

Organizing and understanding a winter's seagrass foodweb network through effective trophic levels

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Abstract

Trophic structure of ecosystems is a unifying concept in ecology; however, the quantification of trophic level of individual components has not received the attention one might expect. Ecosystem network analysis provides a format to make several assessments of trophic structure of communities, including the effective trophic level (i.e. non-integer) of these components. We applied network analysis to a *Halodule wrightii* community in Goose Creek Bay, St. Marks National Wildlife Refuge, Florida, USA, during January and February 1994 where we sampled a wide variety of taxa. Unlike most applications of network analysis, the field sampling design was specific for network construction. From these data and literature values, we constructed and analyzed one of the most complex, highly articulated and site specific foodweb networks to be done. Care was taken to structure the network to reflect best the field data and ecology of populations within the requirements of analysis software. This involved establishing internally consistent rules of data manipulation and compartment aggregation. Special attention was paid to the microbial components of the food web. Consumer compartments comprised effective trophic levels from 2.0 (herbivore/detritivore) to 4.32 (where a level 4.0 represents 'secondary carnivory'), and these values were used to organize data interpretation. The effective trophic levels of consumers tended to aggregate near integer values, but the spread from integer values increased with increasing level. Detritus and benthic microalgae acted as important sources of food in the extended diets of many consumers. 'Bottom-up' control appeared important through mixed trophic impact analysis, and the extent of positive impacts decreased with increasing trophic level. 'Top-down' control was limited to a few consumers with relatively large production or biomass relative to their trophic position. Overall, ordering results from various network analysis algorithms by effective trophic level proved useful in highlighting the potential influence of different taxa to trophodynamics. Although the calculation of effective trophic level has been available for some time, its application to the evaluation of other analyses has previously not received due consideration. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Seagrass community; Network analysis; Effective trophic level; Carbon flow

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1. Introduction

Trophic structure is one of the primary ways by which ecologists organize communities and ecosystems. Although trophic levels are often considered as discrete integers (Lindeman, 1942); individual consumers, their populations or guilds often feed across several trophic levels (Odum and Heald, 1975). Thus, populations or guilds may have 'effective trophic levels' that are fractional (Odum and Heald, 1975; Levine, 1980). For example, a consumer that feeds as a herbivore (level 2) for 50% of its diet and as a primary carnivore (level 3) for 50% would have an effective trophic level of 2.50. The calculations are done by both of the most commonly used software packages for ecosystem network analysis; *ECOPATH II* (Christensen and Pauly, 1992) and *NETWRK4* (Ulanowicz, 1987).

Although effective trophic level has been used to characterize food webs, the full application of this classification has not been realized. Odum and Heald (1975) used it to group various taxa into common feeding categories. Other researchers have used it to compare trophic structures among ecosystems (e.g. Ulanowicz, 1984; Ulanowicz and Wulff, 1991). Recently, Pauly et al. (1998) applied the concept to evaluate fishery trends. It has even been used to examine theoretical issues of energy flow (Burns, 1989). The emphasis in all of these studies has been at the ecosystem level. Little effort has been expended on the actual interaction of specific components and their contribution to within-system regulation. Effective trophic level can be used as a scaling metric for other analyses to infer various attributes and contributions to trophodynamics. For example, populations with higher effective trophic levels would be expected to contribute less to the energetics of the ecosystem than those with lower levels. Deviations from this trend may indicate that a consumer is particularly important or unimportant to the food web. Also, the potential for top-down or bottom-up control may be related to a population's effective trophic level. In this report effective trophic level was used to organize a seagrass food web and investigate these issues in that context.

The seagrass communities along the coasts of the southeastern United States and the Gulf of Mexico support substantial populations of benthos, nekton and waterfowl (Zieman and Zieman, 1989). The primary producers in these communities may include several species of Submerged Aquatic Vegetation (SAV), their epiphytes, phytoplankton, benthic microalgae, and macroalgae. Birds and large fish represent important top consumers, and the relative importance of each organism may vary with season. In winter waterfowl are particularly abundant. The links between the primary producers and the top consumers are often poorly understood, with several trophic steps between producer and top consumers. These trophic steps may be mediated by microbes and animals in both sediments and water column. Ecosystem network analysis has been used to assess the foodweb interactions (Wulff et al., 1989; Christensen and Pauly, 1993). The links between primary producers and birds, a potentially important consumer group, is rarely included in complex network analyses (Baird and Ulanowicz, 1993; Biujse et al., 1993). An effort was made here to include these consumers and evaluate their potential roles in trophodynamics.

The foundation for our research has been a priori collection of data to support the construction and analysis of a winter's seagrass foodweb. Sampling was specifically designed for network construction and to be inclusive of the full range of trophic groupings (Luczkovich et al., 1997; submitted). We measured standing stocks of microbes, benthos, plankton, nekton, birds and organic carbon as well as selected flows and diets. The collection was a joint effort by us and staff of the National Wetlands Research Center, US Geological Survey (USGS). The focal ecosystem was the seagrass communities within Goose Creek Bay of St. Marks National Wildlife Refuge, St. Marks, FL, USA. Further, Livingston and coworkers have amassed considerable information on the ecology of the northern Gulf of Mexico and its coastal and estuarine ecosystems (Heck, 1979; Stoner, 1979, 1980; Livingston, 1980, 1982, 1984; Lewis and Stoner, 1981; Leber, 1983; Lewis, 1984; Luczkovich, 1987). From the field and laboratory studies and the literature, foodweb networks were

constructed and analyzed with ECOPATH II for winter 1994. Three broad objectives were identified with corresponding manuscripts. Luczkovich et al. (1997; submitted) addressed sampling design related to the needs for network construction following the guidelines of Cohen et al. (1993). In Baird et al. (1998) networks were reconstructed for analysis by NETWRK4 and evaluated for uncertainties of input and output variables with emphasis on systems-level attributes. In the present paper the trophic structure of the system is evaluated with special attention to

trophic position and potential importance of the different taxa in relation to position. Furthermore, the issue of adapting field data for network analysis is addressed.

2. Methods

2.1. Sample site and design

Sampling was conducted from January and February 1994. Three sites were sampled in each

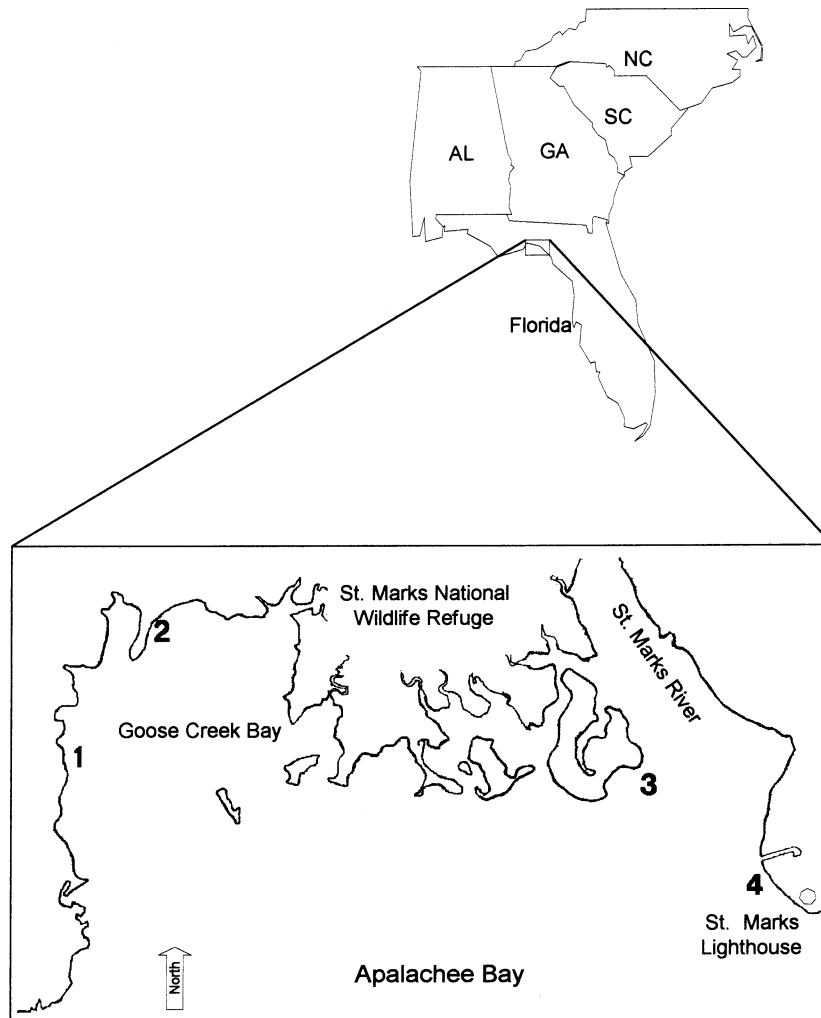


Fig. 1. Sample sites within St. Marks National Wildlife Refuge, St. Marks, Florida, USA. Numbered areas are sample sites.

month: in January sites 1, 2, and 3; in February sites 1, 2, and 4 (Fig. 1). Sites 1 (Live Oak Island) and 2 (Wakulla Beach) were within Goose Creek Bay and similar in community structure and hydrologic regime (Baird et al., 1998). Therefore, only they were used for this network construction and analysis. At each site sampling occurred at 3 transects, running perpendicular to the shore and extending through a *Halodule wrightii* community to approximately 150 m offshore. As a general minimum one sample was collected from each of the three transects within a site, but the different variables measured required different sampling procedures. Some variables were collected with much greater replication.

2.2. Sampling and sample analysis overview

Methods for field sampling and diet determinations are described in depth elsewhere by Luczkovich et al. (1997, submitted) and Baird et al. (1998). Here we give an overview.

Primary productivity and standing stocks of primary producers were estimated largely by USGS personnel directed by W. Rizzo and H. Neckles. Ground cover along transects at each site was determined with periodic biomass sampling. Biomass was divided by macrophyte species (above- and below-ground), microepiphytes, 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 productivities were estimated from changes in dissolved oxygen concentrations with incubation in light and dark.

Benthic bacteria and sediment organic matter were sampled at each transect by coring to 5 cm, and water samples were taken at each transect for dissolved and particulate carbon, bacterioplankton and planktonic microprotozoans. The densities of these organisms were estimated by epifluorescence microscopy with appropriate fluorochromes. During each month at Wakulla Beach, bacterioplankton growth and grazing rates were estimated by modification of the method of Landry and Hassett (1982).

Zooplankton samples were obtained with a 90 μm mesh plankton net and preserved. In the laboratory, the samples were sieved through a series of screens, and the contents of each screen were counted as various taxa. Sieve fractions were then dried at 60°C for 48 h and the biomass l^{-1} in the original sample calculated, using the counts to estimate proportional contribution of each taxonomic group.

Meiofauna were sampled by coring sediments, preserved, and later separated from sediment, sorted, identified to the lowest possible taxon, and enumerated. Dimensions of representative organisms were measured for conversion to biomass (Higgins and Thiel, 1988).

To estimate the standing stock of macroinvertebrates associated with seagrasses, 30 cores (7.62-cm inside diameter) were taken per site (Lewis and Stoner, 1981). The core samples were sieved through 500 μm mesh in the field and placed into jars with 10% formalin with rose bengal stain. In the laboratory, animals in the sieved portions were sorted and identified to taxonomic groups. Polychaetes were identified to family level. Amphipods, molluscs, decapod crustaceans and isopods were identified to species. Other invertebrate groups were identified as necessary. Biomass of each taxon was determined after drying. In the case of molluscs, ophuroids, polychaetes, isopods, decapods, and amphipods, ash-free dry masses were obtained by ashing representative samples and subtracting the mass of the remaining ash from the dry mass. All ash-free dry masses were converted to g carbon by multiplying by 0.45; for samples in which dry masses alone were determined, they were converted to g carbon by multiplying by 0.40 (Jørgensen et al., 1991).

A technique developed for this study, the barrier seine, and gill nets were used to sample fishes and large mobile decapods at each station. All fishes caught in both gill nets and seines were preserved in 10% formalin and taken back to the lab where they were identified, counted, and weighed.

Waterfowl standing stocks were estimated by surveys conducted during field campaigns and by D. Everette (The Florida State University, Department of Biological Science). Everette made

five trips to Wakulla Beach and Live Oak Island from 4 February to 14 March 1994. On each occasion and at each site, he counted birds within a $500 \times 500 \text{ m}^2$ area for 1 h.

To determine the structure of the diet matrix required for ECOPATH II, dietary analyses were conducted. Stomach content analysis was performed on the most common fish species found in the collections. Stomach contents of the fishes were analyzed following the sieve fractionation methodology of Carr and Adams (1972, 1973) as modified by Luczkovich and Stellwag (1993). In other cases, where fish samples were too small to conclude anything about diets, and for the invertebrate groups, estimates of dietary composition were obtained from the literature (see Baird et al., 1998).

2.3. Modelling and analysis approach

Biomass, given as mgC m^{-2} , was estimated for the various taxa collected in January and February from sites 1 and 2. Estimation came from either direct measurement of dry mass or conversion from density based on estimated dimensions of the organisms. Taxa were then organized to represent living compartments based on probable diet and life history characteristics. The 'detritus' compartment was the sum of sediment organic carbon and dissolved and estimated non-living particulate carbon in the water column. The conversion of volumetric to aerial data assumed a depth of 0.75 m for the water column and 5 cm for the sediment.

ECOPATH II was used for network analysis (Christensen and Pauly, 1992). Version 2.1 was used initially, but studies were completed with version 3.0 for Windows. The program required estimates of biomass (B) per compartment, Productivity: Biomass (PB), Consumption: Biomass (QB), fraction of unassimilated food, and/or some combined variable (e.g. Gross food conversion Efficiency (GE as PB/QB)). Some of these values were derived from field data, especially primary productivity of algae; but most came from literature. Three important sources were Christensen and Pauly (1993), Jørgensen et al. (1991) and Peters (1983). PB values for most poikilotherms

were derived from allometric relationships to body mass as summarized by Peters (1983) and lowered to 75% of annual values to correct for winter temperatures. QB values were then derived assuming set fractions of GE based on diet, where the fractions for detritivores, herbivores, omnivores and carnivores were 0.15, 0.20, 0.20, and 0.25, respectively. Homeotherms (birds) were assumed to produce 1.5% of body mass per day with food gross efficiencies of either 3 or 6% of consumption. Lastly, diet distributions were estimated for each consumer compartment from either gut analyses of field samples when available or the literature.

Ecosystem network analysis is actually a collection of mathematical algorithms to evaluate the structure of networks and ecosystems by inference. For this presentation interpretive efforts concentrated on evaluating trophic structure and the impacts of different organisms on trophodynamics. ECOPATH II outputs of effective trophic level (Levine, 1980), the mixed trophic impact matrix (Ulanowicz and Puccia, 1990) and omnivory index (Christensen and Pauly 1992) were used here. The algorithms for the three analyses are found in the cited references. Documentation for these and other algorithms within the ECOPATH II software are found in Christensen and Pauly (1992).

3. Results and discussion

3.1. Input variables and applying field data to network construction

A listing of the compartments used in the food-web network of a *H. wrightii* community in Goose Creek Bay averaged from January and February 1994 is presented in Table 1. There are 48 compartments. As with most representations of food webs, the living compartments represent different degrees of aggregation (Cohen et al., 1993). Compartments range from single species (e.g. 25 and 26) to a few species (e.g. 24 and 38) to large groupings of taxa, especially of small organisms (e.g. 1 and 3). Similarities in diet and habitat are the two main distinguishing characteristics for a

Table 1
Summary of compartments for ECOPATH II network^a

No.	Compartment name	Biomass (mgC/m ²)	PB (d)	QB (d)	Unassimilated food	Growth efficiency	Fraction imported
1	Benthic bacteria	262.50	0.2500	1.0000	0.10	0.25	
2	Microfauna	94.00	0.2000	0.6066	0.20	0.33	
3	Meiofauna	1038.50	0.0476	0.1590	0.50	0.30	
4	Bacterioplankton	10.90	1.5214	6.0855	0.00	0.25	
5	Microprotozoa	4.70	1.0000	3.1250	0.20	0.32	
6	Epiphyte-grazing amphipods	69.00	0.0103	0.0513	0.50	0.20	
7	Suspension-feeding molluscs	6.76	0.0073	0.0364	0.50	0.19	
8	Hermit crabs	178.52	0.0033	0.0222	0.50	0.14	
9	Spider crabs (herbivores)	0.07	0.0002	0.0012	0.50	0.15	
10	Omnivorous crabs	175.08	0.0007	0.0033	0.50	0.20	
11	Blue crabs	12.74	0.0008	0.0031	0.50	0.25	0.1
12	Isopods	61.22	0.0066	0.0328	0.50	0.20	
13	Brittle stars	370.83	0.0026	0.0129	0.50	0.20	
14	Deposit-feeding peracaridan crustaceans	73.60	0.0086	0.0570	0.50	0.15	
15	Herbivorous shrimps	24.58	0.0033	0.0165	0.50	0.20	
16	Predatory shrimps	50.66	0.0031	0.0126	0.50	0.25	
17	Catfish and stingrays	54.87	0.0025	0.0100	0.20	0.25	0.9
18	Tonguefish	1.44	0.0150	0.0599	0.20	0.25	
19	Gulf flounder and needlefish	35.14	0.0061	0.0243	0.20	0.25	
20	Southern hake and sea robins	9.34	0.0101	0.0402	0.20	0.25	
21	Atlantic silverside and bay anchovies	7.90	0.0105	0.0418	0.20	0.26	
22	Sheepshead minnow	8.39	0.0105	0.0700	0.20	0.16	
23	Killifishes	2.26	0.0126	0.0628	0.20	0.21	
24	Gobies and blennies	1.86	0.0183	0.0733	0.20	0.25	
25	Pinfish	2.44	0.0351	0.1402	0.20	0.25	
26	Spot	98.31	0.0289	0.1156	0.20	0.25	
27	Pipefish and seahorses	1.41	0.0267	0.1066	0.20	0.25	
28	Red drum	35.35	0.0026	0.0105	0.20	0.25	0.535
29	Deposit-feeding gastropods	974.93	0.0049	0.0325	0.50	0.15	
30	Predatory gastropods	283.36	0.0099	0.0496	0.50	0.20	
31	Epiphyte-grazing gastropods	6.46	0.0162	0.0811	0.50	0.20	
32	Other gastropods	15.49	0.0110	0.0549	0.50	0.20	
33	Deposit-feeding polychaetes	132.10	0.0104	0.0692	0.50	0.15	
34	Predatory polychaetes	84.16	0.0043	0.0170	0.50	0.24	
35	Suspension-feeding polychaetes	6.74	0.0129	0.0647	0.50	0.20	
36	Zooplankton	2.50	0.0660	0.3301	0.50	0.20	
37	Benthos-eating birds	1.89	0.0150	0.2400	0.25	0.06	0.02
38	Fish-eating birds	36.93	0.0150	0.2400	0.25	0.06	0.935
39	Fish and crustacean-eating birds	1.17	0.0150	0.2400	0.25	0.06	0.49
40	Gulls	7.17	0.0150	0.2400	0.25	0.06	0.855
41	Raptors	1.85	0.0150	0.2400	0.25	0.06	0.69
42	Herbivorous ducks	0.35	0.0150	0.2400	0.25	0.06	0.11
43	Halodule	4963.00	0.0020	0.0000	0.00		
44	Micro-epiphytes	259.90	0.7500	0.0000	0.00		
45	Macro-epiphytes	54.10	0.0300	0.0000	0.00		
46	Benthic algae	1073.50	0.0997	0.0000	0.00		
47	Phytoplankton	71.10	1.5000	0.0000	0.00		
48	Detritus	369500					

^a Average input values for winter 1994 in Goose Creek Bay, St. Marks National Wildlife Refuge, FL.

compartmental grouping. Details of groupings are described in Luczkovich et al. (1997) and summarized in Appendix A. Compartments are ordered numerically in the sequence with which data were entered into ECOPATH II. In general, the order is microbes, benthic and epiphytic arthropods and bivalves, fish, gastropods and polychaetes, zooplankton, birds and at the end primary producers and detritus.

Most taxa were found during both months. Catfish and stingrays (17), tonguefish (18), gulf flounder and needlefish (19), Atlantic silversides and bay anchovies (21), and gobies and blennies (24) were not found in January. Sheepshead minnow (22), red drum (28), and killifish (23) were not found in February. Herbivorous spider crabs (9) and herbivorous ducks (42) were not found in January. All of these were included in the winter's network. Values of zero were used for the month when the organisms were not present, and the zeros were averaged with values obtained for the month when the organisms were present.

The 48 compartments are associated with 333 individual transformations and transfers: 9 imports, 47 respirations, 230 feeding pathways, and 47 returns to detritus (Tables 1 and 2). Cohen et al. (1993) addressed the difficulty in presenting large food webs through box and arrow diagrams, indicating that graphical representations may be too complicated to be meaningful. Therefore, information used for network construction here is given in tabular form as required for analysis by ECOPATH II. The input variables in Table 1 include biomass, PB, QB, their ratio as gross efficiency, fraction of consumed food that is unassimilated, and fraction of consumption imported from outside the site. The diet matrix in Table 2 includes feeding pathways from all food sources to each consumer, as fractions of the consumer's diet. All consumers contributed to detritus through mortality, egestion and excretion.

As seen in Table 1 the largest biomass was in detritus, primarily because of sediment organic carbon. The primary producers, *H. wrightii* and benthic microalgae had biomasses greater than 10^3 mgC m⁻². The only consumers to have biomasses around 10^3 mgC m⁻² were benthic fauna: i.e. meiofauna and deposit-feeding gas-

tropods. As calculated for input to the network, PB and QB values generally were inversely related to body size, being highest in the plankton. Growth efficiencies for microbes and poikilotherms ranged from 0.14 to 0.33. The lower efficiency of 0.06 was used for birds.

Although the populations of organisms in the field fluctuated over time, construction of a steady state network was attempted. Steady state was considered achieved for any prey grouping that had an ecotrophic efficiency, i.e., fraction of production going to predation, harvest and export (Christensen and Pauly, 1992) of 1 or less. To do this, one has several choices for modification of a compartment's attributes; biomass, parameter ratios associated with metabolism, and food source. It was considered that the biomass data were the most reliable, as these were collected most directly. These data were not manipulated to achieve steady state. As described in the Methods section, rules for parameter ratios were internally consistent for all, or at least related, groupings, and these were not modified. Diet distributions, especially those from the literature, were subjected to the greatest manipulation because they were considered to be a flexible parameter. Diets often vary significantly across time and space in response to availability of different food items (Polis, 1995). If a prey grouping had an ecotrophic efficiency greater than 1 (i.e. predation exceeded production in the network), the diet distributions of its predators were altered to reduce predation on it. After all reasonable alterations of this kind, only three groups were allowed to remain slightly overgrazed; predatory shrimp (16), sheepshead minnow (22), and deposit-feeding gastropods (29) (Table 3).

As a first assumption, most organisms were considered to spend their time in the seagrass community or in similar communities. Thus, there was no import or export of material, unless dictated by the organism's energetic balance and biology. This appeared reasonable for many of the benthos and ichthyoplankton (Tolan et al., 1997). During the process of adjusting ecotrophic efficiencies of prey, it became evident that some predators could not be supported by the amount of prey measured within the system. These preda-

tors were either nekton or birds, which are quite able to leave the area within the time scale of minutes to hours. They all had high biomasses relative to their trophic position and high areal consumption rates (Table 3). Blue crabs (11), catfish and rays (17), and red drum (28) were the nekton groups, with the catfish and rays needing 90% of their diet imported (Table 1). Rays may actually eat more frequently within the community, e.g. feeding on polychaetes not readily sampled by our techniques (P. Wilbur, personal communication). All of the birds imported some carbon within a range varying from 2% for benthos-eating birds to 93.5% for fish-eating birds. The latter is largely the result of a flock of Amer-

ican white pelicans that were frequently found at the site for much of the winter. As a result of the importation of carbon associated with the steady state assumption, the significance of bird feeding on community structure could not be truly quantified.

Aggregation of species into trophic guilds is required for network analysis of most, if not all, natural ecosystems. This results from both the fact that identification and characterization of all species in an ecosystem are beyond the abilities of current science (Cohen et al., 1993; Polis, 1995) and the limitations of network analysis software (e.g. ECOPATH II has a limit of 50 compartments). Gardner et al. (1982) and Cale (1995) addressed

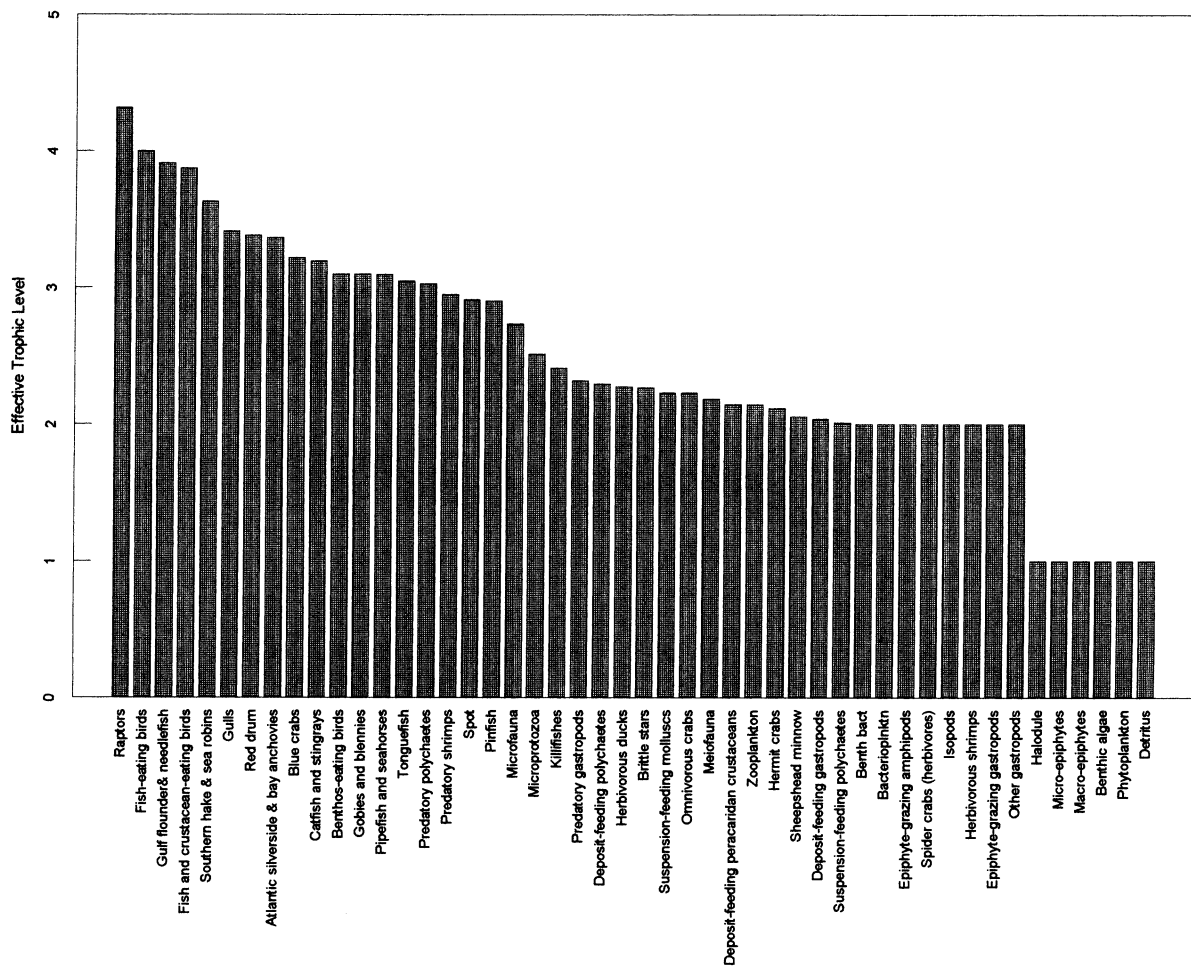


Fig. 2. Effective trophic levels of compartments in the winter's food web.

aggregation strategies and their consequences. Although more needs to be learned, they concluded that aggregation errors may be minimized when aggregation involves (1) components with similar turnover times, (2) parallel components, (3) components with common inputs and (4) components with common outputs. Aggregation of components in series may be more problematic. This would be especially true regarding trophic structure. In the network described here, care was taken to avoid aggregation of components in series (Luczkovich et al., 1997; submitted). The part of the St. Marks food web wherein this may be of greatest concern is the microbial community. However, identifying the trophic structure of the microbial food web is a general problem of investigation (Pomeroy and Wiebe, 1988; Christian, 1994). Several microbial compartments were incorporated into both the benthic and water column habitats at the St. Marks, and feeding among these compartments was included. The often hidden food web of microbes was thus made explicit which expands the number of trophic levels; however an uncertainty about this part of the web remains.

3.2. *Scaling by effective trophic level.*

Although others have computed effective trophic levels (e.g., Odum and Heald, 1975; Ulanowicz, 1984; Johnson et al., 1995), effective trophic levels have not been used to structure understanding of control and activity individual compartments, as done here. The compartments listed in Table 1 were reordered and ranked by 'effective trophic level' (Odum and Heald, 1975; Levine, 1980), as determined within ECOPATH II and listed in Table 3 with selected output variables. These variables include the effective trophic level; omnivory index; rates of consumption, production and respiration ($\text{mgC m}^{-2} \text{d}^{-1}$), and ecotrophic efficiency. The groups representing the highest trophic levels are listed at the top with levels descending to primary producers and detritus at the bottom.

Effective trophic level represents the continuous, rather than integer, trophic position of a compartment and is a good index by which com-

partments can be ordered for evaluation and comparison (Fig. 2). Effective trophic levels tended to cluster around integer values. Fifty per cent of the consumer compartments had effective trophic levels at or near a level of 2 (≤ 2.32) signifying the importance of herbivory and/or detritivory. There was then a small group which had values bridging levels between 2 and 3 (three compartments with levels from 2.41 to 2.74), a larger group near 3 (ten from 2.90 to 3.22), a smaller group of four from 3.37 to 3.63, and four predators with levels > 3.88 . Clustering near integer values may be the result of lack of trophic distinctions made for smaller, prey organisms or a product of the aggregation of compartments. Small organisms tend to be aggregated in food webs, whereas larger organisms are often identified to species or distinct guilds (Cohen et al., 1993). This certainly was the case here. Although distinctions were made between bacteria, protozoans and meiofauna, these groups encompass considerable variability in diets (Kemp, 1990; Sherr and Sherr, 1994). Fish and birds, however, were largely grouped to include one or a few species with similar diets and feeding habits.

The birds divide into a 'herbivorous' group (42) with level 2.28; benthic feeders (37) at 3.10; gulls (40) at 3.41; and three compartments of fish eaters (38), fish and crustacean eaters (39) and raptors (41) ≥ 3.88 . This assumes that feeding off site is comparable to that within the seagrass system. This may be a reasonable assumption for birds that feed in similar environments to the *Halodule* community. Some, however, may feed differently. Gulls may feed in landfills and dump areas. Raptors may feed on prey from terrestrial environments. The influence of such feeding is unknown. Therefore, the conservative interpretation is that the effective trophic levels of organisms that import considerable carbon are representative of their feeding within the system studied.

Two studies of coastal Florida ecosystems presented and discussed effective trophic levels. Odum and Heald (1975) evaluated the effective trophic structure of a mangrove ecosystem in south Florida. After correcting their values to make primary producers and detritus level 1, many of the comparable taxa between our two

Table 3
Selected output values for winter 1994 in Goose Creek Bay, St. Marks National Wildlife Refuge, FL

Number	Compartment name	Effective trophic level	Omnivory index	Productivity	Consumption (mgC m ⁻² d ⁻¹)	Respiration	Ecotrophic efficiency
41	Raptors	4.32	1.69	2.77E-02	4.43E-01	3.05E-01	0.00
38	Fish-eating birds	4.00	0.53	5.54E-01	8.86E+00	6.09E+00	0.00
19	Gulf flounder & needlefish	3.91	0.00	2.14E-01	8.54E-01	4.64E-01	0.59
39	Fish and crustacean-eating birds	3.88	1.06	1.76E-02	2.81E-01	1.93E-01	0.00
20	Southern hake & sea robins	3.63	0.18	9.43E-02	3.75E-01	2.05E-01	0.10
40	Gulls	3.41	0.65	1.07E-01	1.72E+00	1.18E+00	0.00
28	Red drum	3.39	0.83	9.28E-02	3.71E-01	2.14E-01	0.09
21	Atlantic silverside & bay anchovies	3.37	0.25	8.30E-02	3.30E-01	1.79E-01	0.53
11	Blue crabs	3.22	0.14	9.98E-03	3.97E-02	1.00E-02	0.90
17	Catfish and stingrays	3.20	0.42	1.37E-01	5.49E-01	3.02E-01	0.62
37	Benthos-eating birds	3.10	0.03	2.84E-02	4.54E-01	3.12E-01	0.00
24	Gobies and blennies	3.10	0.01	3.41E-02	1.36E-01	7.50E-02	0.08
27	Pipefish and seahorses	3.10	0.04	3.76E-02	1.50E-01	8.30E-02	0.14
18	Tonguefish	3.05	0.01	2.16E-02	8.63E-02	4.80E-02	0.00
34	Predatory polychaetes	3.03	0.12	3.59E-01	1.43E+00	3.79E-01	0.97
16	Predatory shrimps	2.95	0.31	1.59E-01	6.38E-01	1.65E-01	1.17
26	Spot	2.91	0.30	2.84E+00	1.14E+01	6.27E+00	0.59
25	Pinfish	2.90	0.28	8.55E-02	3.42E-01	1.88E-01	0.25
2	Microfauna	2.74	0.26	1.88E+01	5.70E+01	2.68E+01	0.54
5	Microprotozoa	2.52	0.27	4.70E+00	1.47E+01	7.05E+00	0.11
23	Killifishes	2.41	0.48	2.84E-02	1.42E-01	8.50E-02	0.23
30	Predatory gastropods	2.32	0.23	2.81E+00	1.40E+01	4.25E+00	0.00
33	Deposit-feeding polychaetes	2.30	0.27	1.37E+00	9.14E+00	3.24E+00	0.92
42	Herbivorous ducks	2.28	0.21	5.25E-03	8.40E-02	5.80E-02	0.00
13	Brittle stars	2.27	0.26	9.59E-01	4.78E+00	1.45E+00	0.03
7	Suspension-feeding molluscs	2.23	0.22	4.93E-02	2.46E-01	7.40E-02	0.23
10	Omnivorous crabs	2.23	0.22	1.14E-01	5.71E-01	1.58E-01	1.00
3	Meiofauna	2.19	0.21	4.95E+01	1.65E+02	3.27E+01	0.31
14	Deposit-feeding peracaridan crustaceans	2.15	0.16	6.33E-01	4.20E+00	1.47E+00	0.63
36	Zooplankton	2.15	0.16	1.65E-01	8.25E-01	2.48E-01	0.81
8	Hermit crabs	2.12	0.12	5.96E-01	3.96E+00	1.43E+00	0.55
22	Sheepshead minnow	2.06	0.06	8.81E-02	5.88E-01	3.78E-01	1.02
29	Deposit-feeding gastropods	2.04	0.05	4.75E+00	3.17E+01	1.12E+01	1.08
35	Suspension-feeding polychaetes	2.01	0.01	8.72E-02	4.36E-01	1.31E-01	0.90
1	Benthic bacteria	2.00	0.00	6.56E+01	2.63E+02	1.71E+02	0.79
4	Bacterioplankton	2.00	0.00	1.66E+01	6.63E+01	4.98E+01	0.42
6	Epiphyte-grazing amphipods	2.00	0.00	7.08E-01	3.54E+00	1.07E+00	0.86
9	Spider crabs (herbivores)	2.00	0.00	1.77E-05	8.84E-05	0.00E+00	0.00
12	Isopods	2.00	0.00	4.03E-01	2.01E+00	6.06E-01	0.28
15	Herbivorous shrimps	2.00	0.00	8.10E-02	4.05E-01	1.25E-01	0.78

Table 3 (Continued)

Number	Compartment name	Effective trophic level	Omnivory index	Productivity	Consumption (mgC m ⁻² d ⁻¹)	Respiration	Ecotrophic efficiency
31	Epiphyte-grazing gastropods	2.00	0.00	1.05E-01	5.24E-01	1.58E-01	0.02
32	Other gastropods	2.00	0.00	1.70E-01	8.50E-01	2.56E-01	0.53
43	Halodule	1.00	0.00	9.93E+00	0.00E+00		0.18
44	Micro-epiphytes	1.00	0.00	1.95E+02	0.00E+00		0.02
45	Macro-epiphytes	1.00	0.00	1.62E+00	0.00E+00		0.34
46	Benthic algae	1.00	0.00	1.07E+02	0.00E+00		0.74
47	Phytoplankton	1.00	0.00	1.07E+02	0.00E+00		0.07
48	Detritus	1.00	0.42				0.82

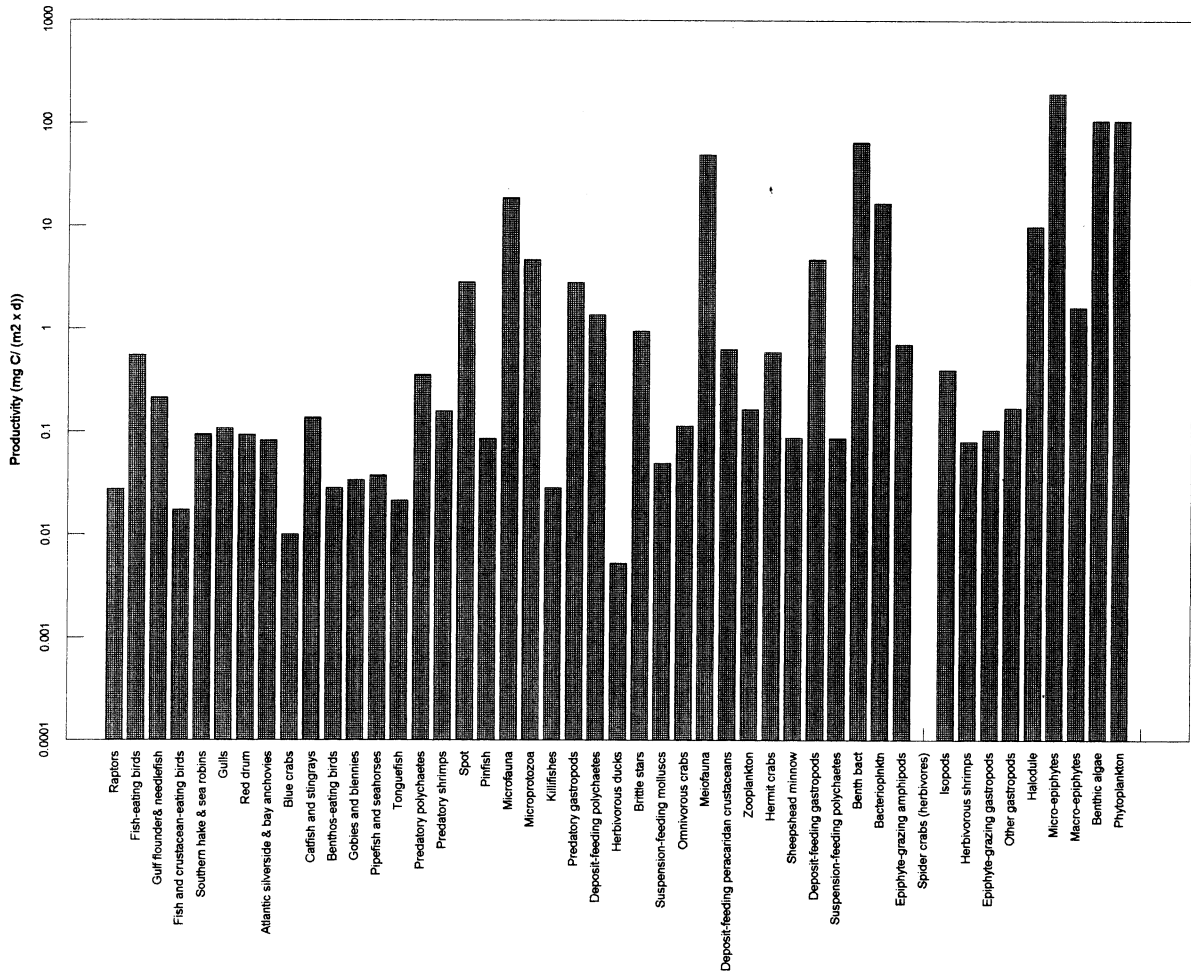


Fig. 3. Productivity of compartments ordered according to effective trophic level in the winter's food web.

systems had similar effective trophic levels. Bacteria and benthos clustered for both systems near level 2. Their smaller, young fish tended to have values similar to those presented here, but these fish groupings appeared to include more adult, small fish with higher values. This is reasonable as Odum and Heald (1975) did not restrict themselves to winter. Continuing up the food web, their top carnivores included raptors that had corrected effective trophic levels higher than for the St. Marks network. Thus, some of the differences may be the result of the timing and boundary conditions of the networks. Ulanowicz (1984) examined the effective trophic levels of 17

compartments in two networks from marsh gut ecosystems within the Crystal River, Florida, near St. Marks. His top carnivores had higher levels than reported here; over 40% of the compartments having a level of 4.0 or greater. Few compartments were at level 2. These results may be hard to compare. Ulanowicz did not recycle material to detritus at level 1; as is done in ECOPATH II, and as he has done in later analyses (Ulanowicz, 1987). Thus, detritus in his networks had trophic position greater than 2, which expanded the overall range.

Others have calculated effective trophic level as done here, including the authors represented in

the compilation of network analyses by Christensen and Pauly (1993). In general the range for the St. Marks' network was not unlike those reported in those studies. A number of ecosystems reported did not have levels above 4.0 (e.g. de la Cruz-Aguero, 1993; de Paula e Silva et al., 1993). Whether the differences are the result of the food webs or perceptions of them is not known. The major differences are that the number of compartments in the study presented here was larger than any reported in Christensen and Pauly (1993). Also, the reports in the compilation did not include explicit description of microbial processing of detritus. Hence the degree of aggregation for many of the compartments reported here is less and the potential for more trophic steps may be greater. Even when microbes have been explicitly included, effective trophic levels have rarely exceeded 4.0 (Baird and Ulanowicz, 1989; Johnson et al., 1995).

Within ECOPATH II and NETWRK4, primary producers and detritus are considered to have a trophic level of 1, and therefore energy cycling can not be tracked through differential trophic positions of detritus; i.e. the trophic level detritus is dependent on the level of the source organism (Burns, 1989). By assigning detritus different trophic levels, different trophic structure, and hence different effective trophic levels, are likely to emerge (Burns et al., 1991). The theoretical value of unfolding energy cycling (Patten, 1985) is not argued. But the position of Baird and Ulanowicz (1989) was adopted to accept what has become the more established calculation of detritus as level 1, as embodied within the available software.

In sampling for and constructing the current network, an emphasis was placed on microbial components associated with the detrital food web. If a consumer feeds on detritus, it also ingests the associated microbial community. The microbial community includes organisms that feed on the detrital substrate and on other members of the community. Unfortunately, little is known about the proportion of a detritivore's diet that comes from the detrital substrate, the microbes feeding on the detrital substrate, and microbial predators (Lopez and Levinton, 1987; Kemp, 1990; Sherr

and Sherr, 1994). Diets for detritivores were partitioned to include both detrital substratum and the associated microbial community. Fractions of diet among these compartments were largely in proportion to relative biomass (Table 2). If detritivores fed only on detritus, they would have an effective trophic level of 2.0. In this network, detritivores have effective trophic levels greater than 2.0, reflecting these perceptions of the microbial food web.

Near steady state canonical or integer trophic levels provide a general trend of decreasing areal productivity as trophic level increases (Lindeman, 1942; Ulanowicz and Kemp, 1979). Fig. 3 shows these general trends for effective trophic levels but with notable exceptions. Some groups with low effective trophic levels are rare and therefore have low productivity values. Rare taxa at low trophic levels, such as spider crabs (9), would not be out of the ordinary. Individual taxa (or compartments) can be rare, but one expects that the composite biomass of a canonical trophic level and/or productivity would be greater than higher levels. Compartments at high trophic levels would be expected to be found in lower abundance and/or secondary productivity. Those at high levels with high productivity might be expected to be quantitatively important controlling elements. Their high rates of productivity would be associated with high rates of consumption and potential for top-down control. This feeding might impact significantly on the community. Interestingly, this potential for top-down control spread across taxa from microscopic predators to overwintering waterfowl. Compartments with relatively high effective trophic levels (≥ 2.41) and relatively high rates of productivity ($> 0.2 \text{ mgC m}^{-2} \text{ d}^{-1}$) included microprotozoans in the water column (5), microfauna in sediments (2), spot (26), predatory polychaetes (34), Gulf flounder and needlefish (19), and fish-eating birds (38).

3.3. *Mixed trophic impact analysis*

Mixed trophic impact analysis identifies the cumulative impacts of each compartment on each other, whether positive or negative (Ulanowicz and Puccia, 1990). Positive impacts promote 'pop-

ulation' growth and occur when one compartment acts as a food source, reduces predation, or reduces competition on another compartment. Negative impacts, which reduce 'population' growth, occur when one group acts as a competitor or a predator on another, or acts indirectly to promote competition or predation on another compartment. The impacts can be the result of direct interaction between one compartment and another or the result of indirect interactions mediated through other compartment flows. Thus, the

analysis sums the impacts of each compartment on each other across all trophic paths. To focus on important interactions, only impacts greater than or equal to $|0.1|$ (i.e. a 10% effect) were considered.

Compartments were grouped along their effective trophic levels to determine the trends of positive (Fig. 4) and negative (Fig. 5) impacts. The number of positively impacted compartments was generally inversely proportional to effective trophic level (Fig. 4). This may indicate bottom-

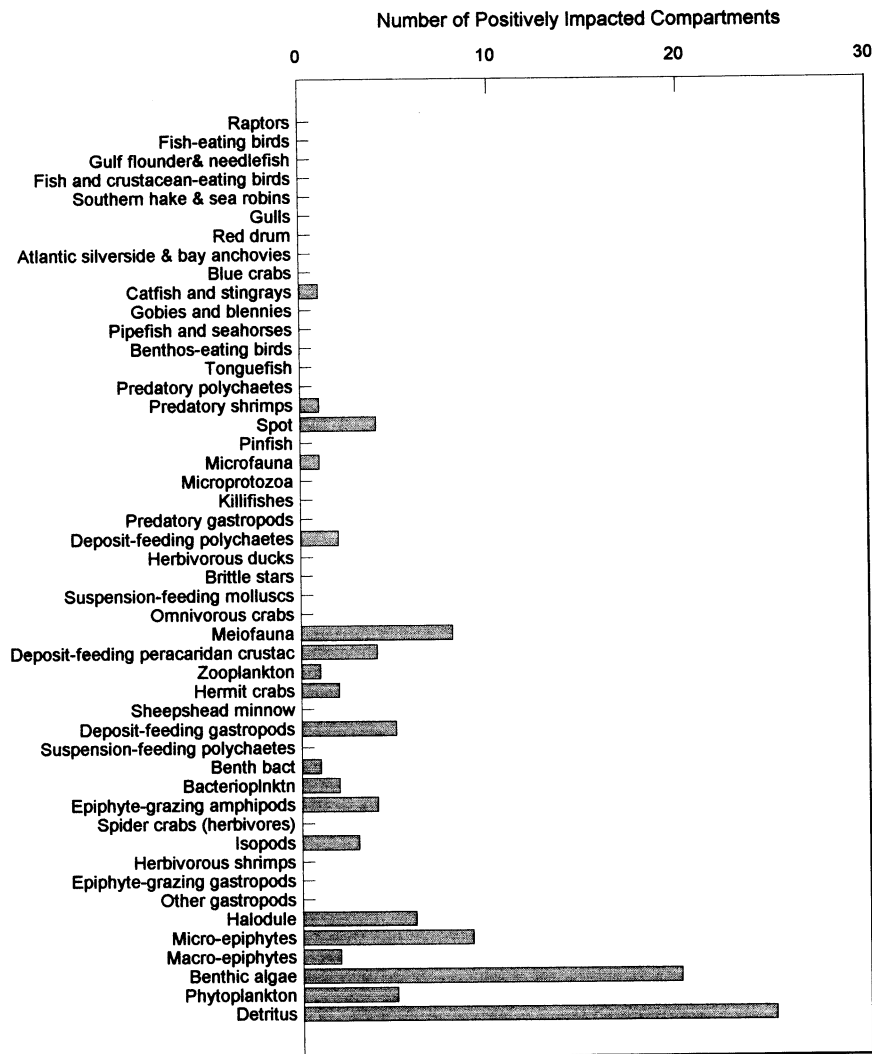


Fig. 4. Positive trophic impacts for the winter's food web with compartments ordered by effective trophic level. The number of impacted compartments represent those with coefficients ≥ 0.1 in the mixed trophic impact matrix.

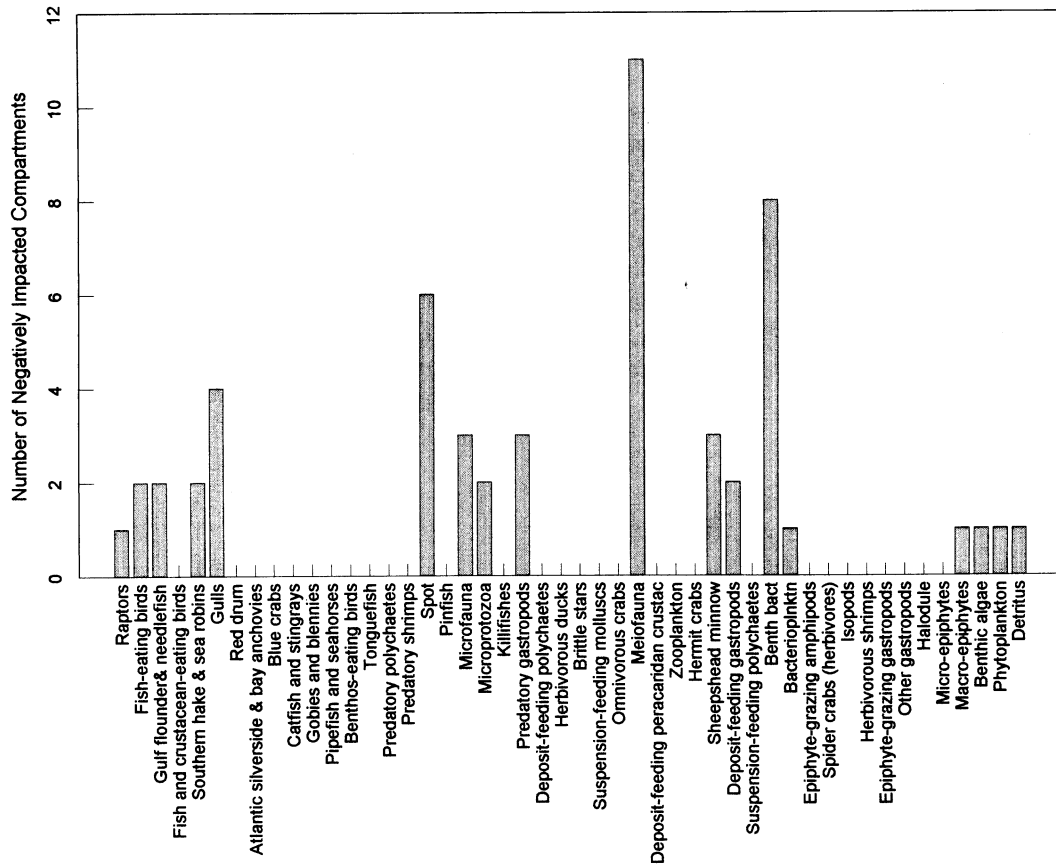


Fig. 5. Negative trophic impacts for the winter's food web with compartments ordered by effective trophic level. The number of impacted compartments represent those with coefficients ≤ -0.1 in the mixed trophic impact matrix.

up control or the presence of multiple, diverse prey for the animal compartments, preventing strong linear foodchain linkages. All primary producer compartments and detritus positively impacted multiple consumer compartments. Benthic microalgae (46) and detritus (48) provided the greatest potential for bottom-up control. Among largely herbivorous and detritivorous consumers, meiofauna (eight, at effective trophic level 2.19) and deposit-feeding gastropods (29, at effective trophic level 2.32), with their large biomasses, positively impacted a disproportionate number of compartments. However, epiphyte-grazing amphipods (6), isopods (12), and deposit-feeding peracaridan crustaceans (14) had relatively low biomasses and positively impacted three or more groups. Spot (26, at effective trophic level 2.91)

also had a positive impact on 4 compartments as a prey item and was the only 'carnivore' with so many.

Compartments that provided the greatest numbers of negative trophic impacts were among the herbivores and detritivores, but significant negative impacts were caused by compartments with trophic levels above 3 (Fig. 5). Negative impacts by detritus and primary producers tended to be through competition among primary producers or on the microbial community. Benthic bacteria (1) and meiofauna (3) provided the greatest numbers of negative impacts. These were through a number of mechanisms: competition with other consumers for detritus and benthic algal exudates (considered part of the detrital pool), consumption of benthic algal exudates and detritus de-

creasing their accumulation, and indirect effects with other consumers. Spot (26) and gulls (40) were the two compartments at higher trophic levels that caused the most negative impacts. This was through their roles as predators and competitors. Of the six groups with the highest effective trophic levels, only one [fish and crustacean-eating birds (39)] did not demonstrate negative impacts. In fact three groups of birds (raptors, fish-eating birds and gulls) demonstrated negative impacts within the community despite the fact that much of their food had to be imported to achieve steady state.

3.4. Feeding diversity

Another analysis provided by ECOPATH II is that of an ‘omnivory index,’ the variance of the effective trophic levels of a consumer’s preys (Christensen and Pauly, 1992). The diversity of trophic levels of prey fed upon by a predator increases with the index value. In Fig. 6 the omnivory indices for all compartments are listed in order of effective trophic level. There was a trend for increased index values with increased effective trophic level. Organisms at higher trophic levels seemed to feed over a broader range

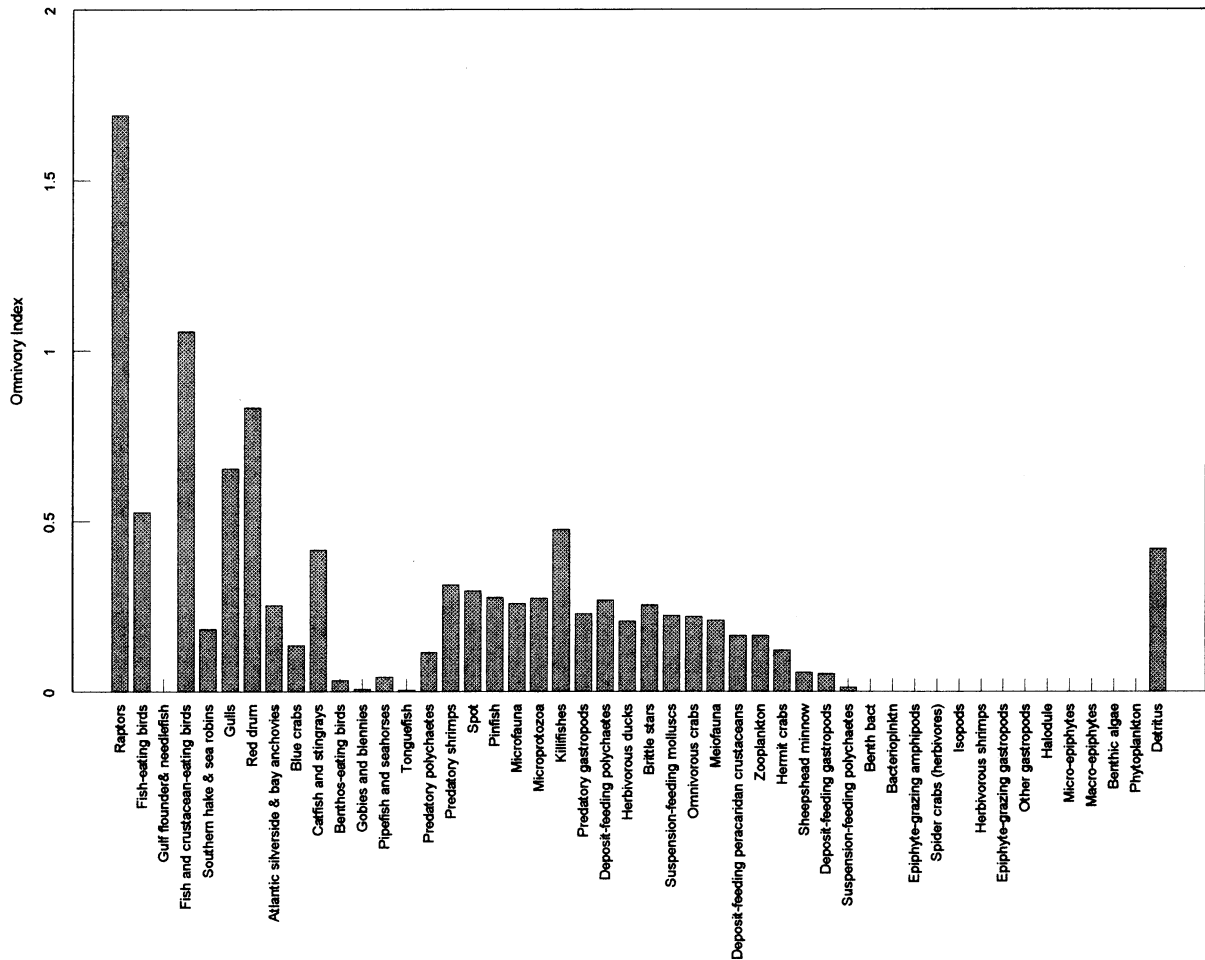


Fig. 6. Omnivory indexes of compartments ordered by effective trophic level.

of levels than do lower levels. But this is not without exceptions. At high trophic levels birds (37–42) generally have higher indices than fish (17–28). Red drum (28) was an exception with the third highest index. The high omnivory index of red drum may have resulted from the fact that juvenile and adult fish were pooled in the network. Different fish life stages often have different diets, so the index reflects ontogenetic changes (Livingston, 1980; Polis, 1995). At lower trophic levels the indices were as low as 0. As in the earlier discussion concerning the distribution of effective trophic levels, the low indices at low trophic levels was in part a result of the inability to resolve diversity among microorganisms and meiofauna. Such resolution would increase the index, but this increase would in all probability extend through higher levels that feed on these groups. Thus the overall trend of increased omnivory indices with increased trophic level may not be changed.

4. Concluding remarks

Network analysis was conducted on a complex and well articulated food web of a winter's *H. wrightii* community in Goose Creek Bay, St. Marks National Wildlife Refuge, FL. Unlike most such networks, much of the data used for network construction came from sampling specific for that purpose. The strategy included field sampling the density and/or biomass of as many taxa as possible, given time and personnel constraints. Data from 4 samplings were averaged in this process, two sites with replicate transects each sampled in January and February 1994. These data, diet estimates from fish stomach content analyses, and selected process rates represented the core of the information base. This data base is more specific in time and space than any other used for foodweb network analysis. Furthermore, the complexity of the food web rivals or exceeds others in the literature (Baird and Ulanowicz, 1989; Christensen, 1995; Ulanowicz et al., 1997). Most energetic processes were derived from literature values using internally consistent rules. First approximations for other diet information came

from the literature with modifications made for relative abundance of prey. Adjustments for steady state were based on diet distribution.

Effective trophic level was used as a metric for ordering compartments in the assessment of their attributes and interactions. As recognized by Lindeman (1942), in a steady state system energy flow decreases with increasing aggregate, canonical trophic level. Thus, as trophic level increases, the energy flow of an average compartment at any effective trophic level decreases. Compartments with attributes that diverge from this average condition would be expected to have greater or lesser influence on the food web. In the *Halodule* community, consumer compartments comprise effective trophic structure from 2.0 (herbivore/detritivore) to 4.32 (where 4.0 represents secondary carnivory). The effective trophic levels of consumers tend to aggregate near integer values, but the spread from integer values increases with increasing level. Based on productivity, several taxa were found to be potentially important to energy flow relative to their trophic position. These included protozoans in both the water column and sediments, spot, predatory polychaetes, Gulf flounder and needlefish, and fish-eating birds. Detritus and benthic microalgae were important sources of food in the extended diets of many consumers. However, the importance of microalgal production may have been underestimated when dissolved photosynthate was modeled to pass through the detritus compartment, losing track of the photosynthate's origins within the analyses. 'Bottom-up' control appeared important through mixed trophic impact analysis. The extent of positive impacts decreased with increasing trophic level. 'Top-down' control, as negative impacts, appeared more limited to a few consumers with inordinately large production relative to their trophic position. Ordering results from various network analysis algorithms by effective trophic level proved useful in highlighting the potential influence of different taxa to trophodynamics.

The energy flow through the winter's *Halodule* community is dominated by detritus and benthic microalgae at the bottom and by waterfowl and piscivorous fish at the top. This pattern changes from winter to summer. SAV productivity in-

creases, and many of the birds emigrate (Zieman and Zieman, 1989). Summer sampling demonstrated the immigration of other piscivorous fish and sea turtles into the community (Luzckovich, unpublished data). Furthermore, many of the fish captured in winter were juveniles. As they age, many change diet ontogenetically (Livingston, 1980, 1984). The results of these changes in community structure will undoubtedly change the trophic structure, a subject for further analysis.

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Appendix A. A list of the compartments and species

Compartment number	Compartment or common name	Species or taxon pooled within a compartment
1	Benthic bacteria	
2	Microfauna	
3	Meiofauna	
4	Bacterioplankton	
5	Microprotozoa	
6	Epiphyte grazing amphipods	<i>Acunmindeutopus naglei</i> <i>Ampithoe longimana</i> <i>Caprella penantis</i> <i>Cymadusa compta</i> <i>Lembos rectangularis</i> <i>Batea catharinensis</i> <i>Elasmopus levis</i> <i>Melita sp.</i> <i>Synchelidium sp.</i> <i>Listriella barnardi</i> <i>Lyssianopsis alba</i>
7	Suspension-feeding molluscs	<i>Brachiodontes exustus</i> <i>Chione cancellata</i> <i>Argopecten irradians</i> <i>Unident bivalves</i> <i>Crepidula fornicata</i> <i>Crepidula convexa</i>

8	Hermit crabs	<i>Pagurus sp.</i> <i>Pagurus mcglaughlini</i>
9	Spider crabs	<i>Libinia dubia</i>
10	Omnivorous crabs	<i>Neopanope texana</i> <i>Pinixia floridana</i>
11	Blue crabs	<i>Callinectes sapidus</i>
12	Isopods	<i>Erichsionella sp.</i> <i>Paracerces caudata</i> <i>Edotea triloba</i>
13	Brittle stars	<i>Ophioderma brevispinum</i>
14	Deposit feeding peracaridan crustaceans	<i>Ampelisca sp.</i> <i>Gammarus mucronatus</i> <i>Cerapus tubularis</i> <i>Corophium sp.</i>
	Detritivorous crustaceans	Unident. Cumacea Unident. Tanaeid Unident. ostracods <i>Mysidopsis</i>
15	Herbivorous shrimp	<i>Hippolyte zostericola</i> <i>Alpheus normani</i>
16	Predatory shrimp	<i>Palaemonetes floridanus</i> <i>Palaemonetes floridanus</i> <i>Penaeus duoarum</i> <i>Processa bermudiensis</i>
17	Catfish and stingrays	<i>Dasyatis sabina</i> <i>Arius felis</i>
18	Tonguefish	<i>Symphurus plagisua</i>
19	Gulf flounder and needlefish	<i>Paralichthyes albigutta</i> <i>Strongylura marina</i>
20	Southern hake and searobins	<i>Urophycis floridana</i> <i>Prionotus scitulus</i> <i>Prionotus tribulus</i>
21	Atlantic silversides and bay anchovy	<i>Menidia beryllina</i> <i>Anchoa mitchelli</i>

22	Sheepshead minnow	
23	Killifishes	<i>Fundulus similis</i> <i>Fundulus confluentus</i> <i>Adinia xenica</i>
24	Gobies and blennies	<i>Microgobius gulosus</i> <i>Gobiosoma robustum</i>
25	Pinfish	<i>Lagodon rhomboides</i>
26	Spot	<i>Leiostomus xanthurus</i>
27	Pipefish and seahorses	<i>Hippocampus zosterae</i> <i>Syngnathus scovelli</i>
28	Red drum (juveniles)	<i>Sciaenops ocellatus</i>
	(adults)	<i>Sciaenops ocellatus</i>
29	Deposit-feeding gastropods	<i>Acetocina candei</i> <i>Swartziella catesbyana</i> <i>Cadulus carolinensis</i> <i>Haminoea succinea</i> <i>Acteon punctostriatus</i> <i>Olivella mutica</i> <i>Truncatella pulchella</i> <i>Nassarius vibex</i>
30	Predatory gastropods	Unident. spirals <i>Urosalpinx perrugata</i> Unident. Nudibranchs <i>Opalia hotessieriana</i> <i>Epitonium albidum</i> <i>Terebra sp.</i> <i>Polinices sp.</i> <i>Busycon spiratum</i> <i>Turbonilla dalli</i> <i>Turbonilla hemphilli</i> <i>Prunum (= Marginella) apicinum</i> <i>Prunum (= Marginella) bellum</i> <i>Prunum (= Marginella) aureocincta</i> <i>Natica pusilla</i> <i>Hylina veliei</i> <i>Acanthocitona pygmaea</i> <i>Odostomia seminuda</i> <i>Seila adamsi</i>
31	Epiphyte-grazing gastropods	<i>Cerithium lutosum</i> <i>Mitrella lunata</i>

		<i>Solariella lamellosa</i>
		<i>Anachis avara</i>
32	Other gastropods	
		<i>Mangelia plicosa</i>
		<i>Hylina veliei</i>
		<i>Jaspidella jaspidea</i>
33	Deposit-feeding polychaetes	
		<i>Aricidea</i> sp.
		Capitellidae
		Cirratulidae
		Maldanidae
		Orbiniidae
		Paraonidae
		Pectanaridae
		Syllidae
		Amphitritidae
		Spionidae
34	Predatory polychaetes and nemertines	
		Glyceridae
		Nereidae
		Onuphidae
		Hesionidae
		Nemertines
35	Suspension-feeding polychaetes	
		Serpulidae
		Sabellidae
36	Zooplankton	
		<i>Acartia tonsa</i>
		Foraminifera
		Harpacticoid
		Nauplii1
		Nauplii2
		Nematode
		Polychaete
		Pycnogonid
37	Benthos-eating birds	
	Clapper Rail	<i>Rallus longirostris</i>
	Bufflehead	<i>Bucephala albeola</i>
	Semi-palmated Plovers	<i>Charadrius semipalmatus</i>
38	Fish-eating birds	
	Great Egret	<i>Casmerodius albus</i>
	Common Loon	<i>Gavia immer</i>
	Great Blue Heron	<i>Ardea herodias</i>
	Louisiana Heron	<i>Hydranassa tricolor</i>
	Red-Breasted Merganser	<i>Mergus serrator</i>
	Double-Crested Comorant	<i>Phalacrocorax carbo</i>
	Belted Kingfisher	<i>Megaceryle alcyon</i>

39	Fish and crustacean eating birds	
	Hooded Merganser	<i>Lophodytes cucullatus</i>
	Willetts	<i>Catoptrophorus semipalmatus</i>
	Greater Yellow Legs	<i>Tringa melanoleuca</i>
40	Gulls and Terns	
	Forster's Tern	<i>Sterna forsteri</i>
	Laughing Gull	<i>Larus atricilla</i>
	Herring Gull	<i>Larus argentatus</i>
	Ring-Billed Gull	<i>Larus delawarensis</i>
41	Raptors	
	Bald Eagle	<i>Haliaeetus leucocephalus</i>
	Northern Harrier	<i>Circus cyaneus</i>
42	Herbivorous ducks	
	Blue-winged teal	<i>Anas discors</i>
43	Seagrass	<i>Halodule wrightii</i>
44	Micro-epiphytes	
45	Macro-epiphytes	
46	Benthic algae	
47	Phytoplankton	
48	Detritus	

References

- Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59, 329–364.
- Baird, D., Ulanowicz, R.E., 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Mar. Ecol. Prog. Ser.* 99, 221–237.
- Baird, D., Luczkovich, J.J., Christian, R.R., 1998. Assessment of spatial and temporal variability in ecosystem attributes of the St. Marks National Wildlife Refuge, Apalachee Bay, Florida. *Estuar. Coast. Shelf Sci.* 47, 329–349.
- Biujse, A.D., Van Eerden, M.R., Dekker, W., Van Densen, W.L.T., 1993. Elements of a trophic model for IJsselmer (The Netherlands), a shallow eutrophic lake. In: Christensen, V., Pauly, D. (Eds.), *Trophic models of aquatic ecosystems*. ICLARM, Manila, Philippines, pp. 90–94.
- Burns, T.P., 1989. Lindeman's contradiction and the trophic structure of ecosystems. *Ecology* 70, 1355–1362.
- Burns, T.P., Higashi, M., Wainright, S.C., Patten, B.C., 1991. Trophic unfolding of a continental shelf energy–flow network. *Ecol. Model.* 55, 1–26.
- Cale, W.G., 1995. Modeling aggregation: ecological perspectives. In: B.C. Patten, S.E. Jørgensen (Eds.), *Complex Ecology: The Part-whole Relation in Ecosystems*. Prentice-Hall PTR, Englewood Cliffs, NJ, USA, pp. 230–241.
- Carr, W.E.S., Adams, C.A., 1972. Food habits of juvenile marine fishes: evidence of cleaning habit in the leather-jacket, *Oligoplites saurus* and the spottail pinfish, *Diplodus holbrooki*. *Fishery Bull.* US 70, 1111–1120.
- Carr, W.E.S., Adams, C.A., 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Am. Fish. Soc.* 102, 511–540.
- Christensen, V., 1995. Ecosystem maturity-towards quantification. *Ecol. Model.* 77, 3–32.
- Christensen, V., Pauly, D., 1992. A Guide to the ECOPATH II Software System (Version 2.1). ICLARM, Manila, Philippines.
- Christensen, V., Pauly, D., 1993. *Trophic Models of Aquatic Ecosystems*. ICLARM, Manila, Philippines.
- Christian, R.R., 1994. Aggregation and disaggregation of microbial food webs. *Microb. Ecol.* 28, 327–330.
- Cohen, J.E., Beaver, R.A., Cousins, S.H., 1993. Improving food webs. *Ecology* 74, 252–258.
- de la Cruz-Aguero, G., 1993. A preliminary model of Mandinga lagoon, Veracruz, Mexico. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*. ICLARM, Manila, Philippines, pp. 193–196.
- de Paula e Silva, R., Sousa, M.I., Caramelo, A.M., 1993. The Maputo Bay ecosystem (Mozambique). In: Christensen, V., Pauly, D. Jr. (Eds.), *Trophic Models of Aquatic Ecosystems*. ICLARM, Manila, Philippines, pp. 214–223.
- Gardner, R.H., Cale, W.G., O'Neill, R.V., 1982. Robust analysis of aggregation error. *Ecology* 63, 1771–1779.

- Heck, K.L. Jr., 1979. Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinum*) meadows. *J. Biogeog.* 6, 183–200.
- Higgins, R.P., Thiel, H., 1988. Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, DC.
- Johnson, C., Klumpp, D., Field, J., Bradbury, R., 1995. Carbon flux on coral reefs: effects of large shifts in community structure. *Mar. Ecol. Prog. Ser.* 126, 123–143.
- Jørgensen, S.E., Nielsen, S.N., Jørgensen, L., 1991. Handbook of Ecological Parameters and Ecotoxicology, Elsevier, Amsterdam.
- Kemp, P.F., 1990. The fate of benthic production. *Rev. Aquatic Sci.* 2, 109–124.
- Landry, M.R., Hassett, R.P., 1982. Estimating the grazing impact of marine micro-zooplankton. *Mar. Biol.* 67, 283–288.
- Leber, K.M., 1983. Feeding Ecology of Decapod Crustaceans and the Influence of Vegetation on Foraging Success in a Subtropical Seagrass Meadow. Ph.D. dissertation. The Florida State University, Tallahassee, FL.
- Levine, S., 1980. Several measures of trophic structure applicable to complex food webs. *J. theor. Biol.* 83, 195–207.
- Lewis, F.G., 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule*, and bare sand substrata. *Mar. Ecol. Progr. Ser.* 19, 101–113.
- Lewis, F.G., Stoner, A.W., 1981. An examination of methods for sampling macrobenthos in seagrass meadows. *Bull. Mar. Sci.* 31, 116–124.
- Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 399–418.
- Livingston, R.J., 1980. Ontogenetic trophic relationships and stress in a coastal seagrass system in Florida. In: Kennedy, V.S. (Ed.), *Estuarine Perspectives*. Academic Press, New York, pp. 423–435.
- Livingston, R.J., 1982. Trophic organization of fishes in a coastal seagrass system. *Mar. Ecol. Progr. Ser.* 7, 1–12.
- Livingston, R.J., 1984. Trophic response of fishes to habitat variability in coastal seagrass systems. *Ecology* 65, 1258–1275.
- Lopez, G.R., Levinton, J.S., 1987. Ecology of deposit-feeding animals in marine sediments. *Quarterly Rev. Biol.* 62, 235–259.
- Luczkovich, J.J., 1987. The Patterns and Mechanisms of Selective Feeding on Seagrass-Meadow Epifauna by Juvenile Pinfish, *Lagodon rhomboides* (Linnaeus). Ph.D. dissertation. The Florida State University, Tallahassee, FL.
- Luczkovich, J.J., Stellwag, E.J., 1993. Isolation of cellulolytic microbes from the intestinal tract of the pinfish, *Lagodon rhomboides* size-related changes in diet and microbial abundance. *Mar. Biol.* 116, 381–388.
- Luczkovich, J.J., Rizzo, W.M., Neckles, H., Ward, G., Christian, R.R., 1997. Including bacteria to birds in a food web: the sampling design for network analysis of a *Halodule wrightii* ecosystem in the Northeastern Gulf of Mexico during winter. Report submitted to National Wetlands Research Center. US Fish and Wildlife Service, Lafayette, LA.
- Luczkovich, J.J., Rizzo, W.M., Neckles, H., Ward, G., Christian, R.R., 1997. Including bacteria to birds in a food web: the sampling design for network analysis of a *Halodule wrightii* ecosystem in the Northeastern Gulf of Mexico during winter. *Ecol. Monogr.* (submitted).
- Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove community. In: Cronin, L.E. (Ed.), *Estuarine Research*, vol. 1. Academic Press, New York, pp. 265–286.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F. Jr., 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Patten, B.C., 1985. Energy cycling in the ecosystem. *Ecol. Model.* 28, 1–71.
- Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge University Press, New York.
- Polis, G.A., 1995. Complex food webs. In: B.C. Patten, S. E. Jørgensen (Eds.), *Complex Ecology: The Part-whole Relation in Ecosystems*. Prentice Hall, Englewood Cliffs, NJ, USA, pp. 513–548.
- Pomeroy, L.R., Wiebe, W.J., 1988. Energetics of microbial food webs. *Hydrobiologia* 159, 7–18.
- Sherr, E.B., Sherr, B.F., 1994. Bacterivory and herbivory: key roles of phagotrophic protists in pelagic food webs. *Microb. Ecol.* 28, 223–235.
- Stoner, A.W., 1979. Species-specific predation on amphipod crustacea by the pinfish *Lagodon rhomboides*: mediation by macrophyte standing crop. *Mar. Biol.* 55, 201–207.
- Stoner, A.W., 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. Mar. Sci.* 30, 537–551.
- Tolan, J.M., Holt, S.A., Onuf, C.P., 1997. Distribution and community structure of ichthyoplankton in Laguna Madre seagrass meadows: potential impact of seagrass species change. *Estuaries* 20, 450–464.
- Ulanowicz, R.E., 1984. Community measures of marine food networks and their possible applications. In: Fasham, M.J.R. (Ed.), *Flows of Energy and Materials in Marine Ecosystems: Theory and Practice*. Plenum Press, New York, pp. 23–47.
- Ulanowicz, R.E., 1987. NETWRK4: a Package of Computer Algorithms to Analyze Ecological Flow Networks. Univ. of Maryland, Chesapeake Biological Laboratory, Solomons.
- Ulanowicz, R.E., Kemp, W.M., 1979. Toward canonical trophic aggregations. *Am. Nat.* 114, 871–883.
- Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. *Coenoses* 5, 7–16.
- Ulanowicz, R.E., Wulff, F., 1991. Comparing ecosystem structures: the Chesapeake Bay and the Baltic Sea. In: Cole, J.J., Lovett, G.M., Findlay, S.E.G. (Eds.), *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*. Springer Verlag, New York, pp. 140–166.

- Ulanowicz, R.E., Bondavalli, C., Egnotovitch, M.S., 1997. Network Analysis of Trophic Dynamics in South Florida Ecosystems, FY 96: The Cypress Wetland Ecosystem. Ann. Rept. to the USGS Biological Resources Division, U. Miami, Coral Gables, FL.
- Wulff, F., Field, J.G., Mann, K.H. (Eds.), 1989. Network Analysis in Marine Ecology: Methods and Applications, Springer-Verlag, New York.
- Zieman, J.C., Zieman, R.T., 1989. The Ecology of the Seagrass Meadows of the West Coast of Florida: a community profile, US Fish Wildl. Serv. Biol. Rep. 85 (7.25).