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

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Network Analysis of Trophic Dynamics
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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.

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).

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.* (19??) 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).

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.

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.

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.

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

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*).

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*).

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*).

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

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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 & 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 & Anderson 1994).

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.

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

- 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 Kvĕt (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

$^{o}C^{-1}.mole^{-1}$, 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.

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.

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.

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.

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.

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.

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.

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).

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).

Tables 1 and 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.

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.

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 $gC\text{-}bits.m^{-2}.y^{-1}$ and dry = 39,854 $gC\text{-}bits.m^{-2}.y^{-1}$) 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.

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.

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 ($\pm$ 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.

7. ACKNOWLEDGMENTS

8. REFERENCES

ANON 1997. Across-Trophic-Level System Simulation (ATLSS): Approach for analysis of South Florida Ecosystems. Progress Report – DRAFT.

ANON 1997. Strategic plan for the interagency Florida Bay Science Program. Prepared by Florida Bay Progam Management Committee.

Baird, D. & Ulanowicz. R.E. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.*, 59: 329-364.

Banse, K. & Mosher. S. 1980. Adult body mass and annual P/B relationships of field populations. *Ecological Monographs* 50: 355 - 379.

Berner, L. & Pescador, M.L. 1988. *The mayflies of Florida*. Rev. ed. Gainesville: University Presses of Florida.

Birkenholz, D.E. 1962. A study of the life history and ecology of the round-tailed muskrat (*Noefiber alleni* True) in North Central Florida. Thesis U. Florida.

Bjorndal, K.A. 1985. Nutritional Ecology of Sea Turtles. *Copeia* 1985(3): 736-751.

Bolte, W. & Bass, O.L.Jr. 1980. Twenty-nine year synopsis of the Coot Bay Christmas bird count, Everglades National Park. South Florida Research Center Report T-605. 19pp.

Browder, J.A., Cottrell, D., Brown, M., Newman, M., Edwards, R., Yuska, J., Browder, M. & Krakoski, J. 1982. Biomass and primary production of Microphytes and Macrophytes in Periphyton habitats of the Southern Everglades, Report T-662, South Florida Research Center, Homestead, Fla. 49 pp.

Brown, R.B., Stone, E.L. & Carlisle, V.W. 1990. Soils. *In:* Myers, R.L. & Ewel, J.J. (Eds.) *Ecosystems of Florida.* University of Central Florida Press, Orlando. Pp. 35-69.

Burt, W.H. & Grossenheider, R.P. 1961. *A field guide to the Mammals. Giving field marks of all species found north of the Mexican Boundary*. Sponsored by the National Wildlife Federation and National Audubon Society. Houghton Mifflin Company, Boston. 200p.

Burt, W.H. & Grossenheider, R.P. 1976. *A field guide to the Mammals. Field marks of all North American species found north of Mexico*. Sponsored by the National Wildlife Federation and National Audubon Society. Houghton Mifflin Company, Boston. 290p.

Busch, D.E., Loftus, W.F. & Bass, O.L.Jr. 1998. Long-term hydrologic effects on marsh plant community structure in the southern Everglades. *Wetlands* 18(2): 230-241.

Caprio, A. C., & Taylor, D. L. 1984. Effect of frost on a subtropical Muhlenbergia prairie in south Florida. *Florida Scientist,* 47, 27-32.

Christian, R.R. & Luczkovich, J.J. 1999 Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. *Ecol. Mod.* 117: 99-124.

Croop, J.D. 1996. A quantitative comparison of sampling techniques and habitat use for the apple snail in the Florida Everglades. Masters Thesis, University of Florida.

Dalrymple, G.H. 1988. The herpetofauna of the Long Pine Key, Everglades National Park, in relation to vegetation and hydrology. Pages 72-86 in Management of Amphibian, Reptiles and small Mammals in North America. USDA Forest Service General Technical Report RM-166.

Daoust, R.J. & Childers, D.L. 1999. Controls on emergent macrophyte composition, abundance, and productivity in freshwater Everglades wetland communities. *Wetlands* 19(1): 262-275.

Davis, W. P., Thornton, K.W. & Levinson, B. 1994. Framework for assessing effects of global climate change on mangrove ecosystems. *Bulletin of Marine Science* 54 (3): 1045-58.

DeAngelis, D.L., Gross, L.J., Huston, M.A., Wolff, W.F., Fleming, D.M., Comiskey, E.J. & Sylvester, S.M. 1998. Landscape Modeling for Everglades Ecosystem Restoration. *Ecosystems* 1: 64-75.

Dierberg, F.E. & Ewel, K.C. 1986. The effects of wastewater on decomposition and orgatic matter accumulation in cypress domes. *In: Cypress Swamps*, K.C. Ewel and H.T. Odum, (Eds.), University of Florida Press, Gainesville.

Diffendorfer, J.E., Richards, P.S., Dalrymple, G.H. & DeAngelis, D.L. 1999. Using ecosystem and food web methods in conservation: an example from the herpetological assemblage of the Everglades. Part I. Paper submitted to *Ecosystems*.

Dineen, J.W. 1984. Fishes of the Everglades. In P.J. Gleason (ed). *Environments of South Florida: Present and Past II.* Memoir II, Miami Geological Society, Miami, Florida.

Dunning, J.B. Jr. 1993. CRC Handbook of avian body mass.

Finn, J.T. 1976. Measures of ecosystem structure and function derived from analysis of flows. *J. theor. Biol.,* 56:363-380.

Flora, M.D. & Rosendahl, P.C. 1982. An analysis of surface water nutrient concentrations in the Shark River Slough, 1972-1980. *South Florida Research Center, Report T-653.*

Foster, M.L. & Humphrey, S.R. 1995. Use of highway underpasses by Florida Panthers and other wildlife. *Wildlife Society Bulletin* 23(1): 95-100.

Fournier, R.A. & Weber, J.M. 1994. Locomotory energetics and metabolic fuel reserves of the Virginia Opossum. *Journal of experimental Biology.* 197:1-16.

Franz, R. & Franz, S.E. 1990. A review of the Florida crayfish fauna, with comments on nomenclature, distribution, and conservation. *Florida Scientist* 53(4): 286-296.

Frederick, P.C. & Collopy, M.W. 1989. The role of predation in determining reproductive success of colonially-nesting wading birds (Ciconiiformes) in the Florida Everglades. *Condor*, 91: 860-867.

Fury, J.R. 1999. Everglades fisheries investigations project, F-56: completion report, 1995-1998. State of Florida. Game and Fresh Water Fish Commission.

Gaines, M.S., Diffendorfer, J.E., & Lind, L. 1997. The effect of high water on small mammal populations inhabiting hammock islands in Everglades National Park. Unpublished Report.

Gaiser, E., Richards, J., DeCellis, S. & Ugarte, C. 1998. Periphyton. In: Jones, R.D., Trexler, J. & Childers, D.L. (Eds.) *Numerical Interpretation of Class III narrative nutrient water criteria for Everglades Wetlands.* Annual Report, Southeast Environmental Research Program, FIU (Flume Experiment).

Givnish, T.J. 1989. Ecology and evolution of carnivorous plants. In: Abrahamson, W.G. (Ed.) *Plant-animal interactions.* McGraw-Hill, New York. Pages. 243-290.

Goodrick, R.L. 1984. The wet prairies of the northern Everglades. *In*: P.J. Gleason (ed.) *Environments of South Florida: Present and Past II.* Memoirs II, Miami Geological Society, Miami, Florida.

Gunderson, L.H. 1994. Vegetation of the Everglades: Determinants of Community Composition. *In* S.M. Davis & J.C. Ogden (eds.) *Everglades: The Ecosystem and Its Restoration.* St. Lucie Press, Delray Beach, Florida.

Gunderson, L.H. & Loftus, W.F. 1993. The Everglades. In: W.H., Martin, S.G. Boyce, & A.C. Echternacht (Eds.), *Biodiversity of the Southeastern United States: Terrestrial communities,* John Wiley & Sons, New York, Chapter 6.

Haake, P.W. & Dean, J.M. 1983. Age and growth of four Everglades fishes using otolith techniques. Tech. Rep. SSFRC-83/03, Everglades National Park, Homestead, Florida.

Hannon, B. 1973. The structure of ecosystems. *J. theor. Biol.,* 83:195-207.

Herndon, A.K. & Taylor, D. 1986. Response of a *Muhlenbergia* prairie to repeated burning: changes in above-ground biomass. South Florida Research Center Rep. 86/05, Everglades National Park, Homestead, FL.

Hoffman, W., Bancroft, G.T. & Sawicki, R.J. 1990. Wading bird populations and distributions in the water conservation areas of the Everglades: 1985 through 1988. Report prepared for the Environmental Sciences Division, South Florida Management Unit. Contract #396-M87-0345.

Hirata, H. and R.E. Ulanowicz. 1984. Information theoretical analysis of ecological networks. *Int. J. Systems Sci.,* 15(3): 261-270.

Humphrey, S.R. 1982. Seasonal habitat use by river otters and Everglades Mink in Florida. *J. Wildl. Manage.* 46(2): 375-381.

Humphrey, S.R. (ed.) 1992. Volume I: Mammals. In R.E. Ashton Jr. (series ed.) *Rare and Endangered Biota of Florida*. University Presses of Florida, Gainesville, Florida.

Humphrey, S.R. & Zinn, T.L. 1982. Seasonal habitat use by river otters and Everglades Mink in Florida. *Journal of Wildlife Management* 46(2): 375-381.

Hunt, B.P. 1952. Food relationships between Florida spotted gar and other organisms in the Tamiami Canal, Dade County, Florida. *Transactions of the American Fisheries Society* 82: 14-33.

Janzen, D.H. & Schoener, T.W. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96-110.

Jordan, F., Jelks, H.L. & Kitchens, W.M. 1994. Habitat use by the fishing spider *Dolomedes triton* in a northern Everglades wetland. *Wetlands* 14(3): 239-42.

Jørgensen, S.E., S.N. Nielsen, and L.A. Jørgensen. 1991. *Handbook of Ecological Parameters and Ecotoxicology*. Pergamon Press, Amsterdam.

Kale, H.W.II (editor). 1978. *Volume Two: Birds*. In P.C.H. Pritchard (series editor). *Rare and Endangered Biota of Florida*. University Presses of Florida, Gainesville, Florida.

Kautz, R.S., Gilbert, D.T. & Mauldin, G.M. 1993. Vegetative cover in Florida based on 1985-1989 Landsat Thematic Mapper Imagery. *Fla. Sci.* 56 (3): 135–151.

Kitchell, J.F. & Windell, J.T. 1972. Energy budget for the lizard, *Anolis carolensis*. *Physiol. Zool*. 45: 178-188.

Kleiber, M. 1961. *The fire of life: an introduction to animal energetics*. John Wiley & Sons, Inc., New York.

Kushlan, J.A. 1990. Freshwater marshes. In: Myers, R.L. and J.J. Ewel (Eds.) *Ecosystems of Florida*. University of Central Florida Press, Orlando.

Kushlan, J.A. & Hunt, B.P.1979. Limnology of an alligator pond in South Florida. *Florida Scientist* 42(2): 65-83.

Kushlan, J.A. & Kushlan, M.S. 1980. Function of nest attendance in the American Alligator. *Herpetologica* 36(1): 27-32.

Kushlan, J.A., Voorhees, S.A., Loftus, W.F. & Frohring, P.C. 1986. Length, mass, and calorific relationships of Everglades animals. *Florida Scientist* 49(2): 65-79.

Kvĕt, J. 1982. Production of organic matter in macrophyte stands. In: Proc. Conf. Macrophytes in Water Management, Water Hygiene and Fishery, Dům Techniky ČSVTS, České Budějovice, 73 (In Czech) – quoted in Vymazal (1995) p.171.

Labisky RF & Boulay MC. 1998. Behaviors of bobcats preying on white-tailed deer in the Everglades. *American Midland Naturalist*, 139(2) 275-281.

Labisky, R.F., Boulay, M.C., Sargent, R.A., Miller, K.E., Zultowsky, J.M. 1995. Population ecology of white-tailed deer in Big Cypress National Preserve and Everglades National Park. Final Report to USDI, University of Florida, Gainesville.

Layne, J.N. 1978. *Volume 1: Mammals*. In: Prichard, P.C.H. (Series Ed.) Rare and endangered biota of Florida. University Presses of Florida, Gainesville.

Layne, J.N. 1984. *The land mammals of southern Florida*. *In* P.J. Gleason (ed.) *Environments of South Florida: Present and Past II*. Memoir II, Miami Geological Society, Miami, Florida.

Leontief, W. 1951. *The Structure of the American Economy 1919-1939*. 2nd edn. Oxford University Press, New York.

Levine, S.H. 1980. Several measures of trophic structure applicable to complex food webs. *J. theor. Biol.*, 83:195-207.

Light, S.S. & Dineen, J.W. 1994. Water control in the Everglades: A historical perspective. *In* S.M. Davis & J.C. Ogden (eds.) *Everglades: The Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, Florida. p. 47-84.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23: 399-418.

Lodge, T.E. 1994. *The Everglades handbook: Understanding the ecosystem*. St. Lucie Press, Delray Beach, Florida.

Loftus, W.F. & Edlund, A.M. 1994. Long-term dynamics of an Everglades small-fish assemblage. *In* Steven M. Davis & John C. Ogden (eds.) *Everglades: The Ecosystem and Its Restoration.* St. Lucie Press, Delray Beach, Florida.

Loftus, W.F. & Kushlan, J.A. 1987. Freshwater fishes of southern Florida. *Bulletin Florida State Museum, Biological Sciences* 31(4): 147-344.

Loftus, W.F., Chapman, J.D. & Conrow, R. 1986. Hydroperiod effects on Everglades marsh food webs, with relation to marsh restoration efforts. *Proceedings of the Conference on Science in the National Parks* 6: 1-22.

Loftus, W.F., Trexler, J.C. & Jones, R.D. 1998. Mercury transfer through an Everglades aquatic food web. Final Report (Contract SP-329) to Florida Department of EPA. (also PhD).

Loveless, C.M. 1959. A study of the vegetation in the Florida Everglades. *Ecology* 40: 1-9.

MacDonald, K. 1997. Site fidelity and its effects on survival of *Odocoileus virginianus seminolus* during a catastrophic flood in the Everglades. Masters Thesis, University of Florida, Gainesville.

Marian, M.P. 1982. Ecophysiological studies in frog culture (*Rana tigrina* Daud). Ph.D. Thesis, Madurai Kamaraj University, Madurai, India.

Mazzotti, F.J., Ostrenko, W. & Smith, A.T. 1981. Effects of the exotic plants *Melaleuca quinquenervia* and *Casuarina equisetifolia* on small mammal populations in the Eastern Florida Everglades. *Florida Scientist* 44(2): 65-71.

McCormick, P.V., Chimney, M.J. & Swift, D.R. 1997. Diel oxygen profiles and water column community metabolism in the Florida Everglades, USA. *Arch. Hydro.* 140:117-129.

McLusky, D.S. 1989. *The Estuarine Ecosystem.* 2nd Edition. Blackie,

McNab B.K. 1980. Food habits, energetics and the population biology of mammals. *Am. Nat.,* 116(1): 106-124.

Miller, K.E. 1993. Habitat use by White-tailed deer in the Everglades: Tree Islands in a seasonally flooded landscape. Masters Thesis, University of Florida, Gainesville.

Moler, P.E. 1992. Amphibians and Reptiles. Volume 3. *In:* Ashton, R.E.Jr. (Ed.) *Rare and Endangered Biota of Florida.* University Presses of Florida.

Moore, W.J. 1962. *Physical Chemistry*, 3rd Edition. Prentice Hall, New Jersey.

Newman, D.G. & Griffin, C.R. 1994. Wetland use by River Otters in Massechusetts. *J. Wildl. Manage*. 58(1): 18-23.

Odum, E.P., Connell, C.E. & Davenport, L.B. 1962. Population energy flow of three primary consumer components of old-field ecosystems. *Ecology* 43(1): 88-96.

Odum, W.E. & McIvor. C.C. 1990. Mangroves. In: Myers, R.L. and J.J. Ewel (Eds.) *Ecosystems of Florida*. University of Central Florida Press, Orlando.

Olmsted, I.C., Loope, L.L. & Rintz, R.R. 1980. A survey and baseline analysis of aspects of the vegetation of Taylor Slough, Everglades National Park. Nat. Park Ser., South Florida Research Center Report T-586.

Patten, B.C., R.W. Bosserman, J.T. Finn and W.G. Cale. 1976. Propagation of cause in ecosystems. Pages 457-479 in B.C. Patten, Ed. *Systems Analysis and Simulation in Ecology*. Vol. 4. Academic Press, New York.

Pennak, R.W. 1978. *Freshwater Invertebrates of the United States* (second edition). John Wiley & Sons, New York, New York.

Pimm, S.L. 1982. *Food Webs*. Chapman and Hall, London. 219p.

Pough, F.H. 1973. Lizard energetics and diet. *Ecology* 54(4): 837-844.

Powers, J.G., Mautz, W.W. & Pekins, P.J. 1989. Nutrient and energy assimilation of prey by bobcats. *J. Wildl. Manage.* 53(4): 1004-1008.

Robertson, W.B.Jr. & Kushlan, J.A. 1984. *The southern Florida avifauna. In* P.J. Gleason (ed.) *Environments of Southern Florida: Present and Past II*. Memoir II, Miami Geological Society, Miami, Florida.

Roman, C. T., Aumen, N. G., Trexler, J. C., Fennemma, R. J., Loftus, W. F., & Soukup, M. A. 1994. Hurricane Andrew's impact on freshwater resources. *BioScience,* 44(4): 247-255.

Ryser, J. 1992. The mating system and male mating success of the Virginia opossum (*Didelphis virginiana*) in Florida. *Journal of Zoology, Part 1*: 228: 127-139.

SCOR. 1981. *Mathematical Models in Biological Oceanography*. T. Platt, K.H. Mann, and R.E. Ulanowicz, Eds. UNESCO Press, Paris.

Seale, B.D. 1987. Amphibia, In: Pandian,T.J. & Vernberg, F.J. (Eds.), *Animal Energetics. Volume 2 Bivalvia through Reptilia.* Academic Press. NY. p.467-552.

Smith, A.T. 1980. An Environmental Study of Everglades Mink (*Mustela vison*). South Florida Research Center Report No. T-555.

Smith, A.T. & Cary, D.M. 1982. Distribution of Everglades Mink. *Florida Scientist* 45(2): 106-112.

Smith, G.C. 1976. Ecological energetics of three species of ectothermic vertebrates. *Ecology* 57: 252-264.

Smith, T.R. & Bass, O.L.Jr. 1994. Landscape, White-tailed deer, and the distribution of Florida Panthers in the Everglades. In: Davis, S. & Ogden, J. (eds.) Everglades: The Ecosystem and Its Restoration, St. Lucie Press, Delray Beach, FL. Pp. 693-708.

Smith, T.R., Hunter, C.G., Eisenberg, J.F. & Sunquist, M.E. 1996. Ecology of white-tailed deer in eastern Everglades National Park: an overview. Bulletin of the Florida Museum of Natural History 39(4): 141-172.

Sowder, A. & Woodall, S. 1985. Small mammals of *Melaleuca* stands and adjacent environments in Southwestern Florida. *Florida Scientist* 48(1): 44- (Not all).

Stevenson, H.M. and Anderson, B.H. 1994. The birdlife of Florida. University Press of Florida, Gainnesville. 892pp.

Swift, D.R and Nicholas, R.B. 1987. Periphyton and water quality relationships in the Everglades Water Conservation Areas, 1978-1982. South Florida Water Management District, Technical Publication 87-2.

Szyrmer, J. and R.E. Ulanowicz. 1987. Total flows in ecosystems. *Ecological Modeling*, 35:123-136.

Thompson, F.G. 1984. *Freshwater Snails of Florida.* University of Florida Press, Gainesville, Florida.

Tilmant, J.T. 1975. Habitat utilization by round-tailed muskrats (*Neofiber alleni*) in Everglades National Park. M.Sc. Degree Humboldt State University.

Trexler, J.C., Richardson, R. & Spitze, K. 1996. Effects of Hurricane Andrew on the structure and function of Everglades aquatic communities, Florida International University.

Ulanowicz, R.E. 1980. An hypothesis on the development of natural communities. *J. theor. Biol.* 85:223-245.

Ulanowicz, R.E. 1983. Identifying the structure of cycling in ecosystems. *Mathematical Biosciences,* 65:219-237.

Ulanowicz, R.E. 1986. *Growth and Development: Ecosystems Phenomenology.* Springer-Verlag, New York. 203p.

Ulanowicz, R.E. 1989. A generic simulation model for treating incomplete sets of data. Pp. 84-89 in F. Wulff, J.G. Field, and K.H. Mann (Eds.) *Network Analysis in Marine Ecology: Methods and Applications.* Springer-Verlag, Berlin.

Ulanowicz, R.E. 1994. Modeling lower trophic components of the Everglades ecosystem. Final Report to National Biological Survey, South Florida/Carribean Research Center, Homestead, FL.

Ulanowicz, R.E. 1995a. Ecosystem trophic foundations: Lindeman exonerata. pp. 549-560 in B.C. Patten and S. Jorgensen (Eds.) *Complex Ecology: The Part-Whole Relation in Ecosystems*. Prentice-Hall, Englewood Cliffs, New Jersey.

Ulanowicz, R.E. 1997. *Ecology, the Ascendent Perspective*. Columbia University Press, 201p.

Ulanowicz, R.E., and D. Baird. 1999. Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community." *J. Mar. Systems* 19:159-172.

Ulanowicz, R.E., Bondavalli, C. and M.S. Egnotovich. 1997. *Network Analysis of Trophic Dynamics in South Florida ecosystems: The Cypress Wetland Ecosystem.* Annual Report to USGS/BRD, Coral Gables, FL. 33p.

Ulanowicz, R.E., Bondavalli, C. and M.S. Egnotovich. 1998. *Network Analysis of Trophic Dynamics in South Florida ecosystems: The Florida Bay Ecosystem.* Annual Report to USGS/BRD, Coral Gables, FL. 33p.

Ulanowicz, R.E., Bondavalli, C. Heymans, J.J. and M.S. Egnotovich. 1999. *Network Analysis of Trophic Dynamics in South Florida ecosystems: The Mangrove Ecosystem.* Annual Report to USGS/BRD, Coral Gables, FL. 39p.

Ulanowicz, R.E. and J.J. Kay. 1991. A package for the analysis of ecosystem flow networks. *Environ. Software,* 6(3): 131-142.

Ulanowicz, R.E. and W.M. Kemp. 1979. Toward canonical trophic aggregations. *Am. Nat.*114: 871-883.

Ulanowicz, R.E. and J.S. Norden. 1990. Symmetrical overhead in flow networks. *Int. J. Systems Sci.*, 21: 429-437.

Ulanowicz, R.E. and C.J. Puccia. 1990. Mixed trophic impacts in ecosystems. *Coenoses* 5(1): 7-16.

Vymazal, J. 1995. Algae and element cycling in wetlands. Lewis Publ. Baco Raton, Fl.

Waldschmidt, S.R., Jones, S.M. & Porter, W.P. 1987. Reptilia *In:* Pandian,T.J. & Vernberg, F.J. (Eds.), *Animal Energetics. Volume 2 Bivalvia through Reptilia.* Academic Press. NY. p.553-619.

Wang, T. & Warburton, S.J. 1995. Breathing pattern and cost of ventilation in the American Alligator. *Respiration Physiology* 102(1): 29-37.

Werner, H.W & Woolfenden, G.E. 1983. The Cape Sable Sparrow: Its habitat, habits and history. *The Seaside Sparrow, Its Biology and Management,* pg. 55-75.