



# Assessment of Spatial and Temporal Variability in Ecosystem Attributes of the St Marks National Wildlife Refuge, Apalachee Bay, Florida

D. Baird<sup>a</sup>, J. Luczkovich<sup>b</sup> and R. R. Christian<sup>b</sup>

<sup>a</sup>Department of Zoology, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth, South Africa

<sup>b</sup>Department of Biology, East Carolina University, Greenville, North Carolina 27858, U.S.A.

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Six carbon-flow networks of a seagrass ecosystem were constructed from comprehensive databases collected at three different sites during January and February 1994, respectively. The flow models, which consisted of 51 compartments each, were analysed by means of network analysis and the resultant outputs compared on spatial and temporal scales. Results on the biomass, species diversity, input, rates of exchange and export of material showed distinct differences between the sites in a month, as well as between months at the same site. System-level attributes, such as total system throughput, ascendancy, the structure and magnitude of recycling, flow diversity, etc., derived from network analysis, also showed noticeable differences from site to site and between months. There was an increase in ecosystem activity and in the magnitude of its global properties between months which are ascribed to a rise in temperature between months, increased rates in respiration and growth of resident species populations, as well as to the immigration of large numbers of fish and birds.

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## Introduction

Spatial and temporal variabilities in ecosystem behaviour are determined to a large extent by biological throughput and the scales over which individuals and populations interact. Recent work on the measurement of material and energy flow between the various ecosystem components has illustrated the efficiency by which material is assimilated, transferred and dissipated, providing significant information on the fundamental structure and function of the whole system (cf. Wulff *et al.*, 1989; Baird & Ulanowicz, 1989, 1993; Baird *et al.*, 1991, 1995; Christian *et al.*, 1996; Halfon *et al.*, 1996). Flow networks of ecosystems, or of subsystems within ecosystems, are more often than not constructed based on data collected of species and communities over periods of months or even years. Data on biomass, diversity and rates of productivity are usually pooled or averaged from many sampling locations and dates and the assumption is made that the information reflects the status of the system in a steady state over time. Although geographical, seasonal and annual variability in biotic and abiotic components are acknowledged, they are rarely incorporated in ecosystem models.

<sup>a</sup>Corresponding author.

In studies of ecosystems where seasonal or inter-annual variability was taken into account, results not only showed substantial differences between structural properties such as biomass, diversity and productivity, but also in system-level attributes such as in the structure and magnitude of recycling, flow diversity and systems throughput. Recent reports by Warwick and Radford (1989) on seasonal changes in an estuarine benthic community, Gaedke and Straile (1994) on seasonal changes and trophic transfer efficiencies in plankton food-webs, Field *et al.* (1989) on the successional development of planktonic communities during an upwelling event, Baird and Ulanowicz (1989) and Baird *et al.* (1995) on the seasonal dynamics of carbon and nitrogen in the Chesapeake Bay, Fores and Christian (1993) and Christian *et al.* (1996) on nitrogen cycling in coastal ecosystems, clearly illustrate the dynamic and variable nature of ecosystem processes over time. Most of these studies used network analysis, a set of algorithms derived from input-output, trophic and cycle analysis, to compute total system properties such as Total System Throughput, Development Capacity, Ascendancy, System Overheads, Finn Cycling Indices, etc. Network analysis has also more recently been used in the field of comparative ecosystem ecology where a

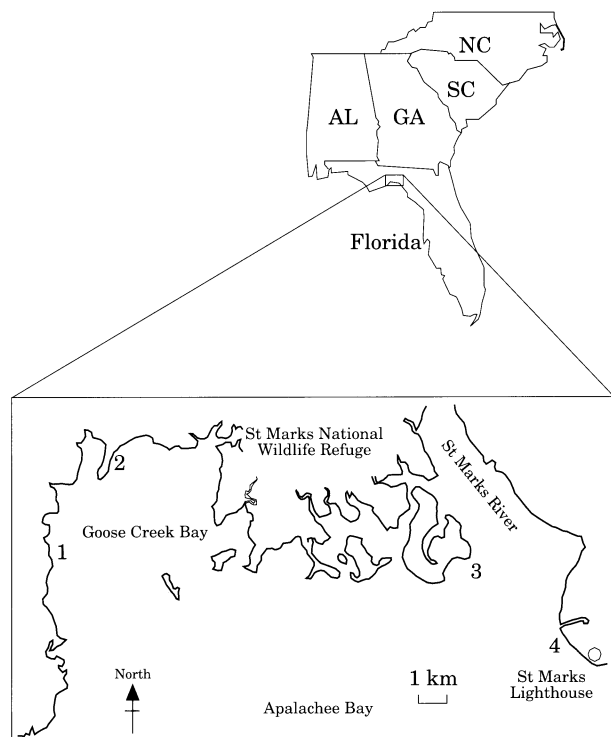


FIGURE 1. Map of the of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida, and sample locations shown by numbers.

particular system has been examined over time (Field *et al.*, 1989; Baird & Heymans, 1996) or where systems from different geographical regions have been compared on spatial scales (Richy *et al.*, 1978; Baird *et al.*, 1991; Baird & Ulanowicz, 1993; Christensen, 1995; Christian *et al.*, 1996). Detailed reference to the basic concepts of network analysis are given by Ulanowicz (1986), Kay *et al.* (1989), Ulanowicz and Kay (1991), while Wulff *et al.* (1989) reviewed the methods and applications of network analysis in marine ecology.

The main objective of this paper is to assess fine-scale temporal and spatial variability in structure and system-level properties, and the influence of averaging over space and time. These are evaluated for a large seagrass ecosystem in the St Marks National Wildlife Refuge, an important overwintering area for migrating waterfowl, in Apalachee Bay, Gulf of Mexico, Florida (see Figure 1). The authors examine the degree to which structural variability over time and space in the ecosystem is reflected in system properties derived from network analysis and to validate this against attributes computed from empirical data. The study is based on extensive databases from three areas in the Refuge sampled during January and February 1994, respectively. The sampling procedures, taxonomic

and trophic refinement, feeding guilds and diet composition were done according to the recommendations of Cohen *et al.* (1993) in order to extract maximum information from the datasets, to standardize procedures and to maximise food-web resolution. Details of the collection and analysis of samples, species diversity and abundance, biomass and trophic classification are given by Luczkovich *et al.* (unpubl.).

Carbon-flow networks were constructed for three different sampling sites in the Refuge during January and February, respectively. Comparisons of networks were made, spatially between sites within each month and temporally between the same site in different months. Networks were then constructed to average the food-web for each month and the overall winter. The networks consist of 51 compartments each and have essentially the same flow structure, topology and degree of aggregation. The same currencies, C (a surrogate for energy), units of biomass ( $\text{mgCm}^{-2}$ ) and flow ( $\text{mgCm}^{-2} \text{day}^{-1}$ ) were used in all nine models.

### Study area, material and methods

The St Marks Wildlife Refuge ( $30^{\circ}06'N$ ,  $84^{\circ}11'E$ ), situated in Apalachee Bay in the north-eastern Gulf of Mexico, contains a diverse landscape of wetlands, interfacing with upland forests and coastal waters with contiguous seagrass beds. The study sites were situated in or near Goose Creek Bay, in an area dominated by the seagrass, *Halodule wrightii*. Three sites were sampled each month: sites 1 (Live Oak Island), 2 (Wakulla Beach) and 3 (Sprague Island) during January 1994; and sites 1, 2 and 4 (Lighthouse Point) during February 1994 (see Figure 1). At each site, replicate samples were taken along three transects, which were delineated 100 m apart, running perpendicular to the shore and extending through *Halodule* communities to approximately 150 m offshore. Each site, about 4.5 ha in size, represents a 'sub-unit' of the seagrass ecosystem. The average water temperatures in the bay during January and February were 12 and 17 °C, respectively. The salinities at sites 3 and 4 were variable, ranging between 15 and 27 due to their closeness to the mouth of the St Marks River. These sites were also more subject to tidal and other currents than sites 1 and 2, which were situated in the inner, calm waters of the bay and where the salinity remained constant during both months at 25. The average depth at all sites was 0.75 m. The inter- and subtidal sediment was predominantly muddy throughout. Details of the sampling design and analytical procedures are described by Luczkovich *et al.*

(unpubl.). Here, the general methodology of the variables sampled at the various study sites is summarized.

Dissolved (DOC) and suspended particulate organic carbon (SusPOC) in the water column and sediment organic matter (SedPOC) were sampled at each transect. Dissolved organic carbon was estimated by wet combustion (Menzel & Vaccaro, 1964). Suspended particulate organic carbon was measured in a Control Equipment Corporation Elemental Analyser. Sediment organic matter was determined by loss on ignition from organic matter sampled from the surface to a depth of 5 cm and converted to C as 45% of the ash free dry mass.

Productivity and standing stocks of primary producers were determined largely by W. Rizzo and H. Neckles (pers. comm., US Geological Survey). Ground cover along transects at each site was determined with periodic biomass sampling. Plant biomass was obtained for macrophyte species (above and below ground), micro-epiphytes and macrophytic algae. Benthic microalgal biomass was estimated from chlorophyll *a* content in surface layers of cores from each site. Phytoplankton biomass was estimated from aquatic chlorophyll *a* concentrations. Benthic microalgal and phytoplankton productivity was estimated from changes in dissolved oxygen concentrations with incubation in light and dark.

Water samples (of 1 l each) were taken at each transect for bacterioplankton and planktonic microprotozoa. Benthic bacteria were sampled at each transect by coring (3.8 cm diameter corer) to a depth of 5 cm. Samples were preserved until counting in 2% formaldehyde. Biomass of bacteria and protozoans were estimated by epifluorescence microscopy by using acridine orange stain for bacterioplankton (Hobbie *et al.*, 1977), 4'-diamino-2-phenylindole (DAP) for benthic bacteria (Porter & Feig, 1980; Schallenberg *et al.*, 1989) and fluorocein isothiocyanate for microprotozoans in the water column (Sherr & Sherr, 1983). Bacterioplankton growth and grazing rates were estimated by modification of the method of Landry and Hassett (1982).

Net zooplankton were collected at each transect (one 45 m net haul per transect), the amount of water filtered during each haul calculated and samples preserved in 5% formalin stained with rose bengal. In the laboratory the samples were sieved through a series of screens (2000, 850, 425, 250, 150 and 75  $\mu\text{m}$ ) and the contents of each screen enumerated under a microscope. Sieve fractions were then dried at 65 °C for 48 h, and the biomass per litre in the original sample calculated.

To estimate the standing stock of meiofauna, five replicate 3.8 cm diameter cores were taken from each transect. Samples were placed in 10% formalin and rose bengal, and later separated from sediment by elutriation onto a 63  $\mu\text{m}$  sieve (Koonsman & Newburg, 1977), sorted, identified to the lowest possible taxon and enumerated. The dimensions of individual organisms of representative taxa were measured for conversion to biomass (Higgins & Thiel, 1988).

The standing stock of macro-invertebrates in the seagrass meadows was estimated by 10 replicate cores (7.62 cm inside diameter corer) per transect to 10 cm depth. Samples were sieved through 500  $\mu\text{m}$  mesh in the field and the organisms identified and counted from the sieved portion of each core sample. Amphipods were identified to species level using the keys of Bousefield (1973), Fox and Bynum (1975) and Myers (1981). Polychaetes were identified to family level using Fauchald (1977) and Uebelacker and Johnson (1984). Molluscs were identified to species using Morris (1975), as were decapod crustaceans and isopods using Williams (1984) and Schultz (1969), respectively. Other invertebrate groups were identified using the keys provided in Gosner (1971) and Fox and Rupert (1985). The biomass of each taxon was determined on a precision balance to the nearest 0.01 mg after drying for 24 h at 60 °C. In the case of molluscs, ophurids, polychaetes, isopods, decapods and amphipods, ash-free dry mass were obtained by ashing representative samples in a muffle furnace at 1000 °C for 4 h. All ash-free dry masses were converted to C by multiplying by 0.45; samples in which dry mass alone were determined were converted to C by multiplying by 0.4.

A barrier seine net, developed specially for this study and gill nets were used to sample fish and mobile decapods quantitatively at each site (see Luczkovich *et al.*, unpubl.). All fish caught were identified to species level, counted and weighed. Waterfowl standing stocks were estimated by surveys conducted in January and February by counting birds feeding at each site. Bird numbers were converted to biomass ( $\text{mgCm}^{-2}$ ) using appropriate wet:dry:carbon weight ratios for each species. The time spent feeding at each site was noted and their diet composition determined from the literature.

The diet composition for the various food-web compartments was determined as follows: stomach contents of representative fish species were analysed according to the sieve fractionation methodology of Carr and Adams (1973) as modified by Luczkovich and Stellwag (1993). This method is consistent with the method used by Livingston (1980, 1982, 1984)

TABLE 1. References to sources on the diet composition of some common invertebrate groups of the St Marks Wildlife National Refuge ecosystem

Feeding type	Food source	Reference
Predatory shrimp [24]	Amphipod, shrimp	Leber (1983)
Herbivorous shrimp [23]	Epiphytes	Leber (1983)
Predatory crab [20]	Fish, molluscs, shrimp, amphipods	Leber (1983)
Herbivorous crab [18]	Seagrass	Leber (1983)
Omnivorous crab [19]	Detritus, plant material, amphipods	Leber (1983)
Deposit feeding amphipods [15]	Detritus, bacteria	Bousefield (1973)
Deposit feeding polychaetes [26]	Detritus, bacteria	Fauchald and Jumars (1979)
Predatory polychaetes [27]	Amphipods, polychaetes	Fauchald and Jumars (1979)
Gastropods [10, 25, 28, 30]	Detritus, epiphytes, polychaetes, bivalves	T. West (ECU, pers. comm.)

Numbers in [ ]s refer to compartment number in flow models.

and Luczkovich (1987) so that comparisons with other dietary studies on fish in the study region are comparable. For the invertebrate groups, estimates of the dietary composition were obtained from the literature, which are listed in Table 1.

#### *Flow network construction*

Carbon-flow networks were constructed for each site in each month, for averages of sites 1 and 2 for each month and for averages of sites 1 and 2 for both months, i.e. nine in all. Sites 3 and 4 were sampled only once, in January and February, respectively, and not used in averaging. Each of the networks consists of 48 living and three non-living compartments and depicts the standing stock of each compartment in  $\text{mgCm}^{-2}$ , and the flows between them in  $\text{mgCm}^{-2}\text{day}^{-1}$ . Not all species, or compartments, were present at all sites. In order to maintain the model structure of 51 compartments throughout the analytical procedures, minuscule amounts ( $1 \times 10^{-5}$  mgC) were entered as biomass imports and exports for those compartments not present in the field samples. These entries do not influence the output results from network analysis whatsoever. The biomass for each species or community was obtained from the samples from each site collected during January and February, which form the primary database for the flow networks.<sup>1</sup>

For primary producers (phytoplankton, macrophytes, micro- and macro-epiphytes, and benthic algae) gross primary production (GPP) was assumed equal to the sum of net primary production (NPP)

and respiration (Rs). Exudation by aquatic plants, considered to be an important source of DOC in aquatic systems (Valiela, 1995), was assumed to be about 25% of the net photosynthate of phytoplankton, epiphytes and benthic algae (Vegter & de Visscher, 1984; Valiela, 1995) and about 2% for macrophytes (Sieburth & Jensen, 1969; Brylinski, 1977; Valiela, 1995). The values for GPP for the various primary producers were considered as inputs into the ecosystem.

Energy budgets were determined for each of the heterotrophic compartments. Consumption of food (Cn) was balanced by production (Pr), respiration (Rs) and egesta (E). Rates of consumption, production and respiration were obtained from the relevant literature, or calculated using appropriate ecological efficiencies such as the Pr/B, Pr/Rs and Pr/Cn ratios. Consumption of some invertebrate groups was obtained from the relationship  $Cn = \text{Assimilation/assimilation efficiency}$  (Baird & Milne, 1981). Fish consumption was estimated from the empirical relationship  $Cn = 1.25(\text{Pr} + 2R)$  (Winberg, 1956; Mann, 1965). The field metabolic and feeding rates of birds at St Marks Refuge were derived from the allometric equations provided by Nagy (1987). Wherever possible and appropriate, metabolic rates of the biota were adjusted to compensate for the 5 °C increase in temperature from January to February.

Each system was assumed to represent a steady-state condition and the inputs into each compartment of the network were balanced by corresponding outputs. Imports into the system were assumed to occur in those compartments whose uptake could not be met by prey production. Exports from the system comprised excess fish production, bird production and egesta. Inputs into the DOC originated mainly from exudates from plants and algae and served as the

<sup>1</sup>The raw data files for each model can be obtained by request on diskette or by anonymous FTP at [FTP://WWW1.ECU.EDU/STMARKS/](ftp://WWW1.ECU.EDU/STMARKS/) or at [HTTP://ECVVAX.CIS.ECU.EDU/~BILUCZKO/DRJOESPG.HTM](http://ECVVAX.CIS.ECU.EDU/~BILUCZKO/DRJOESPG.HTM)

food source for free-living aquatic bacteria. Excess production and egesta by water column organisms (bacteria, micro- and mesozooplankton) were assumed to remain in suspension as particulate POC. About one-third of the daily produced suspended POC was assumed to sink to the bottom, contributing to the sediment POC pool. Egesta of benthic invertebrates and fish, and all unutilized production of the benthos, were assumed to become sediment POC, which was considered as the energy source for benthic bacteria.

The comparison of ecosystems on spatial or temporal scales is simplified if the networks are comparable in general structure, i.e. number of compartments and a similar degree of aggregation. The authors made every effort to construct comparable networks. It should also be noted that calculated system activity measures, such as the total system throughput (TST), are sensitive to the inferred or derived metabolic rate functions (e.g. growth, respiration, food consumption) and ecological efficiencies (e.g. Pr/B, Rs/B, Pr/Cn, assimilation efficiency). Comparable assumptions and procedures were used for all networks.

The networks were analysed by NETWRK IV, a set of algorithms designed to compute various functional indices and system properties of natural ecosystems. The theoretical basis and computational methodology of network analysis are given by Ulanowicz (1986), Kay *et al.* (1989) and Ulanowicz and Kay (1991). A number of system descriptors and indices were calculated for each site and each month from empirical data and NETWRK IV output, such as:

1. The average path length (APL), a system descriptor which measures the average number of compartments a unit of flux will pass through from its entry into the system until it leaves the system. The APL is derived from  $(TST-Z)/Z$  where Z equals the sum of all exogenous inputs (Kay *et al.*, 1989; Baird *et al.*, 1991). The path length is expected to be higher in systems with high degrees of flow diversity and cycling (Christensen, 1995);
2. The average residence time (ART) of energy in the system and which is derived from the ratio between the total system biomass and the sum of all outputs (respiration and exports) from the system (Christensen, 1995);
3. The mapping of each of the complex networks of trophic transfers into a linear food chain, the Lindeman Spine, with discrete trophic levels. The Lindeman Spine illustrates the net amount each trophic level receives from the preceding one, as well as the amount of energy leaving it through respiration, exports, detritus for recycling and the net production passed on to the next higher level. Autotrophs and the non-living detrital pool form the first trophic level. Imported organic matter also enters the system at the first trophic level. The Lindeman Spine also allows the calculation of the trophic efficiency for each level, i.e. the efficiency by which matter and energy is transferred from the level to the next. It also allows the computation of the efficiency for the food-web as a whole, the system trophic efficiency, which is derived from the logarithmic mean of the integer level efficiencies (Baird & Ulanowicz, 1989);
4. Cycling characteristics. The Finn Cycling Index (FCI) gives the proportion of the flow in a system that is recycled as a fraction of the total system throughput, TST (Finn, 1976). The FCI is equal to  $T_c/TST$ , where  $T_c$  is the amount of system activity devoted to cycling. The FCI measures the retentiveness of a system; the higher the FCI, the greater the proportion recycled, and sensu Odum (1969), the more mature or less stressed the system. Network analysis also describes the structure of biogeochemical cycling through the identification and enumeration of all simple cycles in the system. An individual cycle represents a unique pathway which begins and terminates in the same compartment, and contains no repeated compartment. The cycles are grouped into nexuses within each of which all cycles share the same limiting or smallest link, also called the 'weak arc'. The assumption is that a weak arc is the controlling link in a cycle and that by grouping cycles according to the weak arc, one defines the domain of influence of each weak arc (Baird & Ulanowicz, 1989);
5. Global measurements of ecosystem organization such as: (i) total system throughput (TST), which measures the extent of total activity transpiring in the system, is measured as the sum of all flows through all compartments in the system. Total system throughput can be considered as the surrogate for the total power generated within the system (Odum, 1971); (ii) system ascendancy (A) which incorporates both the size and organization of flows into a single index. It is formally expressed as the product of TST and the mutual information inherent in the flow network. The ascendancy of a system should increase as it matures through a series of development stages. Ascendancy is intended to encapsulate the magnitude and diversity of flows between the compartments, and so reflects on the functional attributes of ecosystems (Ulanowicz, 1986; Kay *et al.*, 1989); (iii) development capacity (C) which measures the potential for a system to develop and is the natural upper limit of A; (iv) system overhead which is numerically represented by the difference  $C-A$  and which represents the cost to the

TABLE 2. Biomass (mgCm<sup>-2</sup>) of each compartment of the flow networks of the St Marks national Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida

Compartment number	Compartment name	Jan S1	Jan S2	Jan S3	Feb S1	Feb S2	Feb S4	Mean Jan	Mean Feb	Mean Jan & Feb
1	Phytoplankton	81.00	81.00	81.00	61.20	61.20	61.20	81.00	61.20	71.10
2	<i>Halodule wrightii</i>	4232.00	7744.00	35 328.00	2432.00	5444.00	15 292.00	5988.00	3938.00	4963.00
3	Micro-epiphytes	221.20	402.40	6779.00	105.60	194.40	2934.00	311.80	150.00	230.90
4	Macro-epiphytes	67.60	123.20	115.00	66.00	121.50	500.00	95.40	93.75	94.58
5	Benthic algae <sup>a</sup>	1151.00	624.00	2009.40	657.00	1862.00	186.17	887.50	1259.50	1073.50
6	Bacterio-plankton	8.16	6.93	10.31	15.45	13.01	20.40	7.55	14.23	10.89
7	Micro-protzoa <sup>b</sup>	4.64	8.34	3.21	9.11	3.57	12.02	6.49	6.34	6.42
8	Zooplankton	0.56	0.43	0.22	5.14	5.00	4.94	0.50	5.07	2.78
9	Epiphyte-grazing amphipods	101.48	48.22	338.09	54.15	82.16	243.48	74.85	68.16	71.50
10	Suspension-feeding molluscs	5.80	0.20	0.00	149.85	10.16	4.34	3.00	80.01	41.50
11	Suspension-feeding polychaetes	11.20	8.90	0.00	3.90	5.84	6.55	10.05	4.87	7.46
12	Benthic bacteria	328.00	313.00	322.21	187.00	221.00	215.23	320.50	204.00	262.25
13	Macrofauna	114.40	105.95	108.55	33.71	106.45	72.80	110.18	70.08	90.13
14	Meiofauna	874.80	635.90	1749.70	1579.70	1159.10	638.10	755.35	1369.40	1062.38
15	Deposit-feeding amphipods	53.78	13.88	13.32	35.24	34.72	80.03	33.83	34.98	34.41
16	Detritus-feeding tanaeids & cumaceans	3.68	2.78	0.06	0.26	3.33	11.49	3.23	1.80	2.51
17	Detritus-feeding hermit crabs	492.65	111.97	0.00	287.64	99.77	1.34	302.31	193.71	248.01
18	Herbivorous spider crabs	0.00	0.00	0.00	147.27	0.82	0.27	0.00	74.05	37.02
19	Omnivorous crabs	430.69	162.97	107.94	14.19	299.82	58.01	296.83	157.01	226.92
20	Blue crabs	0.36	0.35	0.00	37.47	19.13	6.84	0.36	28.30	14.33
21	Isopods	142.49	35.96	6.34	17.19	62.48	26.93	89.23	39.84	64.53
22	Brittle stars	496.64	8.95	25.01	619.33	378.05	108.43	252.80	498.69	375.74
23	Herbivorous shrimp	87.71	3.13	0.00	5.70	16.75	0.00	45.42	11.23	28.32
24	Predatory shrimp	52.66	74.09	24.53	65.39	37.81	87.73	63.38	51.60	57.49
25	Deposit-feeding gastropod	704.10	1933.24	1119.38	551.22	1222.49	240.84	1318.67	886.86	1102.76
26	Deposit-feeding polychaetes	101.19	72.58	0.00	2.57	42.19	22.70	86.89	22.38	54.63
27	Predatory polychaetes	121.64	80.35	101.30	846.83	137.91	856.25	101.00	492.37	296.68
28	Predatory gastropods	349.69	33.19	382.21	198.25	1170.83	178.61	191.44	684.54	437.99
29	Epiphyte-grazing gastropods	22.96	0.00	6.45	4.29	0.00	13.87	11.48	2.15	6.81
30	Other gastropods	33.29	1.22	0.00	2.57	42.19	22.70	17.26	22.38	19.82

TABLE 2. Continued

Compartment number	Compartment name	Jan S1	Jan S2	Jan S3	Feb S1	Feb S2	Feb S4	Mean Jan	Mean Feb	Mean Jan & Feb
31	Catfish & stingrays	0-00	0-00	0-00	1410-92	0-00	0-00	0-00	705-46	352-73
32	Tonguefish	0-00	0-00	0-00	7-63	2-02	4-30	0-00	4-83	2-41
33	Gulf flounder & needlefish	0-00	0-00	0-00	50-47	185-60	0-00	0-00	118-04	59-02
34	Southern hake & sea robins	0-44	0-00	1-08	35-41	0-00	10-10	0-22	17-71	8-96
35	Atlantic silversides & bay anchovy	0-00	0-00	0-00	25-07	19-93	17-91	0-00	22-50	11-25
36	Gobies & blennies	0-0	0-00	0-00	3-22	0-00	4-30	0-00	1-61	0-81
37	Pinfish	0-22	0-00	0-45	8-19	2-00	1440-80	0-11	5-10	2-60
38	Spot	3-02	47-49	60-41	25-44	280-16	133-12	25-26	152-80	89-03
39	Pipefish & seahorses	0-61	0-00	0-00	6-34	2-45	3-37	0-31	4-40	2-35
40	Sheepshead minnow	25-88	7-69	6-19	0-00	0-00	0-00	16-79	0-00	8-39
41	Red drum	0-00	141-44	0-00	0-00	0-00	0-00	70-72	0-00	35-36
42	Killifish	5-13	3-90	1-21	0-00	0-00	0-00	4-52	0-00	2-26
43	Herbivorous ducks	0-00	0-00	0-00	0-00	1-41	0-23	0-00	0-70	0-35
44	Benthos-eating birds	0-27	1-77	0-00	5-16	1-10	2-80	0-70	3-08	1-89
45	Fish-eating birds	17-46	7-69	21-27	36-61	103-18	20-00	5-10	68-75	36-93
46	Fish- & crustacean-eating birds	0-00	6-54	0-00	0-00	0-29	0-00	2-20	0-14	1-17
47	Gulls	14-36	17-30	24-79	8-48	15-67	9-51	6-60	7-73	7-17
48	Raptors	3-09	3-38	0-00	2-02	1-70	3-38	2-20	1-49	1-85
49	DOC	3670-00	2984-00	2421-00	4884-00	4792-00	5116-00	3327-00	4838-00	4082-50
50	Suspended POC	276-00	476-00	480-00	414-00	1513-00	245-00	376-00	963-50	669-75
51	Sediment POC	305 000-00	291 000-00	652 000-00	441 000-00	421 000-00	365 000-00	298 000-00	431 000-00	364 500-00

Biomass is given by individual site in January and February 1994 (Jan S1, Jan S2, etc.), pooled data for all sites in January (Mean Jan), all sites in February (Mean Feb) and all sites in both months (Mean Jan & Feb).

\*Benthic algae: meiofauna ratio used to calculate benthic algae biomass for Jan S3 and Feb S4.

\*Microprotozoa: bacterioplankton ratio used to calculate microprotozoa biomass for Feb S1 and Feb S4.

DOC, dissolved organic carbon; POC, particulate organic carbon.

system to operate the way it does. Imports into and exports from the system, dissipation (or respiration) and internal exchanges, or functional redundancy (Rd), all contribute towards the overhead (Baird & Ulanowicz, 1989); (v) internal ascendancy ( $A_i$ ) and internal development capacity ( $C_i$ ), which are functions of internal exchanges alone; (vi) flow diversity, derived from C/TST, measures the number of interactions in an ecosystem and it is thus a much more dynamic concept than species diversity. This index is defined by both the number of interactions and the evenness of flows in the food-web (Mann *et al.*, 1989); (vii) The effective number of connections between any two arbitrary compartments is described by connectance indices, and is given as the log-averaged number of links calculated from the systems overhead. Overall connectance includes the effect of external transfers and internal connectance characterizes only internal exchanges, whilst food-web connectance refers only to transfers among the living compartments in the system (Ulanowicz, 1997).

6. Assorted indices not requiring NETWRK IV output: e.g. the Shannon–Wiener index of diversity ( $H'$ ), with biomass as the importance value, species richness (number of pre-aggregation taxa) and evenness ( $H'/H'max$ ); sum of net primary production (NPP) and of total production (including all compartments of the flow networks); the NPP efficiency (the fraction of NPP grazed by herbivores), Pr/B and Rs/B daily ratios, herbivory, detritivory and the herbivory: detritivory ratio.

To assess the relative variability of selected attributes representing different boundary conditions for network construction, data from each site and month were treated as separate and independent samples, comprising six independent estimates of the ecosystem's attributes during the winter of 1994. *A priori*, the authors suspected that variation in the system attributes, as defined above, would be apparent among stations and between months. Data were compiled into nine separate network analyses: one per station per month ( $N=6$ ), one network each for January and February, respectively by averaging the data from sites 1 and 2 and one for all stations (1 and 2 only) combined for both months. Coefficients of variation (CVs) were calculated for each system attribute for each of the 6 monthly site models, and compared.

## Results

The data are presented under three headings, namely food-web and trophic structure, cycling of material and system-level properties. The authors pay particu-

lar attention to the networks and results of individual sites during the 2 months in order to achieve the objectives of the paper. The results are presented and discussed with particular reference to sites 1 and 2 in the context of spatial and temporal comparisons, because of the similar environmental conditions that prevail at both. Sites 3 and 4, sampled during January and February respectively, differ from 1 and 2, as shown below. Mean values of indices thus do not include sites 3 and 4, but information and data from sites 1 and 2 only.

### *Community, food-web networks and trophic structure*

Separate carbon-flow models were constructed for sites 1, 2 and 3 in January, and sites 1, 2 and 4 in February, for a total of six network models. Each model represents the seagrass ecosystem of a particular subunit of the Refuge, as it existed at that time and place. Not all species were present at all times and sites during the 2 months, and considerable variability in the biomass of the various components was also observed. Biomass information for each ecosystem compartment at each site and month is given in Table 2, as well as mean biomass values. The Shannon–Wiener diversity indices calculated with biomass ( $H'$ ), number of taxa and evenness ( $H'/H'max$ ) are given in Table 3.

There were generally more taxa present in February, with the exception of site 1, where the highest number of taxa were noted in January. However, higher indices of diversity ( $H'$ ) and evenness ( $H'/H'max$ ) were observed during February at most sites, indicating a greater diversity and a more even distribution of biomass across the components than during January. There was also a noticeable decline in these two indices from site 1 to site 3 or 4 in both months (see Table 3).

The standing stocks of most of the primary producers (compartments 1–5, Table 2) were higher during January at all sites. The biomass of *Halodule* was particularly high at site 3 during January. Daily production rates (excluding site 3 in January) increased from January to February, probably due to increased metabolism because of a 5 °C increase in ambient temperature. The daily NPP rate ranged between 261 and 332 mgCm<sup>-2</sup> day<sup>-1</sup> at sites 1 and 2 in January and from 211 to 411 mgCm<sup>-2</sup> day<sup>-1</sup> at the same sites in February. This rate was 4294 mgCm<sup>-2</sup> day<sup>-1</sup> at site 3 in January. There was a marked increase in the biomass and productivity of heterotrophic planktonic communities (compartments 6–8) at all three sites from January to February. The collective increase in biomass and daily



TABLE 3. Structural and system-level attributes of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida

Attribute	Jan S1	Jan S2	Jan S3	Mean Jan	Feb S1	Feb S2	Feb S4	Mean Feb	Mean Jan & Feb
Sum biomass [1-48]	10 365.9	12 784.3	48 7468.6	11 601.0	9820.2	13 473.2	23 557.1	11 640.8	11 620.9
H' (Shannon-Weiner Diversity)	0.88	0.5767	0.3729	0.7427	1.1969	1.0388	0.7111	1.1743	—
S (Species richness)	101	73	48	109	85	77	79	95	113
Sum NPP	261.43	331.93	4293.7	298.65	271.65	411.3	210.66	310.61	296.1
H'/H' max (evenness)	0.4414	0.2566	0.1242	0.3662	0.6203	0.4988	0.3483	0.6636	—
NPP efficiency [%] no	55.1	20	2.7	34.5	74	42.1	56	58.27	46.6
Sum of production [1-48]	404.9	454.9	4430.6	430.9	446.5	584.9	433.7	482.9	449.1
Sum respiration [1-48]	429.4	430.3	3522.3	438.3	478.9	542.9	723.0	589.2	467.2
Herbivory [H]	144.0	66.5	114.0	103.0	201.0	173.0	118.0	181.0	138.0
Detritory [D]	223.1	215.7	223.5	217.64	239.9	264.6	285.0	252.9	236.6
H:D ratio	1:1.96	1:3.24	1:1.96	1:2.11	1:1.19	1:1.53	1:2.42	1:1.40	1:1.71
P/B ratio (per day)	0.0391	0.0353	0.0909	0.0371	0.0455	0.0433	0.0443	0.0414	0.0386
R/B ratio	0.033	0.033	0.072	0.038	0.049	0.04	0.031	0.051	0.04
Sum imports, Z [1-51]	444.64	600.83	7677.85	545.62	591.7	800.89	1427.78	648.88	587.3
Sum of exports, E [1-51]	70.21	170.01	3251.34	112.36	233.34	646.88	142.83	120.33	24.81
APL [1-51]	3.12	2.31	1.66	2.44	2.71	2.4	2.01	2.58	2.51
Average residence time [1-51]	20.75	21.44	7.2	21.08	16.32	17.35	17.79	15.90	19.78
System trophic efficiency [%]	1.85	2.66	4.76	4.91	6.98	5.12	2.69	3.33	11.04
No of cycles	531	584	373	608	990	555	541	1006	1058
Finn cycling index [FCI]	19.03	12.54	1.9	15.53	21.56	16.71	8.16	19.9	18.03
Total system throughput	1830.4	1985.9	20 461.0	1876.6	2192.3	2722.2	4298.3	2321.3	2064.3
Development capacity [C]	9853.6	9236.4	60 412.0	9517.3	12 443.0	14 568.0	19 006.0	13 072.0	11 264.0
Ascendancy [A]	3294.4	3627.8	31 979.0	3391.8	4043.3	4850.5	7715.6	4210.0	3725.7
Overhead imports [Oi]	1267.6	926.9	5301.9	1095.6	1829.4	1974.5	2571.4	1831.5	1487.5
Overhead exports [Oe]	194.4	350.3	3950.6	300.1	372.6	560.1	970.0	403.7	352.9
Respiration overhead [Or]	2106.5	1765.0	7234.5	1962.6	2425.5	2709.9	3295.5	2548.3	2266.6
Redundancy [R]	2990.7	2566.0	11 946.0	2767.2	3772.1	4473.5	4453.6	4078.3	3431.6
Internal C [Ci]	4846.1	4313.2	19 836.0	4546.2	6170.1	6988.6	7876.1	6485.5	5506.6
Internal A [Ai]	1855.4	1746.9	7890.0	1779.0	2398.0	2515.1	3422.5	2407.5	2075.0
Internal R [Ri]	2990.7	2566.3	11 946.0	2767.2	3772.1	4473.5	4453.6	4078.3	3431.6
A/C [%]	33.4	39.3	52.9	35.6	32.5	33.3	40.6	32.2	33.1
Ai/Ci [%]	38.3	40.5	39.8	39.1	38.9	36.0	43.5	37.1	37.7
Oi/C [%]	12.9	10.0	8.8	11.5	14.7	13.6	13.5	14.0	13.2
Oe/C [%]	2.0	3.8	6.5	3.2	3.0	3.8	5.1	3.1	3.1
Or/C [%]	21.4	19.9	12.0	20.6	19.5	18.6	17.3	19.5	20.1
R/C [%]	30.4	27.8	19.8	29.1	30.3	30.7	23.4	31.2	30.5
Ri/Ci [%]	61.7	59.5	60.2	60.9	61.1	64.0	56.5	62.9	62.3
Overall connectance	2.332	2.005	1.469	2.189	2.521	2.393	1.875	2.536	2.414
Internal connectance	2.819	2.358	1.643	2.636	2.825	2.952	2.056	2.986	2.880
Food-web connectance	3.570	3.298	2.694	3.583	2.959	3.426	3.443	3.347	3.543
Flow diversity	5.383	4.651	2.953	5.072	5.676	5.352	4.422	5.631	5.457

production rates of these components averaged 76 and 109%, respectively, over all sites.

The biomass of individual benthic invertebrate compartments (9–30) increased by about 22% from January to February at most sites. Large increases in the number of species and in the biomass of fish and birds were observed between January and February. Increase in fish biomass was mainly due to the combined effect of growth of resident fish, and to the influx of large numbers of pinfish, *Lagodon rhomboides* (in the size range 1–20 mm SL) and spot, *Leiostomus xanthurus* (15–30 mm SL) (compartments 37 and 38, respectively) at all sites in February. The increase in bird numbers was mainly due to the greater abundance of benthos- and fish-eating birds (compartments 44 and 45 respectively).

The total biomass in February, summed over all living compartments of sites 1 and 2 (see Table 3), is only 0.3% higher than in January. Differences between the months at these two sites are, however, more strongly emphasized in  $H'$  indices and production rates, as shown in Table 3. The sum of the production of all living compartments increased by 12% (mean of sites 1 and 2) from January to February.

Herbivory, or that fraction of NPP directly consumed by herbivores and expressed as the NPP efficiency, shows large variation between individual sites and different months. This NPP efficiency fluctuated between 3 and 55% in January and between 42 and 74% in February. Herbivory was particularly low at site 2 during January, possibly because of the lower abundance of epiphyte grazing amphipods (nine) and gastropods (29). The herbivory: detritivory ratio (H:D) ratio remained fairly constant at all sites during both months, except at site 2 in January, where detritivory exceeded herbivory more than three-fold (see Table 3), which is partly due to the virtual absence of the two groups (compartments 9 and 29) mentioned above and, secondly, to the presence of large numbers of detritus feeding gastropods (25).

The daily Pr/B ratios and TST are both considered indices of trophic and functional activities of ecosystems, respectively (Baird *et al.*, 1991; Christensen, 1995). The Pr/B ratios lie between 0.0353 and 0.0391 during January at sites 1 and 2, respectively, but it was about 3 times higher, viz. 0.0909, at site 3, where the TST was approximately 10 times higher (see Table 3). Daily Pr/B ratios fluctuated within a narrow range (0.0433–0.0455) at all sites in February. The TST was slightly higher at site 4 than at the other two sites during this month (see Table 3). Variability in activity, or TST, is also noted between sites in the same month. For example, TST was about 9% higher

at site 2 than at site 1 during January, whereas in February, the TST was 24% higher at site 2 than at site 1. Both TST values and Pr/B ratios were higher at the river mouth sites 3 and 4 than at the inner bay sites 1 and 2 (see Table 3), due to the higher standing crops and production rates of *Halodule* (2) and spot (38) at site 3 in January and of pinfish (37) at site 4 in February.

Pr/B and TST values were generally higher during February than January at all sites. The TST increased from January to February at sites 1 and 2 by 20 and 37%, respectively, and the Pr/B ratio similarly by 16 (at site 1) and 23% (at site 2). The Rs/B ratios follow the same pattern as the Pr/B ratios and showed an increase of about 34% from January to February (see Table 3).

Two other indices which also reflect on the trophic function of an ecosystem are the average path length (APL), i.e. the average number of steps a unit of energy will experience before it leaves the system, and the average residence time (ART) of energy in the system. In both months the APL appear to decrease moving from sites 1 and 2 toward the river mouth at sites 3 and 4. It ranges between 3.12 (site 1) and 1.66 (site 3) in January, and from 2.71 (site 1) and 2.01 (site 4) in February (see Table 3). The ART values at sites 1 and 2 in January are very close (20.75–21.44, see Table 3), but differ drastically from that of site 3, where a short residence time of 7.2 days was computed. This index varies marginally, from 16.33 to 17.79, between sites during February. The difference between months, particularly at sites 1 and 2, is noteworthy. Both ART and APL values at sites 1 and 2 are longer during January than February.

The carbon flow networks for each site and month were mapped into simplified Lindeman Spines and illustrated in Figure 2. The first trophic level consists of primary producers and detritus combined, and includes that portion of consumer demand dependent on imports. Returns to the detrital pool from each integer trophic level are also shown, as well as external inputs and detrital production from plants in the first level. The flow of energy from one level to the next is also shown, whilst the trophic efficiency, defined as the fraction of total carbon received at one level that is passed on to the next one, is given as percentages in the boxes. Respiration and exports from each level are also indicated. Nine to 10 trophic levels were identified for each of the models with the trophic efficiencies generally decreasing with ascending levels. The exception is at site 3 in January, where the efficiency of energy transferred from the first level to the second was low (4.2%) compared to other sites and months, due to the high production of *Halodule*

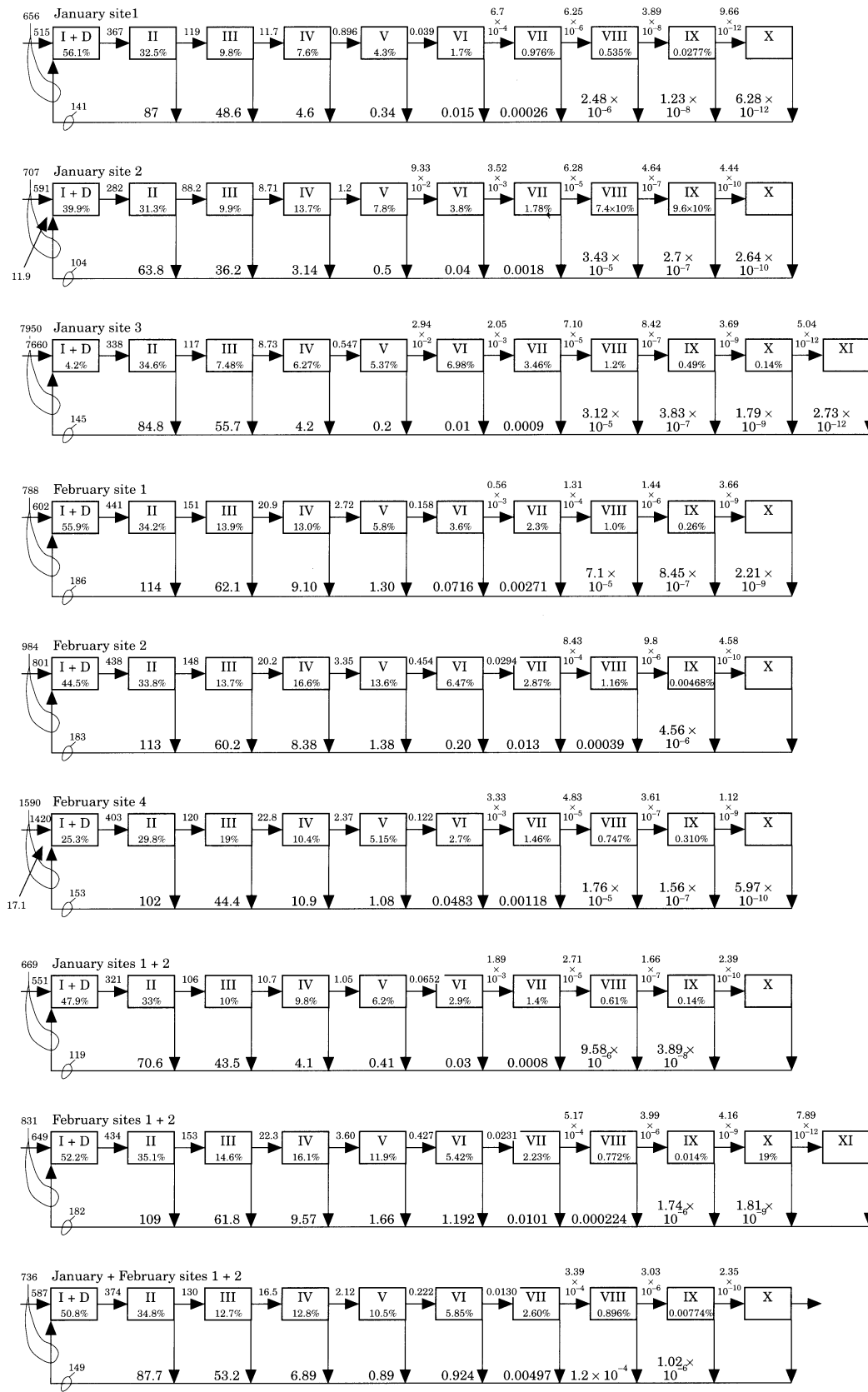


FIGURE 2. Lindeman Spines for each network of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida. Numbers over arrows indicate the biomass flux ( $\text{mgCm}^{-2} \text{ day}^{-1}$ ) between trophic levels (upper line) and into detrital pool (lower line). The percentages in each box indicate the trophic efficiency of carbon transfer between levels.

and micro-epiphytes and the proportionally lower grazing rate relative to the high production. At most sites the highest transfer efficiencies occur at the first three to four trophic levels. The logarithmic mean system efficiencies for the individual spines, including the lower nine trophic levels, are given in Table 3. These efficiencies differ marginally from site to site and from month to month, with the exception of site 1 in January, where this efficiency was the lowest at 2.9%. The mean efficiency for sites 1 and 2 is, however, higher by about 34% in February (5.58) compared to January (4.14). There are also clear differences in this attribute between stations in the same month. The difference in trophic efficiencies are even more accentuated if they are calculated for only the first five trophic levels between which the bulk of transfers occur. The mean efficiencies then are 11% for January and 15% for February; suggesting an increase in efficiency between months of about 35%.

#### *Structure and magnitude of cycling*

The cycling of material and energy is recognized as an important function and universal characteristic of natural ecosystems, contributing to their autonomous behaviour (Ulanowicz, 1986). Cycling occurs through a number of cycles of different path lengths, and materials are considered to cycle more slowly through longer path lengths, whilst short path lengths indicate fast cycling rates (Baird & Ulanowicz, 1989).

Three aspects of cycling are considered here, namely: (1) the cycling structure, i.e. the number of cycles and their distribution against cycle length; (2) the amount of material cycled over different path lengths; and (3) the FCI. The number of cycles at individual sites varied from 373 at site 3 in January to 990 at site 1 in February (see Table 3). The distribution of the number of cycles per nexus is given in Table 4, which shows that more than 50% of cycles are clustered in nexuses containing >20 cycles at each site and month. Only at site 2 in February was a smaller fraction (42%) of the cycles distributed in larger nexuses. Some nexuses contained as many as 128 cycles (February, site 1; Table 4). At most sites, however, the larger nexuses contained less than 80 cycles. The weak arc in most of the large nexuses (>20 cycles) occurred between compartments 38 (spot) and 42 (killifish), between 37 (pinfish) and 42 (killifish), and between 14 (meiofauna) and 26 (deposit-feeding polychaetes). Large nexuses also contained, in general, longer cycle pathways, often including higher predator compartments. Single cycle nexuses comprise between 3.4% (February, site 1) and 7.6% (February, site 4) of all cycles. The paucity of single

cycle nexuses, involving three to four compartments, and the greater frequency of large cycle nexuses indicate a rather complex cycling structures at each ecosystem site. In contrast to the cycles in large nexuses, single cycle nexuses usually involve only benthic compartments, particularly benthic bacteria (12), micro-fauna (13), meiofauna (14) and sediment POC (51). Of interest is that during both months and at all sites, the vast majority of cycles begin and end in sediment POC (51) and involve benthic bacteria (12). Even long cycles which include top level predators follow this pattern. Benthic interactions are thus of particular importance, whereas cycling via grazing pathways plays a small part in these systems.

The amount of recycled carbon over various path lengths is shown in Table 5, which show that the path lengths of recycling involve from two to as many as 11 compartments. Long cycle pathways (six compartments or more), occurred at all sites and both months. Most of the recycled flow occurred over loops involving two to five compartments, and the largest proportion (>50%) of cycled flow took place with path lengths of 3 or more.

The FCI indices varied considerably between sites in the same month and between the same site in different months (see Table 3) and were considerably higher in February, than in January. This index was also much lower at the St Marks river-dominated sites 3 and 4, than at the Goose Bay sites. This index was particularly low (1.9%) at site 3 in January, coinciding with high production and standing crops of *Halodule* and micro-epiphytes. The total amount cycled there ( $389 \text{ mgCm}^{-2} \text{ day}^{-1}$ ), however, was of the same order as cycled elsewhere, but the high TST value for that site resulted in the low FCI. Individual site values of FCI, as well as the mean monthly values (for sites 1 and 2 only), are consistently higher in February, but considerably lower compared to reported FCI values for other coastal systems (cf. Baird & Ulanowicz, 1989, 1993; Baird *et al.*, 1991).

#### *System-level attributes*

Global measures of system organization, e.g. TST, C, A, Overheads, Rd, Flow diversity and Connectance, of each month and site are given in Table 3. The TST, C and A were consistently higher during February than in January, as is the case with other system properties such as flow diversity, system trophic efficiency, APL and FCI. Most of these indices, however, were either lowest or highest at sites 3 and 4 in January and February, respectively. For example, the TST, C and A values were highest at sites 3 and 4, whereas others such as flow diversity and

TABLE 4. Cycle analysis: percentage distribution of cycles per nexus at of each network of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida

Cycles/ nexus	Jan S1 (%)	Jan S2 (%)	Jan S3 (%)	Feb S1 (%)	Feb S2 (%)	Feb S4 (%)	Jan S1 & S2 (%)	Feb S1 & S2 (%)	Mean Jan & Feb (%)
1	6.0	4.3	5.6	3.4	4.9	7.6	5.4	3.4	3.6
2	4.5	3.4	7.0	3.0	3.6	3.7	3.9	2.8	3.4
3	2.8	2.6	2.4	1.5	4.3	2.2	3.0	2.7	3.7
4	11.3	6.8	7.5	1.2	6.5	3.7	6.6	4.0	3.0
5	0.0	0.9	1.3	0.5	0.0	3.7	0.8	0.0	0.9
6	1.1	3.1	3.2	2.4	2.2	3.3	3.9	3.6	3.4
7	2.6	0.0	0.0	3.5	1.3	0.0	2.3	0.7	0.0
8	3.0	9.6	2.1	0.8	2.9	0.0	2.6	0.8	0.8
9	1.7	0.0	0.0	1.8	1.6	1.7	1.5	1.8	2.6
10	0.0	3.4	0.0	2.0	1.8	1.8	1.6	0.0	0.0
11	0.0	0.0	2.9	0.0	2.0	4.1	3.6	0.0	1.0
12	2.3	2.1	3.2	3.6	6.5	0.0	0.0	3.6	3.4
13	0.0	0.0	0.0	1.3	2.3	0.0	0.0	0.0	0.0
14	2.6	7.2	0.0	1.4	2.5	2.6	2.3	1.4	1.3
15	5.6	0.0	0.0	1.5	0.0	0.0	4.9	3.0	4.3
16	3.0	0.0	4.3	1.6	2.9	3.0	0.0	1.6	1.5
17	0.0	0.0	0.0	0.0	3.1	0.0	2.8	1.7	0.0
18	0.0	0.0	0.0	1.8	3.2	6.7	0.0	1.8	5.1
19		0.0	0.0	0	3.4	3.5	0.0	0.0	0.0
20		3.4	0.0	4.8	3.6	0.0	0.0	2.0	0.0
	[26] 4.9	[24] 8.2	[22] 5.9	[24] 2.0	[22] 4.0	[22] 4.1	[21] 3.5	[21] 2.1	[21] 2.0
	[60] 22.6	[30] 5.1	[36] 9.7	[25] 2.5	[24] 4.3	[31] 5.7	[22] 10.9	[31] 3.1	[22] 4.2
	[62] 11.7	[32] 5.5	[39] 10.5	[26] 2.6	[31] 5.6	[32] 5.9	[24] 3.9	[34] 3.2	[23] 2.2
	[75] 14.1	[42] 7.2	[48] 12.9	[30] 3.0	[34] 12.2	[36] 6.7	[27] 4.4	[34] 3.4	[26] 2.5
		[63] 10.8	[80] 21.4	[60] 6.1	[36] 6.5	[40] 7.4	[33] 5.4	[36] 3.6	[27] 2.6
		[96] 16.4		[68] 6.9	[52] 9.4	[47] 8.7	[42] 6.9	[40] 4.0	[29] 2.7
				[74] 7.5		[76] 14.1	[44] 7.2	[40] 4.1	[30] 8.5
				[78] 7.9			[75] 12.3	[42] 4.2	[33] 6.2
				[120] 12.1				[46] 4.5	[36] 3.4
				[128] 12.9				[62] 6.2	[50] 4.7
								[65] 6.5	[52] 4.9
								[206] 20.4	[54] 5.1
									[57] 5.4
									[81] 7.6
Total no	531	584	373	990	555	541	608	1006	1058

Cycle/nexus categories that are greater than 20 are shown below each network in brackets.

FCI were lowest there compared to sites 1 and 2 during the same month. The ecosystem at these two river-dominated sites appears to behave quite differently from the two Goose Bay stations.

The relative ascendancy ratio,  $A/C$ , varies to a greater degree between sites in January than February and is particularly high at site 3 in January (see Table 3). Values for the internal capacity ( $C_i$ ), ascendancy ( $A_i$ ) and redundancy ( $R_i$ ) are also given in Table 3. The normalized ratios ( $A_i/C_i$  and  $R_i/C_i$ ) differ between sites and months within a remarkably narrow range of about 6%. They also increased consistently at all sites in relation to the  $A/C$  ratios, with the exception of site 3 in January, where the  $A_i/C_i$  ratio declined by about 13%. Relative and normalized  $A/C$  ratios are

considered to be suitable indices for intersystem comparisons (Mann *et al.*, 1989; Baird *et al.*, 1991). Here, lower values in February indicate a lesser degree of organization than during January. The normalized internal redundancy ratio ( $R_i/C_i$ ), a measure of system stability (Rutledge *et al.*, 1976; Christensen, 1995) differed marginally between sites and months.

Other important system-level properties, e.g. flow diversity and connectance indices, are also given in Table 3. Of interest is the flow diversity ( $C/TST$ ) index which measures the number and evenness of interactions in a system, which was lower during January than February at all sites and also lower at St Marks River sites 3 and 4 than at the Goose Creek Bay sites 1 and 2. Higher indices in February indicate a

TABLE 5. Cycle analysis: Percentage of cycled flow through loops of various path length of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida

Path length	Jan S1		Jan S2		Jan S3		Mean Jan		Feb S1		Feb S2		Feb S4		Mean Feb		Mean Jan & Feb	
	(mgC)	(%)	(mgC)	(%)	(mgC)	(%)	(mgC)	(%)	(mgC)	(%)	(mgC)	(%)	(mgC)	(%)	(mgC)	(%)	No.	(%)
1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0
2	66.0	19.0	75.7	30.4	64.4	16.6	65.4	22.5	61.3	13.0	70.3	15.5	76.6	21.3	66.8	14.5	65	17.3
3	197.0	56.6	121.0	48.6	235.0	60.4	151.0	51.8	273.0	57.7	243.0	53.5	116.0	32.3	243.0	52.6	196	51.6
4	73.8	21.2	42.1	16.9	81.9	21.1	66.2	22.7	99.6	21.1	94.3	20.7	144.0	40.1	101.0	21.9	89	23.5
5	10.6	3.0	9.3	3.7	7.1	1.8	7.9	2.7	29.0	6.1	34.7	7.6	20.7	5.8	39.1	8.5	16	4.2
6	0.4	0.1	0.9	0.4	0.4	0.1	0.7	0.2	6.6	1.4	10.5	2.3	1.0	0.3	9.0	1.9	3	0.9
7	0.3	0.1	0.1	0.0	0.1	0.0	0.1	0.0	3.3	0.7	1.4	0.3	0.5	0.1	2.5	0.5	1	0.4
8	4E-02	0.0	2E-03	0.0	2E-04	0.0	3E-03	0.0	0.3	0.1	0.2	0.1	1E-02	0.0	0.2	0.0	8	2.1
9	3E-05	0.0	3E-04	0.0	1E-05	0.0	2E-06	0.0	2E-03	0.0	4E-02	0.0	3E-04	0.0	2E-02	0.0	0	0.0
10	5E-10	0.0	1E-08	0.0	1E-07	0.0	0.0	0.0	9E-05	0.0	9E-05	0.0	4E-07	0.0	2E-04	0.0	4E-0	0.0
11					3E-10	0.0	2E-09	0.0	2E-09	0.0	2E-09	0.0	2E-09	0.0	5E-09	0.0		
Sum of cycled flow	348.2	100.0	249.1	100.0	388.9	100.0	291.3	100.0	473.1	100.0	454.5	100.0	358.8	100.0	461.6	100.0	380	100.0

Flows are in  $\text{mgCm}^{-2} \text{day}^{-1}$ .

larger number of interactions and also a greater evenness in the flow structure. As flow diversity is derived from logarithmic indices of complexity, small differences in the value of this index reflect much larger qualitative disparities (Baird & Ulanowicz, 1993).

Three connectance indices are listed in Table 3. These indices vary between sites during months and appear to be generally lower at the river-dominated sites (3 and 4) than at the Goose Creek Bay sites (1 and 2). Only the food-web connectance index at site 4 was higher than at sites 1 and 2. The general trend, namely of higher connectance values from January to February (see Table 3) points to an increase in the magnitude of links between living compartments in February, contributing to a possibly more complex system.

## Discussion

With a growing interest in comparative ecosystem ecology some studies have dealt with ecosystem development on temporal scales, whilst others compared systems on global spatial scales. The common thread in these investigations was the search for common quantifiable properties, or goal functions, of ecosystems which can be used universally in comparative ecosystem studies. Although a large number of indices or functions have been proposed as goal functions, agreement amongst ecologists has yet to be reached, probably due to system complexity (Christensen, 1995). The authors do not attempt in this paper to assess the validity of system indices, but rather the degree to which spatial and temporal differences in ecosystem dynamics are reflected in a suite of structural and system level attributes is explored. The authors used network analysis to calculate system-level attributes and conventional methods to determine most of the structural properties of the St Marks National Wildlife Refuge seagrass ecosystem.

The network models constructed represent 'sub-units' of the St Marks Refuge ecosystem over space and time. Since these subsystems have essentially the same physical, chemical and biological characteristics, differences in system dynamics that may occur over space and time could be subtle and not easily detected. The analyses have produced a substantial amount of information on the variation in a number of indices given in Tables 2 and 3.

An inspection of Table 3 clearly shows differences in system properties between sites (spatially) and months (temporally). These results also show clear differences between the two Goose Creek Bay sites 1 and 2, and the two St Marks River dominated sites 3

and 4. The latter two sites were exposed to a variable salinity regime, whereas salinity remained fairly constant at the Goose Creek Bay sites. Several studies have demonstrated the impact of variable salinity on the composition and productivity of estuarine communities (cf. Jones *et al.*, 1990; Baird & Heymans, 1996). Mannino and Montagna (1997) recently reported on the variation in macrobenthic invertebrate community structures and the importance of salinity in the process of structuring such communities. The authors have made similar observations on community variability on large spatial scales in the St Marks Refuge ecosystem seagrass ecosystem. The influence of the different salinity regimes showed up in a wide spectrum of system properties.

Differences in community structure and system properties were also observed on a temporal scale in the St Marks Refuge seagrass ecosystem (see Table 3). The main reasons for the month-to-month variations are: (1) an increase of 5 °C in the average water temperature and the effect of this on respiration and growth of resident species; and (2) the immigration of fish and birds. The increases in biomass and carbon flow rates are clearly reflected in the TST and other system level attribute values. Numerous studies have reported on the variability in the complexity of physical, chemical and biological structures of ecosystems or components thereof due to changes in ambient temperature. For example, Baird and Ulanowicz (1989), Baird *et al.* (1995) and Warwick and Radford (1989) have shown large swings in C and N dynamics between seasons in the Chesapeake Bay ecosystem and Lyhner Estuary respectively, while Vezina *et al.*, (1995) recorded increased system activity in the St Lawrence Estuary due to a small increase in the ambient temperature of about 3 °C.

Other significant studies of seagrass ecosystems in North Florida have been conducted by Livingston and his students at the Florida State University. Some of the results of the authors' network analyses can be interpreted in the light of their findings. *Halodule wrightii* infaunal densities decline as fish densities increase during the period from the winter months (January and February) through the summer months (June, July), suggesting that fish predation has a major impact on the benthic community (Sheridan & Livingston, 1983). The two epibenthic fishes with the greatest biomass that consume infauna and meiofauna in the *H. wrightii*-dominated estuary at St Marks are pinfish (37) and spot (38). Livingston (1982) also demonstrated that in a nearby estuary in Apalachee Bay (the Ecofina River ecosystem), the density of pinfish and spot of the same size range as reported here, were negatively correlated with salinity. Thus,

TABLE 6. Per cent shift in TST, C, A and overheads at sites 1 and 2 from January to February at the St Marks National Wildlife Refuge

Attribute	Site 1	Site 2
	Jan to Feb	Jan to Feb
TST	+20	+37
C	+26	+58
A	+23	+34
Overhead on imports	+44	+113
Overhead on exports	+92	+60
Overhad on respiration	+15	+54
Redundancy	+26	+74
P/B day-1 ratio	+16	+23
FCI	+13	+33
A/C	-3	-15
Ai/Ci	+2	-11

+, increase; -, decrease.

TST, total system throughput; C, development capacity; A, system ascendancy; P/B production/biomass; FCI, Finn cycling index; Ai/Ci, internal ascendancy/internal development capacity.

differences observed between the Goose Creek Bay stations, where salinity was high and constant, and the St Marks River dominated stations, where salinity was low and variable, could have greatly influenced the abundance of these two important epibenthic predatory fishes, with corresponding and cascading trophic level effects on the behaviour of the entire system. Indeed, the biomass of pinfish and spot combined was lowest in the high salinity areas in these studies [3.24 and 47.49 mgCm<sup>-2</sup> at Station 1 (January) and Station 2 (January); 33.63 and 282.16 mgCm<sup>-2</sup> at Station 1 (February) and Station 2 (February), respectively] and greatest at the St Marks river-dominated stations [60.86 mgCm<sup>-2</sup> at Station 3 (January) and 1573.92 mgCm<sup>-2</sup> at Station 4 (February), respectively]. The increase in biomass at all stations from January to February of these two species also parallels the seasonal increase observed

for these species by Livingston (1982) and Sheridan and Livingston (1983). The authors suggest that these two predatory fish components may have a disproportionate impact on the benthic macrofaunal and meiofaunal compartments, accounting for some of the difference observed among stations and months. These patterns may be examined in more detail using mixed trophic impact analysis in the future (Ulanowicz and Puccia, 1990).

The percentage shift in magnitude of selected system-level properties such as TST, C, A and overheads from January to February at the two Goose Creek Bay sites are shown in Table 6. The table shows a general increase from January to February at both sites, with the exception of the A/C and A<sub>i</sub>/C<sub>i</sub> ratios. The A/C ratio declined at both sites in February as did the A<sub>i</sub>/C<sub>i</sub> at site 2. The reason for the higher A/C and A<sub>i</sub>/C<sub>i</sub> ratios in January is that although the absolute values of C and A were higher in February, the overheads (on imports, respiration and exports) and redundancy (R), were also collectively higher by about 28 and 49% in February at sites 1 and 2 respectively.

It is clear that the magnitude of the various attributes listed in Table 6, including cycling and the Pr/B ratio, are strongly influenced by the total activity, or TST, of the system. By dividing these capacities, (C, A and overheads) by TST, the resultant normalized values, given in Table 7, are scaled to remove the singular effect of TST (cf. Baird & Ulanowicz, 1989). The normalized capacity is higher at both sites in February, but the ascendancy is lower at site 2 in February. All the overheads have increased from January to February at both sites, with the exception of the respiration overhead at site 1 and export overhead at site 2. The decrease in the dimensionless A/C and A<sub>i</sub>/C<sub>i</sub> ratios, considered indices of 'system maturity' (cf. Mann *et al.*, 1989; Baird *et al.*, 1991; Christensen, 1995) from January to February indicate that the carbon-flow dynamics in February are more dissipative and less organized than during the

TABLE 7. Trends in the normalized system-level attributes at sites 1 and 2 during January and February at the St Marks National Wildlife Refuge, Florida

Attribute	Site 1		Site 2	
	January	February	January	February
Capacity	5.38	5.68	4.65	5.35
Ascendancy	1.80	1.84	1.83	1.78
Overheads on imports	0.69	0.83	0.47	0.73
Overheads on exports	0.11	0.17	1.18	0.21
Overheads on respiration	1.15	1.11	0.89	0.99
Redundancy	1.63	1.72	1.29	1.64



preceding cooler, but less active month. Similar observations were made in the Chesapeake Bay for carbon and nitrogen dynamics in different seasons (Baird & Ulanowicz, 1989; Baird *et al.*, 1995).

Networks and network analysis have tended to be treated in a deterministic way with little regard to the amount of variation associated with either the input variables or output indices. This in part has been due to the large amount of information that is required and the inability to obtain this information from one concerted sampling effort, and this study has allowed us to make a limited evaluation of variability. The authors have calculated coefficients of variation (CVs) on some aggregate measures of model input and model attributes for averages of independent samples gathered at sites 1 and 2 during January and February (yielding a sample size of four), and using all sites in both months (giving a sample size of six) [Figures 3(a,b)]. In Figure 3(a) the top six rows represent the CVs of biomasses of aggregated taxonomic or ecological groupings. Fish and bird biomass vary greatly in the four site average (highest CVs), reflecting immigration from January to February. When all six sites are used, the large biomass of *Halodule* at sites 3 and 4 greatly increases the relative variability of primary producers and total biomass. As might be expected, biomasses of individual species (not shown) can have CV values that exceed the highest values of the aggregated biomasses. Assorted measures of diversity (next three rows), have similar CV ranges for both four and six sites. But in the next and last group of Figure 3(a), which represents simple aggregate calculations of flow, large differences are evident between the small CVs of the Goose Creek Bay sites and the high CVs of all six sites. All the CV values in Figure 3(a), associated with inputs, community structure or simple calculations of flow, are above 10% and 11 exceed 50%.

The 16 rows in Figure 3(b) include attributes from network analysis. For the four Goose Creek Bay sites, five of these attributes have CVs less than 10% and none is above 41%. The lowest relative variability is associated with detritivory, normalized ascendancy measures, flow diversity and food-web connectance. The highest is associated with overheads of import, export and respiration. The low variability associated with detritivory and food-web connectance may reflect a relatively stable detrital food-web which is coexistent with a more variable grazing food web. The former's stability may in part be due to the dominance of microbial processing of detritus and the authors' inability to partition microbes and meiofauna into smaller categories. The relative stability of the normalized ascendancy

measures may reflect covariance of the various components. In contrast, many of the CVs for six sites are considerably higher than for four sites, reflecting the previously noted differences between Goose Creek Bay and St Marks River sites.

The authors can make several inferences from the findings of CV variation. It can be expected that system-level attributes derived from network analysis would generally have less relative variation than at least some input variables; an observation in keeping with hierarchy theory (Pattee, 1973; Allen & Starr, 1982). This appears to be true when only the four Goose Creek Bay sites are considered but not necessarily with all six sites, and This may reflect the fact that the four Goose Creek Bay sites are more representative of the same seagrass habitat than the two river-dominated sites. However, not all attributes would be expected to have the same relative variability. Thus, in comparing networks, what may be considered a significant difference between means of one attribute may not be for another. Attributes with the smallest CVs calculated for four sites but with high CVs when six sites are averaged may be good candidates for evaluating differences between networks. Therefore it is suggested that several attributes that fit this category, although not all possible ones are listed; total living biomass, sum of NPP, sum of respiration, TST, Pr/B, detritivory, ART, FCI, redundancy, A/C, flow diversity and food-web connectance are of general significance and may be particularly useful. In this study, each of these have a coefficient of variation less than 25% for the Goose Creek Bay sites a larger CV for all sites.

The percentages are for small-scale differences in time and location. Thus, those CVs listed for the four sites in Figure 3(a,b) may be taken as near the minimum values for networks of natural ecosystems. Networks that include greater scope in sampling may be expected to have higher values for CVs.

Unfortunately, the lack of analyses of variability in the literature prevents statistical comparisons of networks. Several studies reported on a range of system attributes of a variety of ecosystems measured on various temporal and spatial scales (cf. Wulff *et al.*, 1989; Baird *et al.*, 1991; Baird & Ulanowicz, 1993; Christensen, 1995). A comparison of a few of the attributes mentioned above between the St Marks seagrass ecosystem and those of other coastal systems is shown in Table 8. The table shows that the values (means of sites 1 and 2 for January and February) calculated for St Marks, fall well within the reported range, with the exception of the FCI and flow diversity indices which are, respectively, lower and higher than those of the other ecosystems.

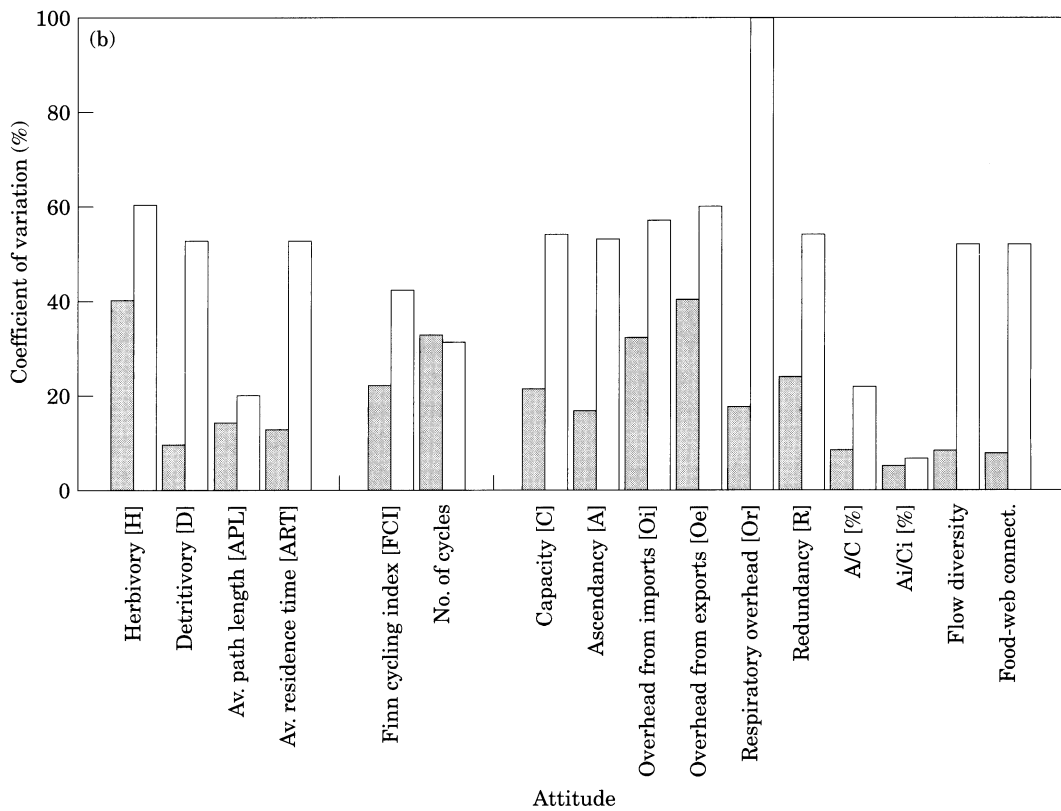
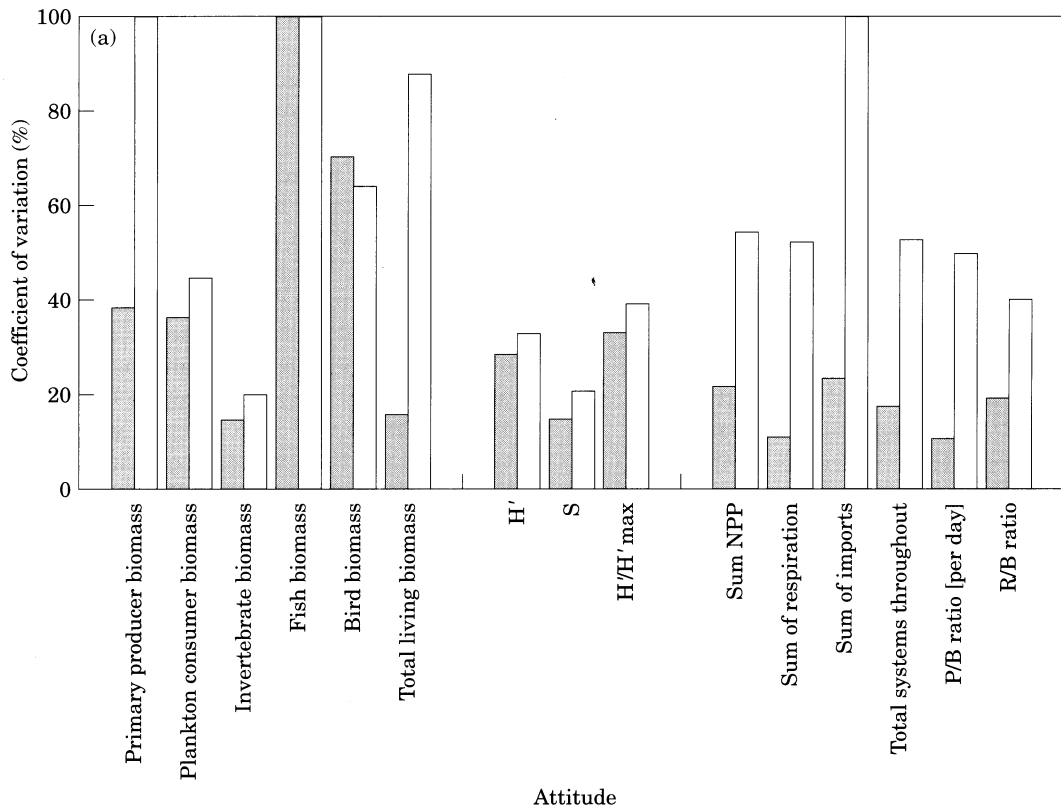


FIGURE 3. (a) Illustration of coefficients of variation in structural attributes of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida. Four sites (shaded columns), Jan S1 & 2, Feb S1 & 2; 6 sites (unshaded columns), 4 sites + averages for January and February. H', Shannon–Weiner diversity index; S, species richness; H'/H' max, Shannon–Weiner index (evenness); NPP, net primary production; P/B production/biomass; R/B, respiration/biomass. (b) Illustration of coefficients of variation in system level attributes of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida. Four sites (shaded columns), Jan S1 & 2, Feb S1 & 2; 6 sites (unshaded columns), 4 sites + averages for January and February.

TABLE 8. Comparison of selected system-level attributes between coastal ecosystems

Attribute	Ecosystem						
	Chesapeake Bay	Swartkops Estuary	Ems Estuary	Baltic Sea	Ythan Estuary	Kromme Estuary	St Marks
FCI	22	44	30	23	25	26	18
A/C	50	28	38	56	34	34	38
P/B day	0.14	0.01	0.04	0.08	0.01	0.002	0.04
Flow diversity	2.9	3.6	4.6	3.1	4.1	3.5	5.46
D:H ratio	5:1	1.5:1	0.5:1	1.5:1	10:1	7:1	1.8:1

FCI, Finn cycling index; A/C, ascendancy/development capacity; P/B, production/biomass; D:H, herbivory/detrivory ratio.

Although the distances between sample sites and time differences between samplings of the seagrass ecosystem discussed here are small, variation within attributes can be large or small depending on the attribute. Data from other seasons may well reveal even greater variability in the system's dynamics on a larger scale. It would, however, appear that the aggregation of information across time and space in the St Marks Refuge seagrass beds masked differences. The importance of such spatial and temporal differences to ecosystem behaviour and dynamics at the scale of ecosystem behaviour remains to be evaluated. This is one of the first studies examining the variability in ecosystem properties over small spatial and temporal scales. These results show that the large variability in input or structural data, is reflected in system level attributes at much smaller scales.

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