBITS. The marsh rabbit (*Silvilagus paulstris*).
49. RACCOONS. Raccoons (*Procyon lotor*) are very abundant in the graminoid wetlands.
50. OPOSSUMS. The Virginia opossum (*Didelphis virginiana*).
51. OTTER. The river otter (*Lutra canadensis*).
52. MINK. The mink (*Mustela vison*).
53. DEER. The white-tailed deer (*Odocoileus virginianus*).
54. BOBCAT. *Lynx rufus*.
55. PANTHER. The Florida panther (*Felis concolor*).

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3.G Birds

Taxonomy, feeding habits and the availability of information were primary concerns in establishing the final list of birds. Species of birds that feed in the graminoids, but do not roost there, were not included, as they have already been accounted for in the cypress and mangrove models. Therefore, the compartments given in this model are mostly those not found in the other models. For lists of all species to be found in the graminoid Everglades, see Stevenson and Anderson (1994).

56. GREBES. Only one species of grebe is found in the graminoids, the pied-billed grebe (*Podilymbus podiceps*).
57. BITTERNS. One species of bittern breeds in the graminoids, the least bittern (*Ixobrychus exilis*).
58. DUCKS. Eight species of Anseriformes breed or roost in the graminoids: fulvous whistling duck (*Dendrocygna bicolor*), green-winged teal (*Anas crecca*), mottled duck (*Anas fulvigula*), mallard (*Anas platyrhynchos*), blue winged teal (*Anas discors*), northern shoveler (*Anas clypeata*), ring necked ducks (*Aythya collaris*) and the ruddy duck (*Oxyura jamaicensis*) (Stevenson and

Anderson, 1994).

59. SNAILKITES. The snail kite (*Rostrhamus sociabilis*) is the most important species of Accipitridae in this system.
60. NIGHTHAWK. Only one species of Caprimulgiformes roosts or breeds in the graminoids, the common nighthawk (*Chordeiles minor*).
61. GRUIFORMES. Including the American coot (*Fulica americana*), limpkin (*Aramus guarauna*), king rail (*Rallus elegans*), common moorhen (*Gallinula chloropus*) and Sandhill crane (*Grus canadensis pratensis*) (Stevenson and Anderson 1994).
62. CAPE SABLE SEASIDE SPARROW. The endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) breeds in the graminoids.
63. PASSERINES. The passerines that roost or breed in the graminoids include the red winged blackbirds *(Agelaius phoeniceus)*, common yellowthroat (*Geothlypis trichas*), swamp sparrow (*Melospiza georgiana*), eastern meadowlark (*Sturnella magna*), boat-tailed grackle (*Quiscalus major*) and the common grackle (*Quiscalus quiscula*) (Stevenson and Anderson 1994).

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3.H Detritus Compartments

Detritus has been divided into three separate compartments:

64. SEDIMENT CARBON. Includes all the non-living organic carbon available in the first 10 centimeters of sediment.
65. LABILE DETRITUS. Liable detritus is organic matter in the water column that decomposes at a relatively fast rate. As with the cypress network, we use the information reported in Dierberg and Ewel (1986) for the decomposition rate of labile detritus (5.7/y.)
66. REFRACTORY DETRITUS. Refractory detritus represents organic matter that decomposes at a relatively slower rate than labile detritus ($0.17.y^{-1}$) (Dierberg and Ewel, 1986).

Seasonality at this latitude is marked more by variations in freshwater input than by changing temperature. Thus, two separate networks mimic seasonality: one for the wet season (from June to November) when freshwater inputs are high and another for the dry season (December to May), when inputs are relatively low.

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4. METHODS

After the "lexical" phase of model building, the next step involves connecting the selected compartments to one another via feeding and detrital pathways. This topology is determined from information about the diets of each taxon. But the purpose here is not merely to formulate a qualitative "food web". We wish to quantify the connections as well. Toward this end, it is useful to concentrate first on assessing the densities, or stocks of the participating taxa. Knowing the concentration of biomass is the key to scaling all the activities of a particular population.

4.1 Estimation Techniques

Four different models were estimated: two for the wet season (long and short hydroperiod) and two for the dry season (long and short hydroperiod). These models were then combined into two models: one for wet season and one for dry season.

The biomass values of some species are known to reasonable precision. For example, the number of animals per cubic meter or liter is available for some of the compartments. As the standard units used in NA are grams of carbon per square meter ($gC.m^{-2}$), the available data had to be transformed to maintain dimensional consistency. Towards this end, information on the average weight (grams) of animals was gathered from technical manuals. The percentage of carbon per gram of dry weight was then combined with wet weight/dry weight ratio to obtain $gC.m^{-3}$. Busch *et al.* (1998) gives the average depth for short and long hydroperiod sites as 22 and 42 cm respectively, and by assuming these average water depths, the carbon biomass in the required units ($g.m^{-2}$) could be calculated. In the case of primary producers, macrophyte biomass data was reported in gram dry weight.m^{-2} (Daoust & Childers, 1999), while periphyton (Browder, *et al.* 1982), floating vegetation and *Utricularia* data were reported in grams ash free dry weight.m^{-2} (Trexler, *pers. comm.*). In this case only the wet weight/dry weight ratio and the percentage of carbon per gram of dry weight (Jorgensen, *et al.* 1991) were necessary to convert the biomass into the correct units.

Water column detritus data for the graminoid marshes includes only TOC (total organic carbon). This compartment includes both dead organic carbon (POC — particulate organic carbon - and DOC — dissolved organic carbon) and living matter (bacteria etc.). The TOC data of Flora & Rosendahl (1982) was then divided into DOC and POC by using a 95% DOC, 5% POC split (Scinto, *pers. comm.*). POC was divided into living and dead POC by using a concentration of 5% living POC (Christian, *pers. comm.*). The remaining 95% dead POC and the DOC were divided into labile and refractory detritus by using a 20% labile, 80% refractory split (Dierberg & Ewel, 1985). Concentrations were reported in $gC.l^{-1}$, and the above procedure was followed. Sediment detritus data was approximated by using bulk densities ($g.cm^{-3}$) and organic carbon percentages of dry weight (45% for long hydroperiod and 0.6% for short hydroperiod) given by Brown *et al.* (1990). Due to lack of information it was assumed that the sediment detritus does not change significantly between wet and dry seasons.

In most cases, suitable estimates of fish and invertebrate density were available. These densities could be used in conjunction with published animal body masses for fishes and common invertebrates (Kushlan, *et al.* 1986) to estimate biomass per unit area. While the primary data on fishes came almost entirely from one source (Trexler, *et al.* 1996), the invertebrate biomass values were estimated from several different data sets.

- Apple snail densities were distinguished as to vegetational substrates, which can serve as an analogue for long versus short hydroperiods (Croop, 1996). This data was split into seasonal

components using monthly data on gastropod densities presented in Ulanowicz (1994). The value from Croop (1996) was taken to be the midpoint for the hydroperiod type, and these densities were subsequently adjusted upward by a factor of 1.07 for the wet season, and down by 0.92 for the dry season to reflect density changes caused by seasonal factors.

- Data for freshwater prawns and crayfish came from Loftus, *et al.* (1990). Their data were easily sorted into the four hydroperiod- and seasonal categories prior to conversion into biomass estimates.
- Estimates of mesoinvertebrates, other marcoinvertebrates and large aquatic insects were derived from data presented in Ulanowicz (1994). Monthly data accumulated over several years from different sites could be assigned to either long or short hydroperiods.
- We were unable to find any density estimates for terrestrial invertebrates and were forced to look to densities of tropical insects in Central American grasslands as surrogates (Janzen & Schoener, 1968). Wet season densities were estimated to be approximately 40% greater than those of the dry season.
- The fishing spider was given its own compartment based on the uniqueness of its trophic role in the Everglades. Density estimates based on habitat type (sawgrass versus wet prairie) were used again as analogues for long and short hydroperiod (Jordan, *et al.* 1994). These estimates were not adjusted by any seasonal factors, since there appear to be no data indicating any sort of seasonal trends in the dynamics of the spider population.
- Fish densities for long and short hydroperiod sites were available in Trexler, *et al.* (1996).

Once the densities were determined, each value was multiplied by an average individual body mass in order to generate estimates of biomass per unit area. In most cases, the individual body masses used were those from Kushlan, *et al.* (1986). For several invertebrate compartments (mesoinvertebrates, other macroinvertebrates and large aquatic insects), body mass estimates appearing in Ulanowicz (1994) were used. In some fish compartments, body masses were calculated using collection data from Fury, *et al.* (1999). These data were used to augment or fill in missing or underrepresented species that were not suitably covered by the body mass estimates reported in Kushlan, *et al.* (1986). Conversion to grams carbon per square meter were carried out under the convention reported in Jorgensen, *et al.* (1991): 20% of wet weight is dry weight, and 45% of dry weight is carbon weight.

Data for all herpetofauna except alligators were obtained from Diffendorfer *et al.* (1999) in grams wet weight per hectare and converted using the wet weight/dry weight ratio and the percentage of carbon per gram of dry weight given by Jorgensen *et al.* (1991). Dalrymple (*pers. comm.*) suggests an average number of 10,000 alligators in the ENP, of which 75% occur in long hydroperiod areas, and with a 50:50 sex ratio. Wulff (*pers. comm.*) suggests that there are about 5,000 adult alligators in the Park and the average weight is 20 kg each. For this study an average value of 10,000 alligators was used, with 30:70 split between adults and juveniles. An average weight of approximately 20 kg was used for adults and 5 kg for juveniles.

Mammals have been very poorly monitored in the graminoid system. In many cases the data for the cypress system had to be used and adjusted to pertain to the graminoids. In general, the average wet mass per animal was obtained from Burt & Grossenheider (1961 or 1976), and the dry weight/wet weight and dry weight/carbon ratios from Jorgensen, *et al.* (1991).

- For mice and rats the densities were presumed to be similar to those in the cypress system. It was assumed that the short hydroperiod values were double those of the long hydroperiod (similar to the cypress data) and the 2:3 conversion of Mazzotti *et al.* (1981) was used for wet and dry season.

- Muskrat biomass was estimated by using the densities of their houses (Tilmant, 1975) and the

number of houses/animal (Birkenholz, 1962). It was assumed that the dry season density was double that of the wet season, and as they only occur in the Shark River Slough (Tilmant, 1975) the biomass was scaled down to apply to the total area of the ENP.

- Marsh rabbit densities were presumed to be similar to those of the cypress system for long hydroperiod areas, as Burt & Grossenheider (1976) report that they occur in wet bottomlands, swamps and hummocks. The short hydroperiod densities were assumed to be 5% of the long hydroperiod densities (the hummock:sawgrass ratio), and, as with the cypress model, the wet season densities were set to half those of the dry season.

- Raccoons are so ubiquitous that they warrant consideration in both the short and long hydroperiod models (Layne, *pers. comm.*). They probably use tree islands for daytime refugia, but it was assumed that they would forage extensively in marshes and prairies during both dry and wet periods. It was assumed that the short hydroperiod density is half of cypress density, that the long hydroperiod densities are half those of the short hydroperiod densities, and that the wet season densities are 0.25 of dry season densities.
- Opossum densities were not available for the graminoids, forcing us to resort to the cypress data. It was assumed that the short hydroperiod density is double that of the long hydroperiod density, as they are reported to prefer farming areas (Burt & Grossenheider, 1961). Ryser (1992) suggests that the opossum population is seasonally stable, whence we presume that the wet and dry season densities are the same.
- River otters occur mostly in long hydroperiod areas (Newman & Griffin, 1994; Burt & Grossenheider, 1976; Dalrymple, *pers. comm.*). It was assumed that the density is higher in the dry season due to seasonal aggregation, and the biomass was calculated by estimating it from the cypress biomass (Humphrey & Zinn, 1982).
- Smith & Cary (1982) found that runways of mink were generally found in sawgrass habitat within 3 m of the edge of the levee and seem to be used frequently. Dalrymple (*pers. comm.*) suggests that they occur in both short and long hydroperiod areas, however, as the biomass was so low in long hydroperiod areas, they were assumed to be negligible in the short hydroperiod areas. Their densities are higher in the dry season (Humprey, 1982) and are reported to be similar to the cypress system (Smith, 1980). The average mass per mink was estimated from Smith & Cary (1982).
- Miller (1993) found that habitat use by white tailed deer did not differ between wet and dry seasons, indicating no seasonal difference in biomass. Smith, *et al.* (1996) gives average number and mass for adults and juvenile deer, and the biomass was reduced by half during the long hydroperiod areas, as they would have less available habitat and they would not occur in the sloughs.
- Bobcats are short hydroperiod residents (Burt & Grossenheider, 1961; Labisky & Boulay, 1998; Foster & Humphrey, 1995). It was assumed that the number of bobcats in the short hydroperiod is half that of in the cypress system, that the density in the long hydroperiod areas is half that of the short hydroperiod and that wet season densities are 0.25 of dry season densities. The average mass for the bobcats of the graminoids was obtained from Powers, *et al.* (1989) and Labisky & Boulay (1998).
- Smith, *et al.* (1996) quotes a number of 6-8 panthers as a possible carrying capacity for the Park. On average only two (one male & one female) of the six panthers monitored by Smith & Bass (1994) were generally found in the mixed marsh or slough areas, while the other four generally occurred in upland/pine forests or outside the Park. Those two panthers spent approximately two-thirds of their time in the short hydroperiod areas and one-third in the long hydroperiod areas (Smith & Bass, 1994). It was assumed that the dry season density was half the number of panthers in wet season.

Bird densities were obtained from the Christmas Bird Count (CBC) and the Breeding Bird Survey (BBS). CBC data from http://www.mbr-pwrc.usgs.gov/cgi-bin/cbcgrids2.pl/numcols=7/cellsize=100?478,578 and BBS from http://www.mbr-pwrc.usgs.gov/id/check/25.html. The BBS (abundance per route) data is converted by using Robbins, *et al.* 1986 methodology, where they observe 50 stops 0.5 miles apart, and observe 0.25 miles in each direction — thus an area of 12.5 miles^2. The CBC data is converted by using the circle with diameter 15km — an area of 458 km^2 (Bolte & Bass, 1980). The relative abundance of birds in the CBC is given in number/100 party hours (John R. Sauer, *pers. comm.*, Patuxent Wildlife Research Center) and this abundance was used as is, as it gives a good abundance for the area of the circle counted (Sauer, *pers. comm.*). It was assumed that the birds that the number of birds that do not feed in the area for the whole day are offset by those birds that were not counted in the survey. Average mass per individual was obtained from Dunning (1993) and Stevenson and Anderson (1994).

Once the biomass had been approximated, information was sought on the production, respiration and consumption rates per unit biomass of each species. Multiplying any biomass density by these factors establishes the total input to and outputs from the compartment in question. If one also has solid data on the dietary proportions of heterotrophs, the total input can be apportioned among the various prey compartments, and the magnitudes of the intercompartmental inputs can be established at this time. Unfortunately, the dietary components of some taxa were not available as quantitative proportions -- only as a list of species. In such cases the total input was assumed to derive from the various prey in proportion to the production or biomass values of those prey.

The consumption, production, respiration and egestion values for each compartment were calculated either by using P/B, P/C, P/R ratios, or by employing known formulas for calculating metabolism, assimilation efficiency, etc. For microbial compartments the P/B, P/R and P/C values from the cypress model were used. For primary producers:

- Ulanowicz (1994) assumed a daily P/B ratio of 0.04 for periphyton, and Browder, *et al.* (1982) reported P/R ratios of 0.92 and 1.39 for the dry and wet seasons, respectively.
- Macrophyte productivity values were obtained from Daoust & Childers (1999) and McCormick, *et al.* (1997) uses a P/R ratio of 1. Vymazal (1995) quote Květ (1982) for the approximate ratios between macrophyte dry mass and other units: 1 g dry mass (ash < 10%) = 0.9-1.0 g organic matter = 0.4 gC = 1.5 g CO_2 = 1.07 g O_2.
- Floating vegetation and *Utricularia* energetics values were approximated by assuming Ulanowicz's (1995a) suggested turnover time of 50 days, and then using the P/B and P/R ratios for macrophytes.

Herpetofauna energetics values were calculated by using the following methodology:

- Salamander production was calculated by using data from Seale (1987) [a salamander of 1g wet weight, produces approximately 6.1 kJ/year], from Jorgensen, *et al.* (1991) [1 g wet weight = 0.25 g dry weight, and 1 g dry weight = 0.45 gC] and from McLusky (1989) [1 gC = 42 kJ]. Diffendorfer, *et al.* (1999) give an annual consumption rate for all herpetofauna of 2.5/y, and Seale (1987) reports P/C and R/C ratios of 0.5 and 0.38, respectively. The proportion of energy lost from salamanders to predators ranges from 0.6 to 0.825 (Diffendorfer, *et al.* 1999), which complements well the P/C and R/C values just cited.
- Marian (1982) gives the consumption, production and respiration values for *Rana tigrina* tadpoles as 959, 883 and 670 $J.g^{-1}.d^{-1}$. These values were used to calculate P/C and P/R ratios of 0.22 and 0.3 respectively. Diffendorfer, *et al.* (1999) suggests that annual consumption in herpetofauna is 2.5 times the biomass. This data was used to calculate the energetics of both tadpoles and

salamander larvae.

- P/C and P/R ratios of 0.36 and 0.95, resepectively, were given by (Smith, 1976) for small, medium and large frogs. Diffendorfer, *et al.* (1999) suggests that annual consumption by herpetofauna is 2.5 times their biomass, and these values were used to calculate the consumption of frogs.
- Turtles have an assimilation efficiency of 80% (Pough, 1973), they consume 3.4 mg dry weight per g wet weight daily (Bjorndal, 1985), and their carbon: dry weight ratio is 30.84 (Jorgensen, *et al.* 1991). Waldschmidt, *et al.* (1987) give their metabolic rate as M ($ccO_2.g^{-1}.h^{-1}$) = 0.066 x (gram wet weight)$^{-0.14}$. Respiration was calculated by using the perfect gas law, PV=nRT (Moore, 1962), where V is the above calculated metabolic rate, P = 1 atm., R = 0.0820575 liter atm.$^{o}C^{-1}$.mole^{-1}, and T = 295 degrees kelvin, along with the fact that free living metabolism is twice the basal metabolism (McNab, 1980) and the conversion factor, 1 mole O_2 = 12 mole C.
- Consumption by snakes (in $gC.m^{-2}.y^{-1}$) was calculated by using Smith's (1976) formula: C (gww.snake^{-1}) = -64.73 + 28.71 x ln (wet weight ±0.91), where the average wet weight of snakes is taken as 291 grams (Dalrymple, *pers. comm.*), the carbon-dry weight conversion for snakes is set at 45% and food conversion is assumed to be 5.5 kcal per gram dry weight (Jorgensen, *et al.* 1991). A P/C ratio of 34% (Smith, 1976) was then used to calculate the production. The metabolic rate for snakes was calculated by the equation M ($ccO_2.g^{-1}.h^{-1}$) = 0.12 x (gww)$^{-0.23}$ (Waldschmidt, *et al.* 1987). Again, the respiration was calculated using the gas law, PV=nRT (Moore, 1962), where V is the above calculated metabolic rate, P = 1 atm., R = 0.0820575 liter atm.$^{o}C^{-1}$.mole^{-1}, and T = 295 degrees Kelvin, along with the fact that free living metabolism is twice the basal metabolism (McNab, 1980) and the conversion factor, 1 mole O_2 = 12 mole C.
- For lizards, daily consumption was calculated from data obtained from Waldschmidt, *et al.* (1987) and applying a carbon: dry mass ratio of 45% (Jorgensen, *et al.* 1991). Respiration was calculated from their metabolic rate ($ccO_2.g^{-1}.h^{-1}$) = 0.096 x (gww)$^{-0.2}$ (Waldschmidt, *et al.* 1987), and by employing the gas law, PV=nRT (Moore, 1962), where V is the metabolic rate, P = 1 atm., R = 0.0820575 liter atm.$^{o}C^{-1}$.mole^{-1}, and T = 295 degrees Kelvin, along with the fact that free living metabolism is twice the basal metabolism (McNab, 1980) and the conversion factor, 1 mole O_2 = 12 mole C. An average assimilation efficiency of 80% was then applied to calculate the production (Kitchell & Windell, 1972; Waldschmidt, *et al.* 1987; Smith, 1976).
- Alligator respiration was calculated by using a metabolic rate of 0.65 ml $O_2.kg^{-1}.min^{-1}$ (Wang & Warburton, 1995), and using the gas law, PV=nRT (Moore, 1962), where V is the metabolic rate, P = 1 atm., R = 0.0820575 liter atm.$^{o}C^{-1}$.mole^{-1}, and T = 295 degrees Kelvin, along with the fact that free living metabolism is twice the basal metabolism (McNab, 1980) and the conversion factor, 1 mole O_2 = 12 mole C. The production and consumption values were calculated from the R/C (0.2563) and P/C (0.5437) ratios for alligators in cypress and mangrove systems, and the egestion was taken to be the residual after applying an assimilation efficiency of 80% (Pough, 1973).

For muskrats, rabbits, raccoons, otter, mink, white tailed deer, bobcats and panthers respiration values were calculated by using Kleiber (1961)'s formula,

Metabolism (Kcal.gww^{-1}.d^{-1}) = 70 x wet weight (kg)$^{0.75}$, the mean food caloric content of 4.5 Kcal.gdw^{-1}, a mean food carbon content of 45% (Jorgensen, *et al.* 1991) and using the rule- of- thumb that free living metabolism is approximately twice basal metabolism (McNab, 1980). Fournier & Weber

(1994) give the average basal metabolism for opossums as 11,150 ml $O_2.kg^{-1}.day^{-1}$ and finds that the cost of transport is 15-80% (we used 50%) higher than for the average of other mammals of equivalent mass. For the remaining mammals, Banse & Mosher's (1980) formula [P/B = 1.11 x wet mass(kg)$^{-0.33}$] was invoked to calculate production in conjunction with a metabolic equivalent of 1.5 kcal = 1gww. An assimilation efficiency of 65% was used to calculate the egestion rates of muskrats, rabbits, raccoons, opossum and white tailed deer, while a figure of 80% was applied to otters, mink and panthers (Jorgensen, *et al.* 1991). Bobcat assimilation efficiency was calculated at 73.75% (Powers, *et al.* 1989).

Respiration values for rats and mice were calculated from an O_2 consumption = 3.27 ml $O_2.g^{-1}.hour^{-1}$ of live weight, to yield an R/C ratio of 0.62 (Odum, *et al.* 1962). Odum *et al.* (1962) give an annual turnover rate (P/B) of 2.5 for mice in unfavorable (long hydroperiod) habitat, and 4.9 in favorable (short hydroperiod) areas. Only 2% of the total energy utilized during a season or annual cycle is channeled into production, so that the P/C ratio is 0.02 (Odum, *et al.* 1962). These ratios were used in conjunction with the estimated biomass of rats and mice to quantify their energetics.

For all bird compartments the annual ratios of P/B (0.015), C/B (0.24) and E/C (0.25) were used to quantify the energetics (Christian & Luczkovich 1999). Respiration was calculated by subtracting the production and egestion from the consumption.

The two seasonal networks were assumed to balance over each period. Although this assumption is not entirely realistic, balance is required for the critical input/output phase of NA (described below). Furthermore, assuming balance facilitates the estimation of many rates. For example, when a component is balanced, its total output can be equated to its total input as a quantity known as the compartmental throughput. It remains to apportion this throughflow among the output processes, namely, respiration, excretion, natural mortality and losses to predation. Fortunately, respiration and excretion rates per unit biomass are available for most species from the literature, so that these outputs can be established immediately. Most of the losses to predation are reckoned from the predator (input) side, as described above.

At this point, the balance is almost complete. It remains to estimate the exchanges of carbon with the outside world. Exogenous imports and exports occur in four different ways: (1) Carbon from the atmosphere may be fixed as biomass through the process of photosynthesis. The magnitude of this import is assessed by multiplying the standing stock of the autotroph with its primary productivity per unit carbon, as mentioned above. (2) Biomass may enter or leave the system with water flowing into and out of the study area. These exchanges are usually estimated from the overall water budget for the area, but in this system that data was not available, and it was therefore assumed that no carbon was imported in this manner. (3) Carbon is accumulated in the sediment and so exported from the system as peat soils. (4) Biomass may enter and leave the system as animal populations migrate across the boundaries of the study area.

Migration applies to many animal species in the model, including invertebrates, fishes and birds. Flowing in the opposite direction are the inputs to the system, for example lizards. Lizards are presumed to stay mostly in the tree hummocks, so that they feed outside the system, and therefore some of their diet would be obtained outside the system. Emigrations of populations, i.e., flows of carbon leaving the system, are considered similar to any other export, but immigrations are treated differently. The network analysis routine, NETWRK, was amended so that migratory imports would be considered separately so as to avoid compartments like lizards from mistakenly being perceived as primary producers. Exactly how this was done will be explained more in detail in the next section.

Movements by avifauna are different than those of fish. Some of the birds may nest or roost on the graminoid prairies, but then leave temporarily to feed elsewhere — such as the cypress and mangroves. Such feeding should be classified as an import to the system. The exclusion of wading birds from this system implies that most of the invertebrates, fishes and herpetofauna consumed by the birds will now appear as an export of carbon to the mangrove and cypress systems. Furthermore, different types of birds exhibit different feeding techniques. For example, some need high water levels and others, low water. These activities are all built into the estimates of imports to- and exports from the ecosystem and impart to the system the role of a "food basket" for the cypress and mangrove systems.

The estimates of all the flows entering and leaving each compartment have now been described. Of course, uncertainties inherent in these partially independent estimations will mean that many of the compartments will not balance exactly. The degree of imbalance can be computed by entering the estimated flows into a spreadsheet format (EXCEL[TM] was used for this purpose). Doing this allows one to compare the marginal sums of inputs to and outputs from each compartment in order to identify those that are most out-of-balance. The investigator has several options for treating an imbalance in a compartment. If the imbalance is severe, it is probably best to check the sources and the arithmetic. Failing the discovery of an error, one might search for other references to crosscheck the data being used.

If no amendments to a compartmental budget can be made on the basis of new data, some investigators prefer to bring the system nearly into balance by adjusting the least-well known flows. Others would rather maintain the flow proportions for each compartment as they appear in the literature and then re-balance the whole system under the covering assumption of linear, donor-control, which always maintains flows positive (Ulanowicz 1989). In this study all compartments could be balanced to within a few percent using literature values, and a final balance was achieved using the program DATBAL, which assumes linear, donor control.

The resulting networks are too large and complicated for easy illustration. Even a matrix representation of one such network spans several pages and is extremely cumbersome to use. For these reasons, detailed results are probably best presented in hypertext format, which can be accessed over the World Wide Web at http://www.cbl.umces.edu/~atlss. Using hypertext, one follow simple instructions to locate the estimated value of any stock or flow in either the wet or dry season. Furthermore, the entire rationale and associated references pertaining to the estimation of any particular value have also been documented in hypertext. Thus, by pointing and clicking one may examine a trophic flow network in minute detail.

This format for disseminating the details of the network should have important benefits for ecosystem science in general and for the visibility of the ATLSS endeavor in particular. We are aware of no other single source where the structural elements of entire ecosystems can be examined and scrutinized so readily. Even if a user has no idea of the benefits of NA, he/she can begin with the species that interests them most and trace the sources and fates of material into and out of that compartment -- simply by pointing and clicking. The presentation also makes it easier to critique the networks, and online suggestions for improvements and amendments are welcomed

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4.2. Network Analysis

4.2.1. Background

Sometime during the mid-1970's it became apparent that ecological modeling in the form of a set of coupled, deterministic differential equations was a problematical undertaking that required support from other, independent methods of systems analysis. In the search for parallel methods of describing the behavior of total ecosystems, various computations performed on the network of trophic flows have figured prominently (SCOR, 1981).

The original impetus for diverting attention from dynamics and concentrating analysis on flow structure came from the field of economics, where success in elucidating indirect economic effects had been achieved by manipulations on matrices of economic flows (Leontief, 1951; Hannon, 1973). Thereafter followed a number of other topological treatments of the underlying flow graph (e.g., Finn, 1976; Levine, 1980; Patten, *et al.* 1976; Ulanowicz & Kemp, 1979). Eventually, Ulanowicz collected most of the methods for analyzing flow networks into a single executable package, called NETWRK (Ulanowicz & Kay 1991.) NETWRK 4.2a is the version used in this analysis.

Four types of analyses are performed by NETWRK. First, input-output structure matrices are calculated. These allow the user to look in detail at the effects, both direct and indirect, that any particular flow or transformation might have on any other given species or flow. Next, the graph is mapped into a concatenated trophic chain (after Lindeman 1942). Then global variables describing the state of development of the network are presented. Finally, all the simple, directed biogeochemical cycles are identified and separated from their supporting dissipative flows. NETWRK 4.2a and its accompanying documentation may be downloaded from the World Wide Web at http://www.cbl.umces.edu/~ulan/ntwk/network.html.

In addition to NETWRK, a package called IMPACTS was used to gauge both the positive and negative, direct and indirect impacts that heterotrophic predation may cause. The method was described in Ulanowicz & Puccia (1990). Of particular interest is how negative impacts at one level can ramify to become positive indirect effects.

The data required to run either of these programs have already been discussed. It was detailed above how, for each compartment, it is necessary to know: (1) all the inputs from outside the system, (2) all the various inputs flowing from other compartments of the system, (3) all the outputs which flow as inputs to other compartments, (4) all exports of useful medium outside the system, and (5) all rates of dissipation of medium. Each of these flows can be represented by a positive scalar element of a matrix or a vector; the absence of a flow can be represented by a zero.

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4.2.2. Input/Output Analysis

The initial section of the NETWRK package is founded upon an ecological variation of economic input-output analysis. "Total contribution coefficients" (Szyrmer & Ulanowicz, 1987) describe exactly what fraction of the total amount leaving compartment i (prey or row designation) eventually enters compartment j (predator or column designation) over all pathways, both direct and indirect. Alternatively, the "total dependency coefficients" portray the fraction of the total ingestion by j, which passed through compartment i along its way to j. The columns of this matrix are particularly useful, because they portray the "extended diet" of the species in question (or, correspondingly, the trophic "pyramid" that supports each heterotroph). As was demonstrated with the cypress wetland ecosystem, such indirect ratios can provide valuable information about how a system is functioning.

As an example of indirect diet coefficients, consider the snail kites (#59). They depend on the apple snails (#7) and other macroinvertebrates (#11) for 100% of their sustenance. These prey items in their turn depend upon primary producers, such as periphyton, macrophytes and other floating vegetation (#3, 4, 5 and 6), and living detritus (#1 and 2), so that ca. 95% of the consumption by snail kites originates from periphyton. Thus, carbon is counted more than once as it passes up the food chain, and the fact that all of the above dependencies sum to over 270% is entirely consistent with the fact that snail kites feed, on the average, at about trophic level 3.

Hannon (1973), Finn (1976), Levine (1980) and Patten, *et al.* (1976) give various examples of how one may employ input-output analysis. One highly useful application is the decomposition of the graph according to each input. That is, the eventual fate of each of the nonzero inputs to the system is traced independently of the other inputs to the system. Not only does this decomposition portray the isolated effects of the various inputs, but these sub-networks can be linearly recombined to recreate what the effects of any arbitrary linear combination of inputs would be, if the flow structure were kept the same.

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4.2.3. Trophic Aggregation

The second section of output from NETWRK interprets the given network according to the trophic concepts of Lindeman (1942). Of course, it is impossible to relegate omnivorous heterotrophs entirely to a single trophic level, but Ulanowicz & Kemp (1979) indicated how input-output techniques could be used to apportion the activities of omnivores among a series of integer trophic levels. This method has been expanded to include the effects of biogeochemical cycles by Ulanowicz (1995a).

In order for trophic aggregation to be meaningful, it is necessary that trophic pathways among living compartments remain finite in length, otherwise one is forced to interpret an infinite regress of trophic levels. Fortunately, Pimm (1982) states that cycles among living taxa are rare in ecosystem networks (although we encountered some interesting exceptions in the three previous networks). The absence of such feeding cycles avoids trophic pathways of infinite length. As a preliminary to trophic aggregation, therefore, all cycles flowing through only living compartments are first removed from the network. So long as the Finn cycling index for such heterotrophic cycling (see below) remains sufficiently small (say, below two percent or so), no appreciable distortion of results should ensue. The 2% requirement is more than satisfied by the graminoid networks.

When the fractions by which each component feeds at a particular trophic level are weighted by the value of that trophic level and the results are summed, one arrives at the effective trophic level for the given species (Levine, 1980.) For example, if a species or compartment is receiving 15 units of medium along a pathway of length 2 and 5 units along a pathway of length 3, then it is acting 75% as a herbivore (trophic level = 2) and 25% as a carnivore (level = 3). The effective trophic position becomes (0.75 x 2) + (0.25 x 3) = 1.75. It is often interesting to compare the average trophic position of species under different circumstances (as, for example, between wet and dry seasons).

The section of NETWRK dealing with trophic aggregation culminates with the partitioning of system activity into a trophic "chain" of transfers, along linear aggregations of heterotrophs. Each such aggregation feeds back into detrital return loops. Such a depiction of the underlying trophic dynamics has been termed "canonical" by Ulanowicz (1995a), because any ecosystem can be mapped into this equivalent and simple form to allow the relative magnitudes of corresponding flows to be compared

directly.

One change made recently as part of NETWRK version 4.2a was to treat migratory inputs of heterotrophs differently than inputs to autotrophs (primary production). NETWRK now treats inputs to heterotrophs as coming into the system at exactly the same trophic level as the receiving compartment would otherwise occupy within the system. Previously such inputs were treated as primary production by default, and this unrealistic assumption artificially deflated many of the reported trophic levels.

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4.2.4. System-Level Indices

The next section of output from NETWRK yields estimates for global attributes of the network that have been defined with the help of information theory to assess the pattern of development in ecosystems (Ulanowicz, 1980,1986; Hirata & Ulanowicz, 1984; Ulanowicz & Norden, 1990). The first such property is the "total system throughput", or the gross sum of all transfers, which provides a measure of the size of the system. Multiplying the total throughput by the system indeterminacy (according to the Shannon Wiener formula) of the individual flows yields what has been termed the "development capacity" of the system. This quantity serves as an upper bound on the ascendency, which is a measure of the network's potential for competitive advantage over other real or putative network configurations. Ascendency is the product of a factor of size (total system throughput) times a factor representing the coherence of the flows (the average mutual information of the flow structure).

The difference between the realized structure and its upper bound is the overhead (Ulanowicz, 1986). Overhead has contradictory interpretations. On one hand, it is a catchall for the system's inefficiencies in processing material and energy. What is a disadvantage under benign conditions can turn in the system's favor when it is perturbed in some novel way, however. Then, the overhead represents a "strength-in-reserve" of degrees of freedom, which the system can utilize to adapt to the new threat. Overhead is generated in any of four ways: three components of overhead are due to indeterminacies in imports, exports, dissipations (respirations), and a fourth is related to the indeterminacy over which of several parallel pathways flow will proceed between any two nodes (flow redundancy). The fractions of the development capacity encumbered by the ascendency and by each of the overhead components provide a profile of the structural composition of the system that often is useful for assessing the organizational status of an ecosystem.

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4.2.5. Cycles

Most networks of ecosystem flows contain cycles of material or energy, and the magnitudes and structure of these cycles are fully assessed by NETWRK. The program enumerates all of the simple cycles in the given matrix of exchanges. Furthermore, the simple cycles are grouped into "nexuses" of cycles that share the same "weak arc." A weak arc is defined here as the smallest flow in a given directed cycle. The assumption is that the weak arc is the limiting or controlling link in a cycle, and that by grouping according to critical links, one identifies the domain of influence for each weak arc. Presumably, any change in a weak arc will propagate throughout its associated nexus. The nexuses are

listed roughly according to ascending order of the magnitude of their defining weak arcs.

The cycles are then subtracted from the network in a fashion described in detail by Ulanowicz (1983). Briefly, the magnitude of flow in the smallest weak arc is distributed over the flows in that particular nexus, and the resulting amounts are subtracted from each arc in that nexus. This process zeroes the weak arc, thereby eliminating all the cycles in that nexus, but it does not disturb the balance around any compartment, nor does it change any exogenous input, export or respiration. None of the remaining arcs of the nexus are driven negative. After that nexus has been removed, the next smallest weak arc is located; and nexuses are subtracted iteratively until all cycles have been removed from the network.

As each cycle is removed, the flow associated with that cycle is added to the magnitudes of other cycles of the same trophic length. The end result is a distribution of the magnitude of cycling according to the trophic length of cycles. This profile could be useful in assessing system response to perturbation. For example, cycling via the larger loops is often more sensitive to disturbance. The cycle distribution is then normalized by the total system throughput. Summing this normalized distribution yields the Finn cycling index, which is the fraction of total activity that is devoted to cycling (Finn, 1976).

Finally, the separation of cycled from transient flow is reported in the form of separate matrices for each type of flow. The row sums and column sums of the matrix of aggregated cycles will always balance; no further reference to exogenous exchanges is necessary. The visual structure of the aggregated cycles existing in more complicated networks very often reveals separate domains of control in the network (e.g. Baird & Ulanowicz 1989). Finally, it should be remarked that the starting network has been neatly decomposed into an acyclic "tree" of dissipative flows and a wholly conservative nexus of cycled flows.

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4.2.6. Trophic Impacts

NETWRK treats only positive mass flows and does not consider the propagation of the negative effects that accompany predation. Ulanowicz & Puccia (1990) outlined how to treat the propagation of both positive and negative trophic effects, and their technique has been implemented in the algorithm, IMPACTS. For any particular component (designated as the "focal taxon"), IMPACTS provides a ranked listing of all the positive and negative impacts (both direct and indirect) upon that focal species. Also a ranked listing of all the direct and indirect trophic effects that focal species has upon all the other taxa is likewise provided. Of special interest are those predators that exert a direct negative impact upon a prey, but whose combined indirect positive influences more than compensate the prey for its direct losses. Such "beneficial predators" are more common than might be supposed and often highlight particular ecological roles that otherwise might have gone unnoticed. In similar fashion, one can identify various prey species that indirectly have an adverse effect upon their predators. These are referred to as "malefic prey". IMPACTS can be downloaded from http://www.cbl.umces.edu/~ulan/ntwk/network.html.

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5. RESULTS

5.1. Input/Output Analysis

Perhaps the most useful indices to result from the Input/Output section of NETWRK are the "total dependency coefficients" (Szyrmer & Ulanowicz 1987) or, more appropriately, the "indirect diets" of each taxon. By reading down the column of these dependency coefficients one notes the quantitative trophic history of material reaching that given compartment.

The total dependency coefficients (TDC's) of the heterotrophs in the graminoid ecosystem reveal that a significant fraction of the carbon reaching many of the predators originates in the periphyton compartment (Figure 1). The aquatic invertebrates (7-12) and fish (14-35) depend on the periphyton compartment (3) on the average for 80% of their sustenance. Periphyton contributes a significant amount of carbon to the diets of some birds, aquatic herpetofauna and aquatic mammals. Tadpoles (#41) have the highest dependency on periphyton ~ 96% in the wet season and 97% in the dry season, while large frogs (#38) depend on periphyton for 94% and 96% of their energy in the wet and dry seasons, respectively. The indirect dependency of otter (51) on periphyton varies between 79-88% between wet and dry season, whereas snail kites depend on periphyton for 94-95% of their sustenance during the wet and dry season respectively. By way of contrast, only very small flows link periphyton with terrestrial mammals and terrestrial herpetofauna, which feed mainly upon terrestrial invertebrate species. Such is the case for lizards (44), muskrats (46), rabbits (48), bobcats (54) and Florida panthers (55), which obtain virtually none of their carbon via periphyton pathways.

One may employ the total dependency matrix to test how dependent each single compartment is on the other major groups. For example, looking at how much various groups are dependent on invertebrates (compartments 7 to 14) reveals that the salamanders and smaller frogs show the highest dependencies (Figure 2). More than 100% of the carbon reaching salamanders (36) during the dry season, medium frogs (39) and small frogs (40) during both seasons passes through invertebrates. Similarly, approximately 100% of the carbon that reaches the snail kites (59) and nighthawks (60) pass through invertebrates. (The values greater than 100% simply mean that the same carbon is spending time in more than one invertebrate compartment.) There is a very low dependency of birds, mammals and herpetofauna upon fishes, with only fishing spiders (14) showing more than 50% dependency on fish (Figure 3).

Dependencies on the remaining three big groups (herptofauna, birds and mammals) do not exceed 20% in most cases. The exceptions here are the dependencies of snakes (24%), alligators (28%) and mink (22%) on lizards during the wet season, although their dependencies on lizards remain much lower during the dry season. Dependency coefficients generally decline as one proceeds from invertebrates up to mammals, however, the dependencies of bobcats and panthers on muskrat are very high — 90% and 94% for bobcats in the wet and dry respectively, and 80% for both wet and dry seasons for panthers.

Summing the dependencies on all primary producers for each compartment, one sees that, in most instances, the result is close to 100% (Figure 4). This indicates that the system depends mainly on internal carbon fixation and receives only a small subsidy from outside the system. There are some exceptions, with lizards (# 44) being the most obvious — it only depends on 2% of internal carbon in both wet and dry season. The very low dependency on internal carbon by lizards is because they import most of their diet from outside the system. Snakes and alligators (#'s 43 and 45) depend on internal carbon for 77-95% and 73-94% respectively (for wet and dry seasons) and import their remaining sustenance from outside the system. Similarly, mink (#52) depend on internal carbon for 78-96% (wet and dry season, respectively), the panthers (# 55) 96-99%, and passerine birds (#63) 91-94% for wet and dry season, respectively.

In general, there is a difference in indirect diets between wet and dry seasons. The dependencies on primary producers (Figure 4), and especially on periphyton (Figure 1), increase from the wet to the dry season. Conversely, the dependencies on invertebrates (Figure 2) are higher during the wet season than during the dry, while dependencies on fish (Figure 3) do not show any trend.

The dependencies of consumers on periphyton are very different from those of the consumers in the mangrove system, although the similarity of the graminoid system to that of the cypress is more evident. In the mangrove system (Ulanowicz, *et al.* 1999) the consumers depend mostly on carbon from the detrital compartments, while in the cypress system most of the consumers are supported via the grazing chain, and the importance of periphyton increases during the dry season (Ulanowicz, *et al.* 1997). This is similar to the increase in dependencies on periphyton seen in the graminoid system, although the magnitude of the dependencies is generally smaller in the cypress system. Comparison of the graminoid dependencies with those in the marine system (Florida Bay) is not as useful, although the dependencies on detritus also seem low in the Bay ecosystem (Ulanowicz, *et al.* 1998).

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5.2. Trophic Impacts

Impact analysis is used to study both positive and negative indirect effects between compartments. In higher-dimensional networks, such as this ecosystem, every pair of compartments is connected in this way, at least indirectly. Coefficients in the impact matrix represent the aggregated net (positive and negative) indirect effects between two species.

Of special interest are those compartments that function as "beneficial predators". The direct impact of a predator on its prey is obviously negative. However, the overall effect can become positive, due to the potential for compensation via multiple indirect pathways. In such cases one speaks of "beneficial predators". In the three previous networks, beneficial predation was quite abundant. In the cypress swamp, for example, the American alligator was a net benefactor to 11 of its prey items. In the graminoid system during the wet season, redear sunfish and warmouth benefited two prey compartments (Table 1). During the dry season, the warmouth, redear sunfish and spotted sunfish benefited more than one (two) of their prey items (Table 2).

Table 1 and table 2 list all the beneficent predators during either season, together with the number of prey that each positively impacts. In the graminoid system there are 13 beneficial predators in the wet season and 17 in the dry, which is much lower than the 218 and 208 that was found in the wet and dry season mangrove systems respectively. The much lower number of beneficial predators in this system could be due to the fact that the main predators of the invertebrates and fish compartments, namely the wading birds, were excluded from this model. Of the 13 and 17 beneficial predator interactions, 8 predators are beneficial in both seasons, which indicates that some predators are beneficial to more than one prey type. In addition to the number of beneficial predators being low, the magnitudes of their actions are not very strong. The most significant positive impact during the wet season is that of gar on other macroinvertebrates — where the impact is 0.027, while the most significant positive impact during the dry season is the impact of snakes on crayfish (0.137).

Although only a small number of beneficial predator interactions achieve significant magnitude, in a few cases more than one predator affects the same prey in a net positive manner. Adding together all the positive effects by multiple predators, one obtains an aggregate positive impact by the several predators (Table 3). In addition to those links cited above, three other prey compartments receive significant

benefit from a combination of predators during both wet and dry seasons: Living sediment (#1), living POC (#2) and periphyton (#3). During the both seasons, living POC receives the most benefit from their prey, but more so during the dry season (0.06 vs. 0.04).

Having considered and identified instances of beneficial predation, one should also consider whether the reverse relationship might be possible, i.e., that the overall effect of a host on its predator over all pathways, direct and indirect, can be negative. As mentioned above, in such case we talk of a "malefic prey". A search of the graminoid network uncovers 111 cases of "malefic" links during the wet season and 103 for the dry. A total of 36 prey affect their predators negatively in the wet period and 33 in the dry (Table 4). The compartment living POC (#2) produces the highest number of negative indirect effects on its predators during both seasons, adversely affecting some 18 prey during the wet season and 17 during the dry period. Next in line is the small frogs compartment (#40) with 6 negative impacts in the wet season, and 5 in the dry season. Similarly, killifishes (#22) and mesoinvertebrates (#10) also have 5 negative impacts on their predators.

The number of malefic prey species and the number of predators that they affect are lower in the graminoids than in the mangroves or Florida Bay systems. There are 186 and 185 malefic prey species in the wet and dry mangrove systems, and they affect 47 and 48 different predators in those two systems, respectively. In Florida Bay, the malefic prey species number 278 and 283 in the wet and dry seasons, respectively; and they affect 70 and 68 predators, respectively. The lower number of malefic prey in the graminoids might simply be due to the lower number of compartments in the system.

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5.3. Trophic Levels

As with most ecosystems studied by Network Analysis thus far, none of the compartments of the graminoid ecosystem feeds, on the average, at or above trophic level 5. In fact, none of the compartments feeds above the fourth trophic level. The highest feeders are the lizards (#44), which feed at an effective trophic level of 3.83 during the dry season and the mink (#52) and alligators (#45) that effectively feed at 3.49 during the wet season. The average trophic levels during both seasons are listed in Table 5. In general, there was very little difference between the trophic levels of the wet and dry seasons, although the trophic levels are generally higher in the dry season than in the wet. Only three compartments have seasonal differences larger than 0.2 — the freshwater prawns (#8), salamanders (#36) and lizards (#44) have differences of 0.21, 0.23 and 0.71, respectively, and all of their trophic levels are higher in the dry season than in the wet.

In the mangrove and Florida Bay systems, the raptors feed one full trophic level higher than the top predators of the graminoid or the cypress systems. In the mangrove system kites & hawks, eagles & ospreys and owls feed at effective trophic levels of 4.3, 4.2 and 4.5 respectively, while the top predators in the cypress are alligators and snakes, both feeding at an effective trophic level of 3.8. By way of inter-habitat comparison, the effective trophic level of alligators, mink and lizards in the graminoids (dry season only) resemble more those of the cypress than those of the mangrove system.

A quick perusal of the Lindeman transformation matrix, which apportions compartments among trophic levels, reveals that there are 16 trophic levels in the overall network. Thus, at least one non-redundant trophic pathway with 16 links can be found in the network. As usual, however, not much carbon persists beyond the fifth trophic stage, and the amounts calculated to reach the 16th level are absolutely

infinitesimal (of the order 10^{-32} grams.) The first six trophic levels during each season are depicted in Figure 5. One notices immediately that the trophic chains in the two seasons are quite similar, although the inputs and through-flows are generally smaller in the dry season, and the efficiencies are higher in the wet season. The efficiencies of the graminoid trophic levels are mostly lower than those observed in the other three ecosystems. The efficiencies of the higher trophic levels (V and VI) are higher, however, than the trophic efficiencies of levels V and VI of the cypress system. Similarly, the efficiency of trophic level V in the graminoid system is also higher than the efficiency of trophic level V in the mangrove system.

The ratio of detritivory:herbivory is a approximately 29:1 in the wet season and 45:1 in the wet season. This is **much** higher than the 7:1, 8:1 and 5:1 calculated for the mangrove, Florida Bay and cypress ecosystems, respectively. This higher detritivory suggests that the recycling of carbon is enormously important in the graminoid system. This result stands in stark contrast to the total dependency analysis, which showed that most compartments depend mainly on periphyton, and dependencies on detritus appear to be decidedly secondary. The discrepancy may be explained by the fact that most excretion and mortality from living compartments becomes refractory detritus (#66) and carbon in the sediment (#64), which in turn is utilized mainly by bacteria (TL2) in the sediment and in the water column (i.e., detritivory by TL2). Similarly, much of the production by plants (periphyton, macrophytes, floating vegetation and *Utricularia*) is not consumed by herbivores, but is broken down into labile and refractory detritus, which is then utilized by bacteria in the sediment and the water column (again detritivory). This augments the magnitude of detritivory and reveals that much of what is produced by the primary producers is not utilized by the higher trophic levels, but rather is recycled into the detritus and subsequently deposited as peat. The high dependencies by most heterotrophs on periphyton owe to the fact that the greater fraction of what is consumable among the primary producers consists of periphyton, and demonstrates how extremely important periphyton is to this system.

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5.4. System Level Indices

The freshwater cypress biome and the mangrove ecosystem surround the graminoid ecotope, which is also proximal to the waters of Florida Bay. All of these networks have been estimated and analyzed previously as part of this contract, making it is possible to compare the system level indices calculated for the graminoid ecosystem to those of its neighbors. It is useful to bear in mind that in certain very real ways the graminoid system *feeds* its neighbors, and its characteristic indices might be expected to reflect that fact.

With respect to total activity, the graminoid system is far more active than any of the neighboring systems (Table 6). Its total system throughput is 19,949 $gC.m^{-2}.y^{-1}$ during the wet season and 10,992 $gC.m^{-2}.y^{-1}$ during the dry, while the throughputs of the other three systems are all approximately an order of magnitude smaller. The development capacity of the graminoid system (wet = 79,572 gC-bits.$m^{-2}.y^{-1}$ and dry = 39,854 gC-bits.$m^{-2}.y^{-1}$) is also significantly higher than that of the other systems. While one might attribute the latter inequality to the fact that the total system throughput serves as a scaling factor of the capacity, we note how the ascendency (normalized as a percentage of development capacity) in the graminoids is 48.6% in the wet season, and 52.6% in the dry season. This is much higher than the ascendency values for the mangroves (36%), Florida Bay (38%) or the cypress system (44%).

These values for ascendency reveal that the graminoid system appears to be the least stressed of the four communities studied. The graminoid system has been stressed by various modifications of its flow patterns, which resulted in loss of transitional glades, modification of flow patterns, reduced hydroperiods, unnatural pooling and over-drainage (Light & Dineen, 1994). The system has experienced the fewest changes to its faunal community, however, and is sustained by an abundance of flora and micro-bacterial communities. The mangrove system and the Florida Bay communities are more stressed than the graminoids because of the variations in osmolarity common to estuaries, and the recent hypersalinities noted in the Bay. The cypress ecosystem, like that of the graminoids is limited by a dearth of nutrients (probably phosphorus), which are abundant in the marine and estuarine waters and sediments. The graminoid system compensates for this dearth of nutrients through its profusion of periphyton, which exhibits a high P/B ratio, even under oligotrophic conditions. The natural stressors affecting the bay, mangroves and the cypress appear to have far greater effects, for they modulate the very rates of material and energy processing.

Information indices are usually applied only to whole systems. Evidence is accumulating however, that the various sub-components of the ascendency-like variables can serve to gauge the contributions of individual system elements to the performance of the whole system (Ulanowicz & Baird, 1999). For example, the ascendency is comprised of terms that are generated by each transfer in the system. If one sums up all the terms generated by the inputs to a given taxon (say, the jth one), the result is a measure of the contribution of that compartment to the full system ascendency (call it A_j). Because ascendency may be viewed as an indicator of efficient system performance (Ulanowicz, 1997), the same partial-sum, A_j, represents the contribution of taxon j to overall system performance. Furthermore, if one then divides A_j by the corresponding throughput for taxon j (call it T_j), the ratio A_j/T_j will represent the contribution per unit of activity of j to the total system ascendency.

Calculating and ranking these "relative contribution coefficients" proves to be a most interesting exercise. When the average trophic levels of the 66 compartments of the graminoid wetland ecosystem were calculated, for example, the lizards, alligators, snakes and large fishes were seen to feed at trophic levels higher than some other "charismatic megafauna", such as the snail kite, nighthawk, Florida panther or bobcat. The relative contributions to ascendency by the latter, however, actually outweighed those of the former. The relative values of these coefficients seem to accord well with most people's normative judgments of the specific "value" of the various taxa to the organization of the system as a whole (Table 7).

The system indices in the graminoid ecosystem show much larger variation between wet and dry seasons than do those of the other three systems. In the grassland prairies, the total systems throughput (T), development capacity (C) and ascendency (A) values are all nearly half in the dry season of what it is in the wet season, although the relative ascendency (A:C) increases during the dry season. This decrease in systems activity during the dry season is due to the lack of input into the system and the shutdown of some of the production activities during the dry season.

The relative contributions of the taxa of the graminoid ecosystem mirror some of the results obtained from the cypress ecosystem (Ulanowicz, *et al.* 1997). The avian and feline predators (snail kites, nighthawks, Florida panther and bobcats) ranked only 48, 39, 52 and 41 in terms of trophic level (average levels 3.13, 3.00, 3.17 and 3.02, respectively). Their relative contributions to the system ascendencies were highest of all taxa during both seasons. They were followed in relative contributions to the system ascendency by the fishing spiders, salamanders and larger fishes. The reduced sensitivity of crayfish (1.4 and 0.99 in wet and dry seasons) in the graminoids was not seen in the cypress, however. Crayfish ranked 16th and 17th in the cypress system with sensitivities of 1.9 and 2.2 respectively.

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5.5 Cycling

With 66 compartments in the trophic flow network the number of potential pathways for recycling carbon is roughly proportional to 66-factorial -- an immense number! The fact that the network is not fully connected reduces the number of potential cycles considerably. Nonetheless, the number of simple cycles in the graminoid network remains enormous. Using the standard algorithm in NETWRK 4.2a to calculate the number of cycles registered ca. 24 billion(!) cycles.

The situation is similar to what happened in previous years with the Florida Bay and mangrove networks, and the same approach taken then was followed with the graminoid systems: Most of the overwhelming number of simple cycles counted above include more than one detrital component. We make the approximation then, that one may choose to ignore those cycles that contain more than one nonliving compartment. The identification of such "single-detritus" cycles can than be achieved first by removing the cycles that contain no detrital links, and then by successively adding the detrital compartments into the search, *one at a time*. The number of cycles counted in this manner will be a radical underestimate of the total number of cycles present, but once they have been extracted from the network, the residual graph will contain no cycles. Even this simplification takes considerable computing power to execute. Unlike the mangrove system, where the dry season contained fewer routes for recycle, and the Florida Bay system, where the wet season showed a greater number of cycles, the number of cycles are the same in the wet and dry season models of the graminoids.

The first stage in the cycle analysis was the removal of the cycles that contain no nonliving compartments. These are generally rare in most ecosystems (Pimm, 1982). There were only 16 such cycles during both seasons in the graminoids. The cycle of greatest magnitude was cannibalism by snakes, but the amount cycled over this route is very small — 5.8 $mgC.m^{-2}.y^{-1}$ in the dry season and 14 $mgC.m^{-2}.y^{-1}$ in the wet season.

By far and away the greatest number of single-detrital cycles was generated by compartment #64, carbon in the sediment, which has 133,657 cycles in the dry season and 183,606 in the wet season. Of this huge number of cycles, only 8 cycles accounted for most of the recycling by the system: 457.29 $gC.m^{-2}.y^{-1}$ or 95.8% in the wet season, and 458.9 $gC.m^{-2}.y^{-1}$ or 96.2% in the dry season. The major routes for recycling were between the detritus compartments (both in the water column and in the sediment) and living sediments (Figure 6). Recycling between the detritus compartments included carbon cycled from living sediment (#1) to sediment carbon (#64), to refractory and labile detritus (#65 and 66) and from labile and refractory detritus to sediment carbon. Other than the cycles shown in Figure 6, the two next largest cycles (in magnitude) are:

1. Between living POC and labile detritus (± 2.6 $gC.m^{-2}.y^{-1}$ — wet and dry season) and
2. Between mesoinvertebrates, sediment carbon, living sediment and labile detritus (±1.1 $gC.m^{-2}.y^{-1}$ in the wet season and 0.7 $gC.m^{-2}.y^{-1}$ in the dry season).

Thus the linkage between the detrital cycle and the higher trophic levels is via the mesoinvertebrates feeding on living sediments and sediment carbon, which is a very small rate. One would expect that feeding on living POC, labile- and refractory detritus would be noticeable in the recycling of this system, because the detritivory:herbivory ratio is so large. This loop is largest, however, when the

mesoinvertebrate-*Utricularia*-labile detritus-mesoinvertebrate loop is incorporated (0.5 $gC.m^{-2}.y^{-1}$ in the wet season and 0.4 $gC.m^{-2}.y^{-1}$ in the dry season).

The aggregate activities devoted to cycling in the graminoid ecosystem during the wet and dry seasons are 477.2 $gC.m^{-2}.y^{-1}$ and 476.8 $gC.m^{-2}.y^{-1}$, respectively, which puts the Finn Cycling Index at 2.4% and 4.3% for the wet and dry seasons, respectively. These Finn Cycling Index values are much lower than the 17.2% of the mangrove system, the 14.4% for Florida Bay, and the 8 - 9% occurring in the cypress swamps. Such a reduction in the FCI probably is due to the lower dependency by the higher trophic levels on the detritus (contrary to the fact that most of the carbon is shunted into the detritus) and the importance of periphyton to the higher trophic levels of the system.

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6. CLOSING REMARKS

The first three reports emphasized the individual characteristics of the cypress, mangrove and Florida Bay ecosystems. With the characterization of the last community, the graminoids, now having been completed, intersystem comparison becomes feasible. The fact that the series cypress—graminoid-mangrove-bay form a gradient from terrestrial, fresh water, estuarine to marine habitats make this comparison even more interesting.

In the graminoid system, the breakdown of carbon to the detritus is very important, which is similar to the importance of detritus in the cypress and mangrove systems. However, unlike the latter two systems, the recycling of detritus in the graminoids seems not to be important. Most of the carbon simply sinks out of the system. Conversely, the periphyton seems to be much more important to the higher trophic levels of the graminoids than is the case in the other systems. This is all borne out by the various analyses as discussed below:

The dependency of the consumers upon primary producers is very different in the graminoids than in the other systems. In the mangrove system (Ulanowicz, *et al.* 1999), the consumers depend mostly on carbon from the detrital compartments. In the cypress system, most of the consumers depend on the grazing chain, and the importance of periphyton increases in that system during the dry season (Ulanowicz, *et al.* 1997). This summer dependency upon periphyton is similar to, although not as spectacular as, the dependencies on periphyton by the higher trophic levels of the graminoid system (Figure 1). In the Florida Bay marine system the dependency on detritus returns to lower values (Ulanowicz, *et al.* 1998). One is led to speculate whether the rigors of the physical environment in the mangroves (osmolarity) might not somehow occasion the greater reuse of detritus in that system?

The analysis of beneficial predators and malefic prey in the graminoids indicates that the living POC and living sediment compartments benefit the most from some of their predators (Table 3). In addition, graminoid living POC is the compartment that is malefic to the most predators (Table 4). This is not the case in the cypress system, where living POC and living sediment benefit at most from only 3 predators (Ulanowicz, *et al.* 1997), or in the Florida Bay system, where bacteria is not malefic to any of its predators (Ulanowicz, *et al.* 1998). In the mangrove system, however, bacteria in the sediment is malefic to most of its predators (Ulanowicz, *et al.* 1999). Thus, with regard to malefic prey species, it seems that the bacterial components of the graminoid and mangrove systems impact the rest of their systems in a negative way, even though bacteria are affected positively by most of their predators in the graminoids. One is led to conclude that the sediment is a natural sink for carbon in the graminoid system.

The extremely high detritivory:herbivory ratios in the graminoids (29:1 in the wet season and 45:1 in the dry season) normally would indicate that recycling is important in this system. The concomitant low FCI values (2.4 - 4.3%) indicate, however, that cycling really isn't that important in the graminoids. This apparent paradox is resolved by concluding that much of what is produced by the primary producers seems to be shunted into the detritus (sediment carbon, labile and refractory detritus), where it is consumed by the bacteria that help make up the living POC and living sediment. Further study of the total dependency analysis reveals that the carbon in the bacteria is not recycled to higher trophic levels, but seems to be deposited as peat. This accords with the other observation that most of the higher trophic levels seem to depend on periphyton instead of detritus or bacteria.

The analysis of cycles also lends support to the theory that cycling in the graminoids is confined mostly to the sediment and water column detritus. Sediment carbon (ETL 1) is at the crux of most of the recycling, and most carbon is recycled among the sediment carbon (ETL 1), living sediment (ETL 2), refractory detritus (ETL 2) and labile detritus (ETL 2) (Figure 6). That is, the detritus-microbial loop accounts for 96% of the recycling in the graminoids and incorporates only compartments at the first and

second trophic levels. The link between the detrital cycle and the higher trophic levels is quite weak. The largest such cycle consists of the mesoinvertebrates feeding on living sediments and sediment carbon (± 1.1 $gC/m^2/yr$ in the wet season and 0.7 $gC.m^{-2}.y^{-1}$ in the dry season). When incorporating the water column detritus, the most significant loop (labile detritus-mesoinvertebrate-*Utricularia)* shows only marginal activity (0.5 $gC.m^{-2}.y^{-1}$ in the wet season and 0.4 $gC.m^{-2}.y^{-1}$ in the dry season). All signs seem to point to a weak interaction between the microbial loop and the upper trophic levels in the graminoid system.

When comparing the key players that effect recycling in the graminoids with their counterparts in the Florida Bay system (Ulanowicz, *et al.* 1998), it becomes evident that the links with the higher trophic levels are more visible in the latter system. In the Florida Bay water column, for example, the main recycling pathways include pelagic flagellates (ETL 2.1), zooplankton (ETL 2.5) and pelagic ciliates (ETL 2.6), and benthic recycling includes meiofauna (ETL 2.3) and benthic ciliates (ETL 2.4). Similarly, in the mangrove ecosystem the key players in recycling carbon are sediment carbon (ETL 1), bacteria in the sediment (ETL 2), flagellates in the sediment (ETL 2.5), ciliates in the sediment (ETL 2.66) and meiofauna in the sediment (ETL 2.74). All such links towards the higher trophic levels remain in the distant background in the graminoid ecosystem.

The fact that the graminoid ecosystem is being used as a feeding ground by many of the migratory species that reside in the cypress and mangrove systems, has influenced how we cast the graminoid model and, consequently, has affected the model properties vis-à-vis its counterparts. The analysis of beneficial predation provides good examples of the differences engendered thereby. For example, there are 13 beneficial predators in the graminoid wet season and 17 in the dry season. This is much fewer than the instances of beneficial predation in the cypress, mangrove and Florida Bay systems, where examples of beneficial predation were far more in evidence. There were 78-67 (wet-dry) beneficial predators in the cypress, 208-218 beneficial predators in the mangrove system and 282-294 in Florida Bay. This reduction in the instances of beneficial predation in the graminoids derives from the exclusion of the wading birds, and of other birds that do not roost there, but still feed in the grassy prairies.

Even though the graminoid ecosystem is represented by fewer compartments (66 vs. the 128 for Florida Bay), it is far more active than either the cypress, the mangrove or the Florida Bay community (Table 6). Its total system throughput is an order of magnitude larger than that of any of the other three systems, and its development capacity is similarly higher than that of the other systems. Furthermore, the leading index of development (the ascendency:capacity ratio) also indicates that the trophic relationships in the graminoid ecosystem are more clearly defined than they are in the other three systems.

The insights gained from this comparative exercise should serve the ATLSS modelers well as they begin their task of executing this most complex of all ecosystem simulations.

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