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*Ecological Monographs*, Volume 59, Issue 4 (Dec., 1989), 329-364.

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*Ecological Monographs*

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## THE SEASONAL DYNAMICS OF THE CHESAPEAKE BAY ECOSYSTEM<sup>1</sup>

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**Abstract.** The full suite of carbon exchanges among the 36 most important components of the Chesapeake Bay mesohaline ecosystem is estimated to examine the seasonal trends in energy flow and the trophic dynamics of the ecosystem. The networks provide information on the rates of energy transfer between the trophic components in a system wherein autochthonous production is dominated by phytoplankton production. A key seasonal feature of the system is that the summer grazing of primary producers by zooplankton is greatly reduced due to top-down control of zooplankton by ctenophores and sea nettles. Some of the ungrazed phytoplankton is left to fuel the activities of the pelagic microbial community, and the remainder falls to the bottom where it augments the deposit-feeding assemblage of polychaetes, amphipods, and blue crabs. There is a dominant seasonal cycle in the activities of all subcommunities, which is greatest in the summer and least in the cold season. However, the overall topology of the ecosystem does not appear to change substantially from season to season.

Matrix operations can be employed to assess the various direct and indirect pathways by which each trophic group obtains energy. Often, indirect linkages reveal interesting differences. For example, although the bluefish and striped bass are both piscivorous predators, 63% of bluefish intake depends indirectly on benthic organisms, whereas striped bass depends mainly on planktonic organisms. Nearly all higher trophic species exhibit significant indirect dependencies upon the upper components of the microbial loop, especially during summer.

The complicated trophic network can be mapped into an eight-level trophic chain in the sense of Lindeman. Such analysis reveals that detritivory is about 10 times greater than herbivorous grazing in the Chesapeake system and that 70% of detritus results from internal recycle. Annual efficiencies of trophic levels decrease as one ascends the chain. Major seasonal shifts in trophic efficiencies at higher levels appear to be modulated by how effectively microscopic zooplankton (mostly ciliates) are cropped by their predators. Average trophic efficiency is 9.6%. Despite the existence of eight trophic levels, the average level at which each species feeds always remains below 5. One “pest” species (the coelenterate *Chrysaora quinquecirrha*) feeds rather high on the trophic pyramid and may exert a heretofore unappreciated level of control on the planktonic food chain.

The number of cycles present in the network is surprisingly few, despite the fact that a relatively large and seemingly constant amount (23.2%) of total system activity is devoted to recycling. This combination of factors possibly indicates a stressed ecosystem. A study of the rate-limiting links in the seasonal networks of recycling of material within the plankton reconfirms the shift of predator control from crustacean zooplankton in springtime to the sea nettle (*Chrysaora quinquecirrha*) during summer months. The collection of cycles present in the system is disjoint; there is no overlap between the cycles among the planktonic community and the circulations among the deposit feeders and nekton. The filter-feeding benthos and fish do not participate in any cycling, but serve rather as bridges to shift carbon and energy from the planktonic community into the benthic-nektonic subsystems. Neither do most of the members of the microbial loop engage in any recycle of carbon, functioning instead as a dissipative shunt of energy out of the system.

**Key words:** ascendancy; Chesapeake Bay; *Chrysaora quinquecirrha*; dependency coefficients; food web structure; input-output analysis; microbial loop; nexus of cycles; population and community energetics; predator control; recycling; seasonal activity levels; seasonal energy flows; structure of recycling; trophic pyramids; trophic structure.

<sup>1</sup> Manuscript received 27 April 1987; revised and accepted 10 October 1988; final version received 6 January 1989.

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## INTRODUCTION

The direction that the quantitative study of whole ecosystems should take is by no means certain. During the late sixties and early seventies there appeared to be an emerging consensus that simulating an ecosystem with a set of coupled, first-order differential equations should become the focal point around which studies of ecological communities are built (Patten 1971, Ott 1976). However, it soon became evident that such efforts were bound to fall short of the high hopes so many had held for this genre of systems ecology. Although simplistic simulation models, such as the Streeter-Phelps calculations for BOD and DO, can often be validated to a reasonable degree (Longhurst 1978), more complicated models involving coupled biological processes seem short on predictive ability, whence the paradox that building finer detail into a model often degrades the performance of the model as measured by most objective standards (Platt et al. 1981).

While some cling to the hope that more complete and more precise data will eventually set matters aright (Vinogradov and Menshutkin 1977), others are less than sanguine about the promise of simulation modeling. For example, Dugdale (1975) shows how difficult it becomes to simulate systems wherein the cast of species changes arbitrarily at a rapid rate. Lorenz (1969) demonstrated how nonlinearities in system equations often give rise to progressive amplification of errors in the data used to start the simulation. Such model instability results from efforts to increase the number of interacting components and to sharpen the fidelity of the expressions (usually by augmenting their nonlinearities) used to describe component processes (Ulanowicz 1979). In the end the behavior of the model can pass into the realm of what is now called "deterministic chaos," where prediction becomes highly problematic (May and Oster 1976).

Clearly, some retrenchment of attitudes on how to treat complex ecosystems has been in order (Innis 1977). We share the opinion that less reliance should be placed on methods that are heavy with a priori assumptions and more emphasis should be shifted toward developing new methods of interpreting the mass of data at hand. In what follows we attempt to demonstrate the efficacy of several new quantitative analyses in providing useful insights into the workings of the ecosystem of the Chesapeake Bay estuary.

To become more specific, biological oceanographers now are being urged to give greater emphasis to quantifying the fluxes of material and energy in marine ecosystems (Platt et al. 1981, Longhurst 1984, Fasham 1985). Quantitative descriptions of energy or material flows provide significant insights into the fundamental structure of an ecosystem and outline the efficiencies with which such currencies are transferred and assimilated. Moreover, these budgets provide a starting point for ecosystem flow analysis and structural comparison (and even simulation modeling), as well as providing a heuristic tool to help shape future research.

The physical, chemical, and biological properties of Chesapeake Bay, the largest estuary in the continental United States, have been studied intensively over the past 60 yr. The Bay is rich in natural resources and its shellfish and finfish species have long been subjected to heavy commercial and recreational exploitation. It also receives large amounts of nutrients and toxic pollutants in runoff from its catchment. In recent years research has increasingly been directed toward studying the interactions among its biotic and abiotic components and to elucidating those processes which influence the productivity of the ecosystem (e.g., Mountford et al. 1977, Holland et al. 1980, Kemp and Boynton 1981, Sellner 1981, Boynton et al. 1982, 1986, Tuttle et al. 1985, 1986, Ulanowicz and Baird 1986).

The objectives of this paper are: (a) to present a quantitative schematic of carbon exchanges within the ecosystem of the mesohaline region of Chesapeake Bay for each of the four seasons (the reason for emphasizing seasonality is that substantial differences in biomass and productivity have been observed over the course of a year, and we feel that averaged annual values would mask significant trends); (b) to determine the seasonal magnitudes of all transfers of carbon occurring over pathways that involve multiple trophic transfers; (c) to elucidate and study the underlying chain of trophic transfers inherent in such a branched web; (d) to illustrate the configuration of cyclic pathways in the system (Ulanowicz 1983); and (e) to characterize each set of seasonal dynamics using recently developed network indices.

## STUDY AREA

The Chesapeake Bay is situated along the Atlantic coast of the United States extending 314 km from latitude 36°50' to 39°40' N (Fig. 1). Hydrographically it is a partially mixed estuary (Pritchard 1967), having an average tidal range of  $\approx 0.6$  m. The Chesapeake Bay can be subdivided on the basis of salinity into three major divisions, namely the oligohaline (0–6 g/kg), mesohaline (6–18 g/kg), and polyhaline ( $> 18$  g/kg) (Fig. 1; Stroup and Lynn 1963). The surface water temperatures range from 21.4° to 28.9°C in summer, 13.1 to 23.3° in fall, 2.3° to 5.7° in winter, and 6.2° to 16.7° in spring (Ritchie and Genys 1975).

The areal and volumetric statistics for the entire Bay have been tabulated by Cronin (1971). The mesohaline region spans  $5.98 \times 10^9$  m<sup>2</sup>, or 48% of total surface area, and its volume is  $3.63 \times 10^{10}$  m<sup>3</sup>, or 47% of total volume of the estuary. Average depth of the mesohaline zone is  $\approx 7$  m.

Freshwater flows into the estuary from a number of rivers (Fig. 1), but the Susquehanna River provides  $\approx 50\%$  of the total of such input into the Chesapeake Bay. By dividing the volume of the Bay by the total freshwater inflows from all rivers (Officer 1976), we have estimated the average flushing time of the entire Chesapeake Bay to be  $\approx 42$  d.

## ESTIMATES AND ASSUMPTIONS

Energy flow models require information on standing stocks of the living and nonliving ecosystem constituents, diets of the feeding species, rates at which ingested materials are utilized, and rates of transfer of energy among various entities in the food web. We calculated the mean seasonal biomass of each of the compartments and the exchange of carbon among them (see Figs. 2–5) from data collected during the years 1983–1986. The data sources are listed in Table 1.

In order to quantify carbonaceous flows in the seasonal networks, it was necessary to estimate the amounts of carbon contained in each population and to establish both the origins of all they consume and the fates of what was ingested. Gross primary production in the autotrophic compartments (phytoplankton and benthic algae) was assumed to equal the sum of net primary production plus algal respiration. These gross production figures represent the major sources (or inputs) to the ecosystem. The net primary production was then partitioned among consumers according to reported herbivore diets and energy requirements (see Results). The residual production contributed to the pools of dissolved and particulate organic carbon in the water column.

Carbon budgets were constructed for each heterotrophic compartment during each season according to the equation:

$$C = P + R + E,$$

where  $C$  = consumption or total intake,  $P$  = secondary production,  $R$  = respiration, and  $E$  = egestion (Crisp 1971). Egestion ( $E$ ) is that portion of the ingested material not assimilated but released back into the environment as fecal material. We have not attempted to include the poorly understood rates of excretion ( $U$ ) into the budgets and have assumed that consumption is balanced by production, respiration, and feces. The carbon available to the next link in the food web was apportioned to predators (according to their diet and demand), detritus, or commercial harvest. Where possible, information on the activities of the various consumers was garnered from the results of local studies; otherwise respiration and production values were estimated using appropriate  $P/B$  and  $P/R$  ratios (McNeil and Lawton 1970, Humphreys 1979, Warwick 1980, McLusky 1981, Mann 1982, Valiela 1984, Schwinghamer et al. 1986).

We assumed that suspended detritus was composed of two components—particulate organic carbon (POC) and attached bacteria. The minimal amount of physical degradation of the POC was neglected, and the losses from this nonliving compartment were attributed either to sedimentation out of the water column or to consumption by attached bacteria and other detritivores. POC concentrations in Chesapeake Bay were measured by Tuttle et al. (1985, 1986), who estimated that the biomass of the bacteria attached to the POC was  $\approx 20\%$

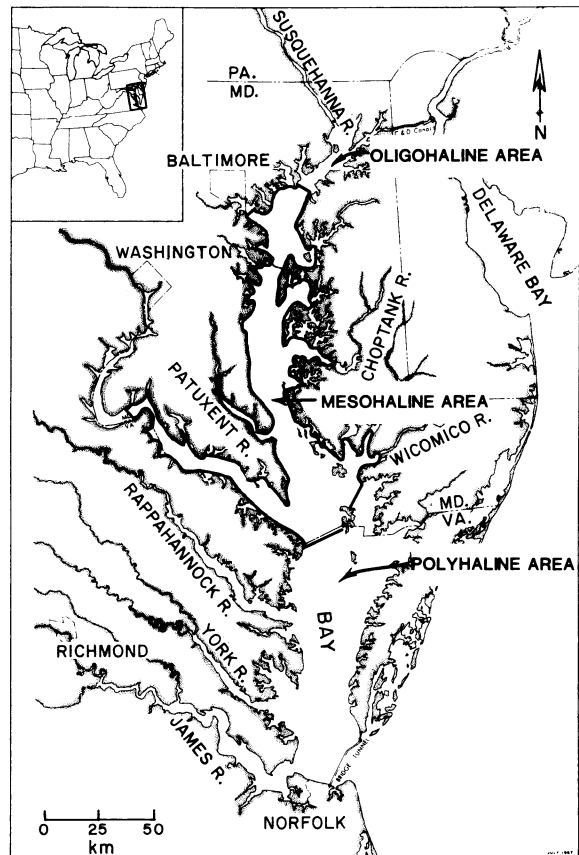


FIG. 1. The Chesapeake Bay.

of the freestanding bacterial stock (Table 1). Doubtless, this latter percentage is variable, but in the absence of better information it will be assumed constant. Zooplankton and other suspension feeders most probably consume detrital particles (either discriminately or indiscriminately) in proportion to the standing stock of detritus relative to that of other food sources such as phytoplankton and microzooplankton ( $> 4 \mu\text{m}$  in size).

Carbon demand by invertebrates (excluding bacteria, flagellates, and microzooplankton) was calculated either from the relationship:

$$C = A \times 100/\text{assimilation efficiency}$$

(Warwick et al. 1979, Baird and Milne 1981), where  $A = P + R$ , or from the growth coefficient  $P/C$ . Fish consumption was estimated from the empirical relationship:

$$C = 1.25(P + 2R),$$

which was derived on physiological grounds and applies to a variety of fish species (Winberg 1956, Mann 1965). The  $P/B$  ratios used to estimate fish production or biomass were calculated from the relationship:

$$P/B = 3K[(L_{\text{max}}/L_t) - 1],$$

where  $K$  and  $L_{\text{max}}$  are parameters of the von Bertalanffy growth equation, and  $L_t$  is length at age  $t$  (Longhurst

TABLE 1. References to data sources and information on biomass and energetics including diet composition and ecological coefficients (model compartment number in parentheses).

Model compartment	Parameter	Reference
Phytoplankton (1)	Biomass ( <i>B</i> ) Production ( <i>P</i> ) Respiration DOC exudates: 25% of net production	Tuttle et al. 1985, 1986 Sellner et al. 1985, Sellner and Brownlee 1986 Flemer and Olmon 1971 Wiebe and Smith 1977, Larson and Hagstrom 1979, Fenchel 1982, Wolter 1982, Vegter and de Visscher 1984, Laanbroek et al. 1985
Bacteria attached to suspended particles (2)	Biomass 10–20% of free-living bacteria. Carbon conversion 40%; daily <i>P/B</i> ratios: summer 0.5, fall 0.3, winter 0.2, spring 0.5. <i>P/R</i> 0.8–0.9	Azam and Hodson 1977, Ducklow 1983, Ducklow and Kirchman 1983, Alldredge et al. 1986
Sediment bacteria (3)	Biomass  Energetics	Anderson and Meadows 1969, Gerlach 1978, Newell and Fallon 1982, J. H. Tuttle, Chesapeake Biological Laboratory, <i>personal communication</i> Newell and Fallon 1982, Rublee 1982, Newell et al. 1981, J. H. Tuttle, Chesapeake Biological Laboratory, <i>personal communication</i>
Benthic algae (4)	Biomass Energetics	Boynton et al. 1985, 1986 Cuff et al. 1983, Asmus and Asmus 1985
Free bacteria in water column (5)	Biomass Production Energetics	Tuttle et al. 1985, 1986 Tuttle et al. 1985, 1986 Payne 1970, Furham and Azam 1982, Azam et al. 1983, Ducklow 1983, Joint and Williams 1985, Findlay et al. 1986
Heterotrophic microflagellates (6)	Biomass ( $\pm 10\%$ of free-living bacterial biomass) Energetics (consumption production of bacteria)	Linley et al. 1983 Haas and Webb 1979, Fenchel 1982, Azam et al. 1983, Ducklow 1983, Linley et al. 1983, Davis and Sieburth 1984, Wright and Coffin 1984, Andersen and Fenchel 1985, Caron et al. 1985, Gast 1985, Rassoulzadegan and Sheldon 1986
Microzooplankton (7)	Biomass  Energetics	Sellner et al. 1985, Taylor et al. 1985, Sellner and Brownlee 1986 Heinbokel 1978, Heinbokel and Beers 1979, Rassoulzadegan and Ettiene 1981, Brownlee 1982, Fenchel 1982, Capriulo and Carpenter 1983, Verity 1985, Andersen and Sorensen 1986
Zooplankton (8)	Biomass and species composition Energetics	Jacobs et al. 1985 Winberg 1956, Heinle 1966, 1974, Paffenhofer and Strickland 1970, Paffenhofer 1971, Frost 1972, Heinle and Flemer 1975, Poulet 1976, Berk et al. 1977, Roman 1977, 1984a, b, Donaghay and Small 1979, Ikeda and Motoda 1979, Price et al. 1983, Robertson 1983, Turner and Anderson 1984, Kiorboe et al. 1985, Stoecker and Sanders 1985, Sheldon et al. 1986, Williamson and Butler 1986
Ctenophores (9) and sea nettles (10)	Biomass  Energetics	Curl 1962, Herman et al. 1968, Jacobs et al. 1985, Shenker 1985, D. G. Cargo, Chesapeake Biological Laboratory, <i>personal communication</i> Cargo and Schultz 1966, Bishop 1967, Miller 1970, Burrell and van Engel 1976, Clifford and Cargo 1978, Reeve and Baker 1978, Reeve et al. 1978, Kremer 1979, Deason and Smayda 1982a, b, Feigenbaum et al. 1982, Kelly 1983, Feigenbaum and Kelly 1984
Other suspension feeders (11) and <i>Mya</i> (12)	Biomass  Energetics	Hiegel 1985, A. Marsh, Chesapeake Biological Laboratory, <i>personal communication</i> Haven and Morales-Alamo 1966, Tenore and Dunstan 1973, Mountford et al. 1976, 1977, Wright et al. 1982, Walker and Tenore 1984, A. Marsh, Chesapeake Biological Laboratory, <i>personal communication</i>
Oysters (13)	Biomass  Energetics	Cabraal 1978, Stagg 1986, Department of Natural Resources, Maryland Haven and Morales-Alamo 1966, 1970, Tenore and Dunstan 1973, Dame 1976, Buxton et al. 1981, Wright et al. 1982

TABLE 1. Continued.

Model compartment	Parameter	Reference
<i>Nereis</i> (15) and other polychaetes (14)	Biomass	Hiegel 1985, A. Marsh, Chesapeake Biological Laboratory, <i>personal communication</i>
	Energetics	Warwick and Price 1974, Tenore et al. 1977, Heip and Herman 1979, Warwick 1980, Tenore 1982, Evans 1984, Baird et al. 1985, George and Warwick 1985, Moller et al. 1985
<i>Macoma</i> spp. (16)	Biomass	Hiegel 1985
	Energetics	Walker and Tenore 1984, Hummel 1985a, b
Meiofauna (17)	Biomass estimated as 10% of macrobenthos	Sanders 1960, McIntyre 1961, Wigley and McIntyre 1964, Gerlach 1971, 1978, Baird and Milne 1981, Kuipers et al. 1981
	Energetics	Gerlach 1971, 1981, Coull 1973, Tenore et al. 1977, Rieper 1978, 1982, Scheimer et al. 1980, Montagna et al. 1983, Montagna 1984
Crustacean deposit feeders (18)	Biomass	Hiegel 1985
	Energetics	Birkland 1977, Mossman 1978, Moller and Rosenberg 1982, Nielsen and Kofoed 1982, Moller et al. 1985
Blue crab (19)	Biomass	Miller et al. 1975, Souza et al. 1980, Department of Natural Resources, Maryland
	Energetics	Darnell 1958, Tagatz 1968, Klein Breteler 1976, Virnstein 1977, Paul 1981, Nelson 1981, du Preez 1983, Evans 1984, Pihl 1985
Fish larvae (20)	Biomass	Wood et al. 1979, Jacobs et al. 1985
	Species composition distribution, seasonal abundance	Dovel 1971, Boynton et al. 1977, McCabe and Miller 1978, Wood et al. 1979, Mihursky et al. 1980, Setzler-Hamilton et al. 1982, Olney 1983
	Energetics	Boynton et al. 1977, Houde and Schekter 1981, 1983, Houde and Alpern Lovdal 1984
Alewife and herring (21)	Biomass	Estimated from commercial catches, 1983–1986
	Feeding	Wells 1970, Hutchinson 1971, Burbridge 1974, Domermuth and Reed 1980
	Energetics	Stewart and Binkowski 1986
Bay anchovy (22)	Biomass	Lunsford et al. 1976, Richkus et al. 1979, Wilson et al. 1979, Dovel 1981, Reis and Dean 1981, Olney 1983
	Feeding	Homer and Boynton 1978
	Energetics	Boynton et al. 1977, Houde and Schekter 1981, 1983
Menhaden (23)	Biomass	Estimated from commercial catches, 1983–1986; Wilson et al. 1978
	Feeding	Homer and Boynton 1978, Peck 1983
	Energetics	Durbin and Durbin 1975, 1983
Shad (24)	Biomass	Estimated from commercial catches, 1983–1986; Wilson et al. 1978
	Feeding	Hildebrand and Schroeder 1927, Bigelow and Schroeder 1953, Domermuth and Reed 1980
	Energetics	<i>P/B</i> from growth curve (Longhurst 1983); Winberg 1956, Mann 1965, Humphreys 1979
Atlantic croaker (25), hog choker (26), spot (27)	Biomass	Estimated from trawl catches, Department of Natural Resources, Maryland, 1983–1986
	Feeding	Homer and Boynton 1978, Overstreet and Heard 1978
	Energetics	<i>P/B</i> from growth curve (Longhurst 1983); Winberg 1956, Mann 1965, Humphreys 1979
White perch (28), catfish (29), blue fish (30), summer flounder (32), striped bass (33)	Biomass	Estimated from commercial catches, 1983–1986; Wilson et al. 1978, Stagg 1986, Department of Natural Resources, Maryland
	Feeding	Welsh and Breder 1923, Hollis 1952, Muncy 1962, Manooch 1973, Merrimer 1975, Chao and Musick 1977, Homer and Boynton 1978, Layher and Boles 1980, Gardinier and Hoff 1982
	Energetics	<i>P/B</i> rates from growth curves (Longhurst 1983); Winberg 1956, Mann 1965, 1982, McNeil and Lawton 1970, Humphreys 1979, Valiela 1984

TABLE 1. Continued.

Model compartment	Parameter	Reference
Dissolved organic carbon, DOC (34)	Seasonal concentrations	Provided by C. F. D'Elia, Chesapeake Biological Laboratory
Suspended particulate organic carbon, POC (35)	Seasonal concentrations	Tuttle et al. 1985, 1986
Sediment POC (36)	Seasonal concentrations	Boynton et al. 1985, 1986, Hiegel 1985

1983). Typical values for annual  $P/B$  ratios range from  $\approx 3.3$  to 4.5.

One of the major problems in this study was to estimate the biomasses of some commercially exploited fish species. For each of these (catfish, alewife and herrings, menhaden, shad, perch, bluefish, summer flounder, and striped bass) the mean seasonal catches for the years 1983–1986 were assumed to constitute 50% of the season's production (Sheldon et al. 1977, Stewart et al. 1981, Mann 1982), and mean seasonal biomass was then estimated using the appropriate  $P/B$  ratio as calculated above. The standing stocks of croaker, hogchoker, and spot were obtained from trawl studies conducted in the mesohaline region of Chesapeake Bay by the Maryland Department of Natural Resources. Scientific names of species for which common names are used in our paper can be found in the Appendix.

The descriptive parameters (biomass, diet, consumption, production, respiration) for each compartment were obtained from a large number of sources. These are listed in Table 1 according to their compartment number as designated in Figs. 2–6. Some of the references provided direct information on diet, diet composition, assimilation, and other ecological coefficients, while others provided estimates of production and/or respiration ratios for the same or related species in similar habitats elsewhere. Detailed documentation of the calculations for estimating the biomasses, the energetics of individual components, and the fluxes between them is available from the Chesapeake Biological Laboratory (Ulanowicz and Baird 1986).

The biomass of each component (as carbon) is given in milligrams per square metre and carbon flux information in milligrams per square metre per season. Data on all planktonic species (e.g., phytoplankton, bacteria, zooplankton, DOC, and suspended POC) were integrated over an average water column depth of 7 m. The four seasons consist of the following months: summer, June–August (92 d); fall, September–November (91 d); winter, December–February (90 d) and spring, March–May (92 d).

## RESULTS

Figs. 2–6 depict the exchanges of carbon among the major ecosystem components resident in the mesohaline region of the Chesapeake Bay as well as the stocks comprising each compartment. The main struc-

tural features of the ecosystem and the temporal changes in biomasses, magnitudes of flow, productivities, and diversities are implicit in the figures. The total inflows to each producer, consumer, and storage compartment are shown, as are their respective outputs (respiration, production, egesta [for compartments 1–33], and flows to other compartments). The living compartments are numbered 1 to 33, and the passive storage compartments, 34–36.

For clarity, flows from suspended POC and attached bacteria and from sediment POC and bacteria are combined in Figs. 2–5 but are illustrated in more detail in Fig. 6. The aggregate flows to the suspended POC (35) and to the sediment POC (36) compartments are shown in Figs. 2–6. Table 2 provides a summary of biomasses and production figures for the main trophic groups, which are aggregated according to their modes of feeding. The egesta ( $E$ ) of compartments 5–10 were assumed to remain temporarily in suspension (as POC), making them available for recycling within the water column (Paffenhöfer and Knowles 1979, Hofmann et al. 1981). Feces from the fish community (20–33) were assumed to sink to the bottom, where they became part of the sediment POC pool (36). Unutilized benthic invertebrate production was assumed to become incorporated into sediment POC (36). Annual demands for sediment POC exceed its available sources by  $\approx 11.6\%$ , but rather than force an artificial balance, we have chosen to retain the ostensible deficit. Most of the excess demand occurs in the summer (32.5% deficit during that season) with lesser shortfalls in the autumn (1.6%), winter (6.9%), and spring (9.7%).

With the exception of phytoplankton and zooplankton, biomasses of most ecosystem components were highest in summer. Phytoplankton biomass peaks during the spring; however, the highest production rates occur during summer (Sellner et al. 1985, Sellner and Brownlee 1986). Mesozooplankton biomass was highest in spring and lowest during the summer. Also, daily rates of spring zooplankton production exceeded those of summer (Figs. 2–5). Productivities of all the other heterotrophic components were higher in summer than during any other season.

Phytoplankton (1) are grazed by a variety of consumers with special vigor during spring and summer, when  $\approx 35\%$  of phytoplankton net production is consumed (compared to 10% in fall and 14% in winter).

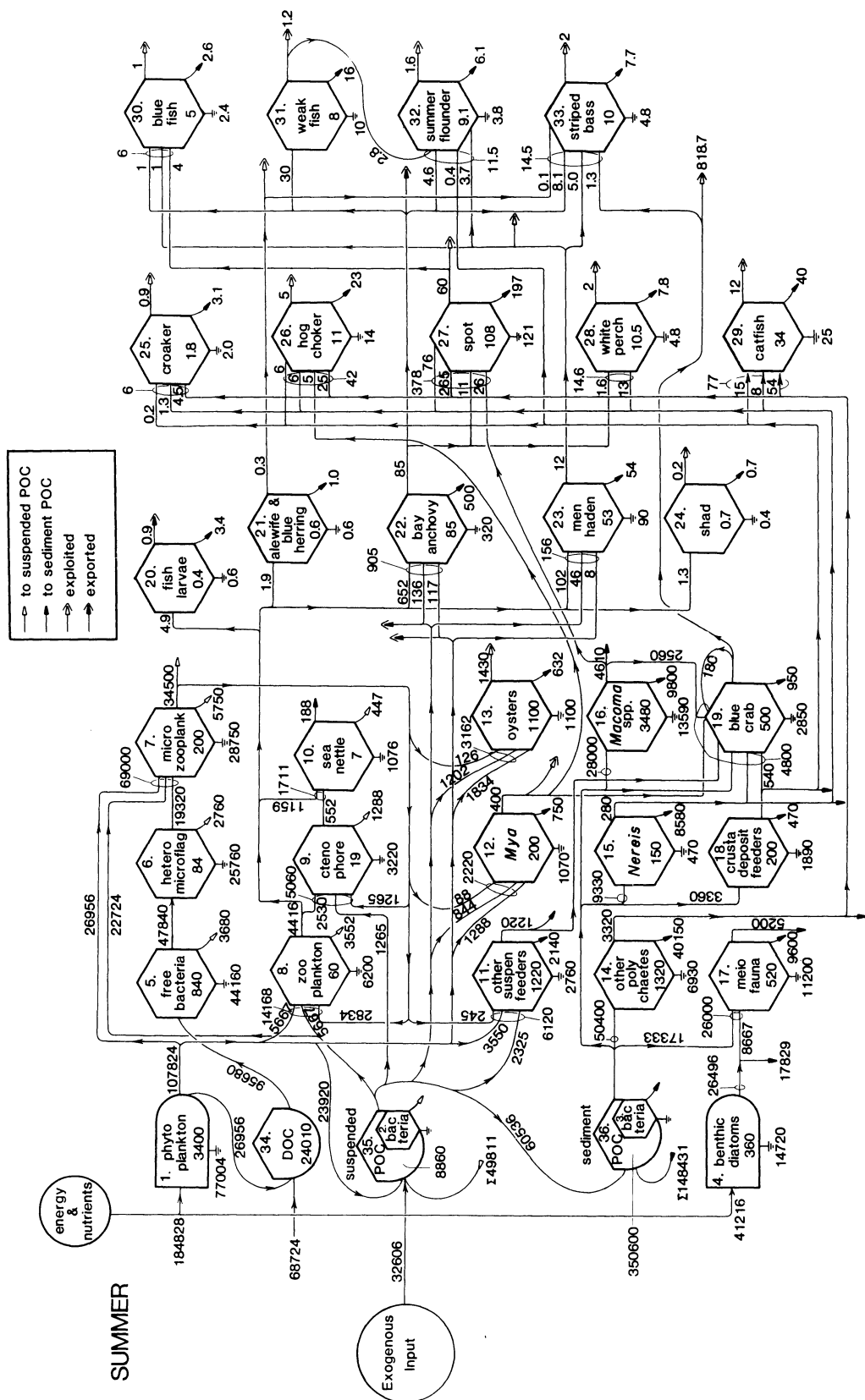
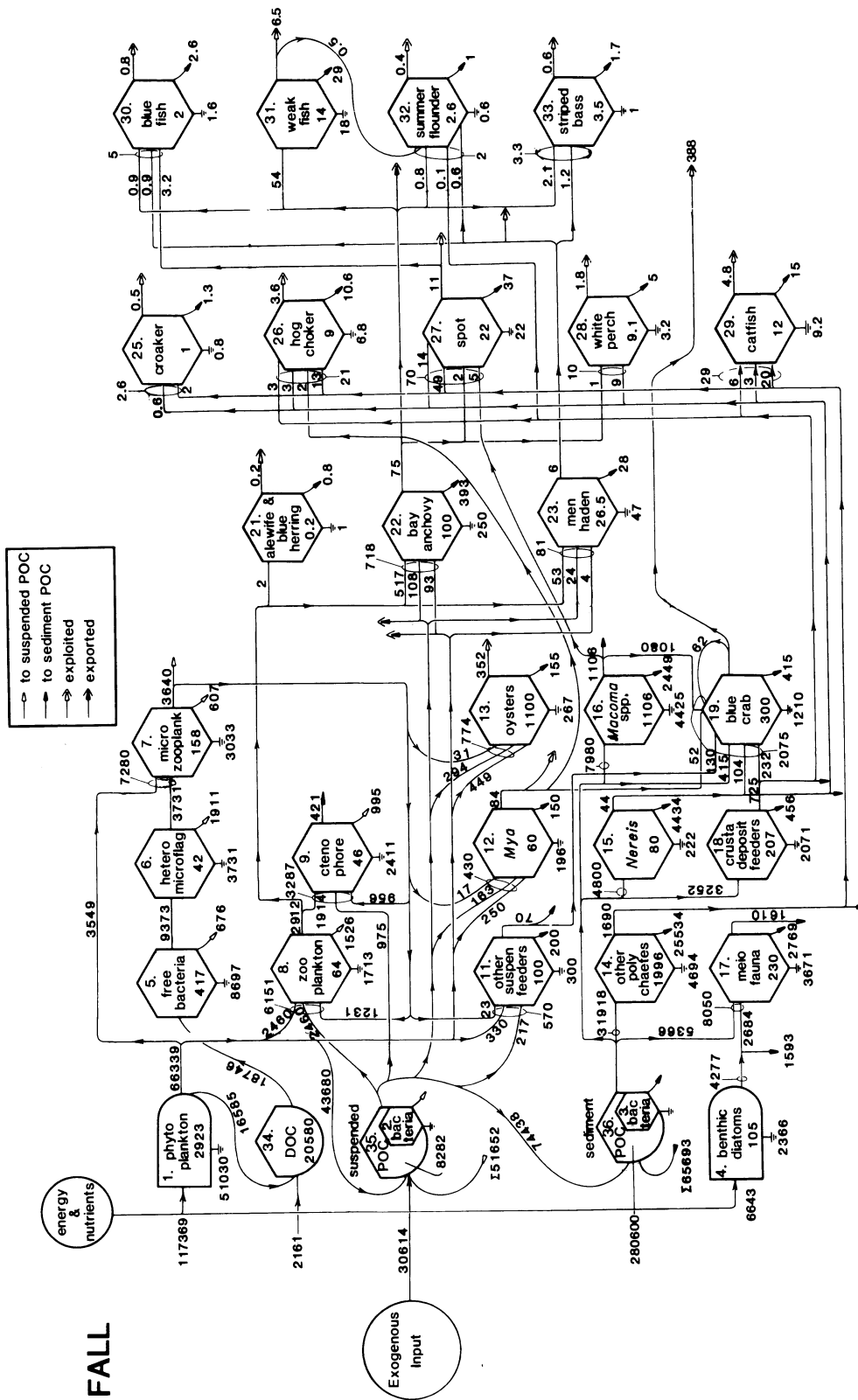


FIG. 2. Energy flow network of the mesohaline area of Chesapeake Bay during summer (biomass C in  $\text{mg}/\text{m}^2$ , carbon flows in  $\text{mg}/\text{m}^2$ , summer  $^{-1}$ ).





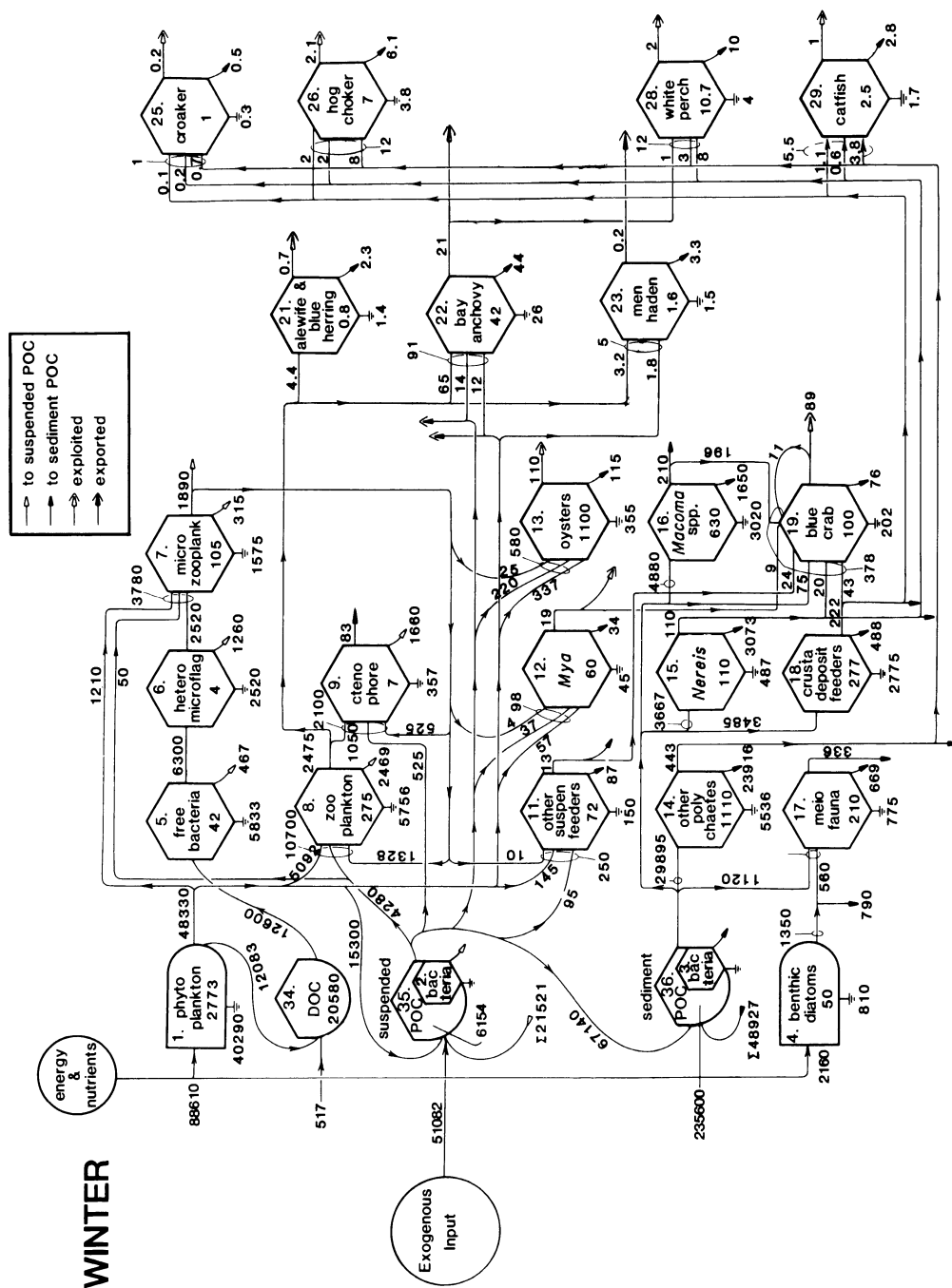


Fig. 4. Energy flow network of the mesohaline area of Chesapeake Bay during winter (biomass C in mg·m<sup>-2</sup>·winter<sup>-1</sup>).



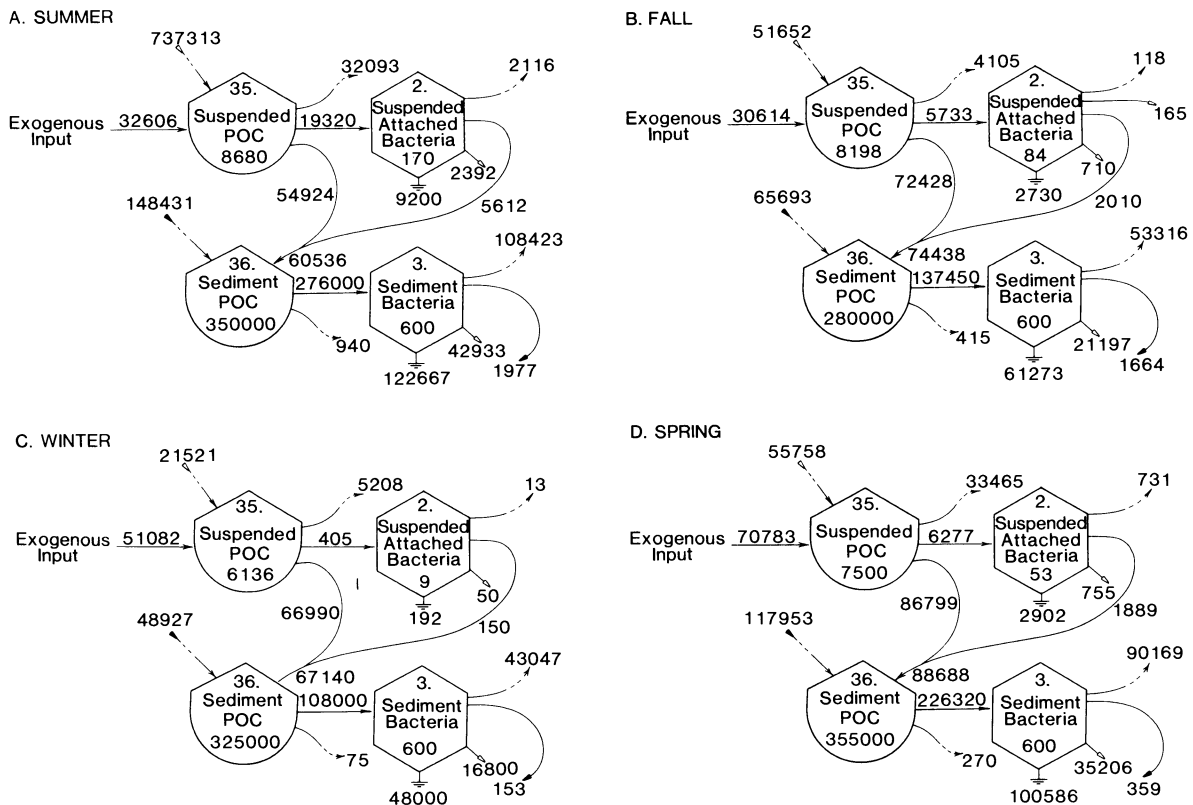


FIG. 6 Seasonal biomass and flows of passive storage compartments (35 and 36), attached bacteria (2) and sediment bacteria (3). Biomass C in  $\text{mg}/\text{m}^2$  and carbon flows in  $\text{mg}\cdot\text{m}^{-2}\cdot\text{season}^{-1}$ . Dotted lines represent aggregated exchanges with other compartments. (n. b., according to available data the sediment POC [particulate organic carbon] is not in balance.)

Zooplankton (8) are the dominant herbivores during spring, when they graze 32% of the phytoplankton production. However, their utilization drops off to only 5.3% in summer, 3.7% in fall, and 10.5% in winter. Ungrazed phytoplankton production would be even greater during summer were it not for significant utilization (25%) by the microzooplankton (7). In addition to mortality from grazing, phytoplankton cells can also die naturally, become part of the suspended detritus pool (35), and possibly sink to the bottom. Sedimentation rates of phytoplankton from the mesohaline photic zone have been measured by Boynton et al. (1985, 1986), who show that  $\approx 65\%$  of the fall, 31% of the winter, 39% of the spring, and 22% of the summer net populations exit the water column in this way. Storm-driven resuspension of organic carbon is insignificant at the scale of the whole system (W. Boynton, *personal communication*). On an annual basis  $\approx 5.8\%$  of the phytoplankton production could not be accounted for, with the excesses appearing mostly in summer (9.4% during that season) and winter (15.9%).

Estimates of the release of dissolved organic material from phytoplankton cells range from 5% to as much as 50% of net photosynthate (Fogg et al. 1965, Berman and Holm-Hansen 1974, Sharp 1977, Larson and Hagstrom 1979, Vegter and de Visscher 1984). In the

absence of information on the temporal variability of exudation we have assumed that a constant 25% of the net production is lost as dissolved organic carbon (DOC), which in turn is eventually utilized by free-living bacteria (Wiebe and Smith 1977, Larson and Hagstrom 1979, Sellner 1981, Wolter 1982, Azam et al. 1983, Ducklow 1983, Linley et al. 1983, Laanbroek et al. 1985, Joint and Williams 1985, Findlay et al. 1986). Taylor et al. (1985) have suggested that carbon released in exudates from bacterivorous protozoans and DOC lost from algal cells during zooplankton grazing also contribute significantly to the DOC pool (Lampert 1978, Copping and Lorenzen 1980).

Biomasses and production figures for bacterioplankton (5), heterotrophic microflagellates (6) (in nanoplankton size range 2–20  $\mu\text{m}$ ), and microzooplankton (7) (20–200  $\mu\text{m}$ , including taxa such as tintinnid ciliates, rotifers, sarcodinians, copepod nauplii stages) were highest in the summer and lowest in winter (Table 2 and Figs. 2–5). Heterotrophic microflagellates (7) appear to be the principal, if not the only, consumers of free planktonic bacteria in aquatic ecosystems (Haas and Webb 1979, Azam et al. 1983, Ducklow 1983, Linley et al. 1983, Davis and Sieburth 1984, Wright and Coffin 1984, Andersen and Fenchel 1985, Caron et al. 1985, Gast 1985, Rassoulzadegan and Sheldon

TABLE 2. Seasonal biomass and production values (both as carbon) for the main trophic aggregations in the mesohaline region of Chesapeake Bay. S = summer, F = fall, W = winter, SP = spring. DOC = dissolved organic carbon. POC = particulate organic carbon.

Aggregation	(Model compartment)*	Biomass C (mg/m <sup>2</sup> )					
		S		F		W	
		$\bar{X}$	(SD)	$\bar{X}$	(SD)	$\bar{X}$	(SD)
Phytoplankton	(1)	3400	(850)	2923	(876)	2773	(582)
Attached bacteria	(2)	170	(100)	84	(34)	9	(3)
Sediment bacteria	(3)	600	(—)	600	(—)	600	(—)
Benthic diatoms	(4)	360	(84)	105	(24)	50	(9)
Microzooplankton	(5–7)	1124	(620)	617	(241)	151	(67)
Zooplankton	(8–10)	86	(18)	110	(25)	282	(85)
Suspension feeders	(11–13)	2520	(1100)	1260	(630)	1232	(1240)
Deposit feeders	(14–19)	6170	(2470)	3919	(1175)	2437	(536)
Suspension-feeding fish	(20–24)	139.7	(34)	126.7	(25)	44.4	(8.8)
Benthic-feeding fish	(25–29)	165.3	(50)	53.1	(13.8)	65.6	(11.8)
Carnivorous fish	(30–33)	32.1	(9.6)	21.6	(4.2)	0	
DOC	(34)	24010	(847)	20580	(1246)	20580	(1246)
Suspended POC	(35)	8680	(3140)	8189	(3200)	6163	(2180)
Sediment POC	(36)	350000	(—)	280000	(—)	325000	(—)

\* Compartment numbers in Figs. 2–6.

1986). Microzooplankton (7) are known to feed most effectively on particles in the nanoplankton size range (Heinbokel 1978, Rassoulzadegan and Ettiene 1981, Jonnson 1986, Sheldon et al. 1986). We have assumed that the microzooplankton community (7) consumes all of flagellate (6) production each season, and that the remainder of its energy demand is satisfied by phytoplankton and suspended detritus in the nanoplankton size range (Heinbokel 1978, Fenchel 1982, 1984, Heinbokel and Beers 1979, Capriulo and Carpenter 1983, Verity 1985). Sherr and Sherr (1987) have suggested that ciliate protozoans may also graze effectively on bacteria.

The direct consumption of microzooplankton (e.g., tintinnids, rotifers, etc.) by various predators (e.g., copepods) has been suggested, but very few quantitative field data are available (most probably because these organisms have no hard body parts and are difficult to detect in samples of stomach contents). Stoeckers and Sanders (1985) have observed preferential feeding on tintinnids (*Favella* spp.) by the copepod *Acartia tonsa*, even when algae (dinoflagellates) were more readily available; hence, microzooplankton may play a much larger role in food web dynamics than had been thought. In the absence of any clear consensus on the contribution of microzooplankton to the diets of their possible predators, we have used available information to estimate that the diets of zooplankton (8) and ctenophores (9) consist of between 15 and 25% microzooplankton and those of suspension feeders (11, 12, 13)  $\approx$  4%.

The zooplankton community (8) is dominated in summer and fall by the calanoid copepod *Acartia tonsa*, and in late winter and spring by another copepod, *Eurytemora affinis* (Heinle 1966, Jacobs et al. 1985). Zooplankton feed mainly on phytoplankton and suspended

detrital particles (Paffenhofer and Strickland 1970, Frost 1972, Heinle and Flemer 1975, Poulet 1976, Roman 1977, 1984a, b, Price et al. 1983). Recent evidence also suggests that microzooplankton, such as tintinnid ciliates, may form a substantial proportion of the zooplankton diet (Berk et al. 1977, Robertson 1983, Turner and Anderson 1984, Stoecker and Sanders 1985, Williamson and Butler 1986). Zooplankton production amounts to  $\approx$  4 or 5% of phytoplankton production from summer through winter, but peaks substantially to 24% during spring.

The ctenophore, *Mnemiopsis leidyi* (9) occurs in Chesapeake Bay throughout the year with greatest densities in summer and fall. It feeds predominantly on zooplankton, and to a lesser extent on suspended detritus and microzooplankton (Bishop 1967, Kremer 1979, Deason and Smayda 1982a). It does not appear to ingest phytoplankton (Deason and Smayda 1982b). The sea nettle, *Chrysaora quinquecirra* (10), present in the Bay only during summer and early fall, feeds voraciously on ctenophores, as well as on zooplankton and fish larvae (Heinle 1966, Miller 1974, Clifford and Cargo 1978, Moller 1980, Feigenbaum et al. 1982, Feigenbaum and Kelly 1984).

The biomass of subtidal, benthic diatoms has been estimated from chlorophyll *a* measurements conducted on live organisms present on the sediment surface (Boynton et al. 1986). Benthic diatom biomass and production are highest in the summer and lowest in winter. About 35% of the benthic microflora production is consumed by meiofauna, with the rest becoming sediment POC (36) (W. Boynton, *personal communication*).

The principal source of benthic POC is the sedimentation of organic matter produced in the photic zone. The sedimentation rate appears in Figs. 2–5 as

TABLE 2. Continued.

Biomass C (mg·m <sup>-2</sup> )		Production C (mg·m <sup>-2</sup> season <sup>-1</sup> )							
SP		S		F		W		SP	
$\bar{X}$	(SD)	$\bar{X}$	(SD)	$\bar{X}$	(SD)	$\bar{X}$	(SD)	$\bar{X}$	(SD)
482	(868)	107824	(84100)	66339	(40000)	48330	(26500)	74520	(44700)
53	(30)	7728		2293		163		2620	
600	(-)	110400		54980		43200		90528	
194	(68)	26496		4277		1350		17848	
421	(158)	101660		16744		10715		38327	
396	(96)	5156		3333		2558		18069	
1283	(650)	3050		506		142		1390	
4656	(1380)	15140		5725		1321		11088	
113.1	(29.4)	98.4		81.2		21.9		78	
131.5	(42)	67.9		21.7		5.3		42.6	
15.3	(4)	8.6		8.8		0		6.1	
Seasonal turnover rates									
22260	(5397)	4.0		0.9		0.6		2.3	
7500	(1890)	12.3		10.0		11.8		16.8	
355000	(-)	0.8		0.5		0.3		0.6	

the flux of suspended POC (35) to sediment POC (36) and was measured using sediment traps placed at various locations in the mesohaline region of Chesapeake Bay (Boynton et al. 1985, 1986). Using Boynton's data we have estimated that  $\approx 53\%$  of the total input to sediment POC was deposited from the well-mixed water column during fall, 58% during winter, and 45% during spring. In the summer, when the water column is stratified (Malone et al. 1986), only 30% of the total inputs into sediment POC came from the water column. Remaining sources of POC were biodeposition (egestion and mortality) from benthic organisms.

Bacterial biomass in the top 6 cm of Chesapeake Bay sediments was estimated by multiplying the observed mean counts of  $10^9$  cells/mL of sediment as averaged over the seasons, by an approximate carbon content of  $10^{-14}$  g/cell. Bacterial productivities during fall, winter, and spring are respectively  $\approx 50$ , 40, and 80% of that during the summer, when the turnover rate is  $\approx 12$  h. Throughout the seasons the carbon conversion efficiency of sediment bacteria was assumed to be 40%.

The benthic invertebrate community essentially consists of three groups, suspension feeders (11–13), deposit feeders (14–18), and the predator/scavenger blue crab (19). The suspension feeders (bivalve molluscs) retain particles  $>4 \mu\text{m}$  with 100% efficiency (Mohlenberg and Riisgard 1978, Wright et al. 1982) and feed mainly on phytoplankton, suspended detritus, and microzooplankton (Figs. 2–5). Because of their commercial importance (Stagg 1986), the clam *Mya arenaria* (12) and the oyster *Crassostrea virginica* (13) were treated separately from "other" suspension feeders (11), such as *Rangia cuneata* and *Mulinia lateralis*.

The deposit feeders consist mainly of *Nereis succinea* (15), "other" polychaetes (14, e.g., *Heteromastus filiformes*, *Scololepides viridis*), tellinid bivalves (16, *Ma-*

*coma* spp.), amphipod crustaceans (18, *Corophium lacustrae* and *Leptocheirus plumulosus*), and meiofauna (17). With the exception of meiofauna, which partially subsist on benthic diatoms (Montagna 1984), these faunal groups obtain their energy primarily from sediment bacteria (Figs. 2–5). The commercially exploited blue crab, *Callinectes sapidus* (19), is the foremost benthic scavenger/predator in Chesapeake Bay. About 60% of its diet consists of mollusc bivalves, and the remainder of polychaetes, amphipods, dead fish, and juvenile blue crabs (Darnell 1958, Tagatz 1968, Virnstein 1977, Nelson 1981, Paul 1981). Rates of consumption, respiration, egestion, production, and predation for the benthic community are shown in Figs. 2–5.

Trophic studies on the most abundant fish species in the mesohaline region of Chesapeake Bay have shown that this community can be grouped into three broad categories. The first group is composed of the suspension feeders, namely fish larvae (20), alewives and herring (21), bay anchovy (22), menhaden (23), and shad (24). These species feed predominantly on phytoplankton and zooplankton (Figs. 2–5 and references in Table 1). The biomass and productivity of this group both reach their maximum levels during the summer. Fish larvae are present in significant numbers in the mesohaline region only during summer and are usually dominated by bay anchovy. Shad migrate out of the area during fall and winter to return the following spring. The second major group of nekton consists of the Atlantic croaker (25), hogchoker (26), spot (27), white perch (28), and catfish (29), all of which feed mainly on benthic macroinvertebrates. Spot was the most abundant of these species during summer and fall, and the white perch was most common during winter and spring. The third group of piscivorous fish (bluefish [30], weakfish [31], summer flounder [32], and striped

TABLE 3. Seasonal production of primary producers, water column, benthic, and nektonic communities expressed as a percentage of total annual productivity.

Community	Season % annual production				Annual produc- tion, as C (g/m <sup>2</sup> )
	S	F	W	SP	
Primary producers (1, 4)*	39	20	14	27	347
Water column invertebrates (2, 5–10)	55	11	6	28	209
Macro- and meiobenthos (11–19)	48	16	4	32	33.7
Nekton (20–33)	41	25	6	28	0.45
All communities	45	17	11	27	595.5

\* Numbers of model compartments in Figs. 2–6.

bass [33]) feed mainly on bay anchovy and menhaden (Figs. 2–5). These species reach their maximum biomasses during summer and are all subject to commercial exploitation. They emigrate from the mesohaline area during winter (Figs. 2–5).

The number of species of waterfowl overwintering in Chesapeake Bay has declined significantly over the past 25 yr, apparently because the reduction in submerged aquatic vegetation has caused them to seek alternative feeding areas (Perry et al. 1981, Perry and Uhler 1982). Six species of diving ducks (Canvasback, scaup, goldeneye, Bufflehead, and scoters) feed mainly on estuarine invertebrates, such as polychaetes, amphipods, and bivalve molluscs (*Rangia cuneata*, *Mulinia lateralis*, *Macoma* spp.). Based on the numbers of diving ducks together with their average daily energy intake (Perry et al. 1981, Perry and Uhler 1982), we have estimated that the consumption (as C) by these species in the mesohaline area during winter is  $\approx 15$  mg/m<sup>2</sup>, which is  $\approx 1.5\%$  of the production of their benthic prey. Hence, we have not included the waterfowl as a component in our budgets.

## DISCUSSION

### Seasonal patterns

Biological activity peaks in summer, decreases through the fall and winter, and rises again during the spring. These features would be lost in any evaluation of only annual means. Estimates of seasonal production in four large aggregated communities are given in Table 3, expressed as the percentage of total annual production of each group. These data clearly illustrate the aforementioned annual pattern of change.

The main inputs of carbon (and energy) to the system take the forms of primary production (mainly by phytoplankton) and, to a lesser extent, influx of suspended detritus (calculated by difference). Nutrient inputs and increasing temperatures during spring are generally considered to trigger the onset of the wave of biological activity that persists through spring and summer (Boynton et al. 1982, Malone et al. 1986).

The ecological roles of free bacteria, microflagellates, and microzooplankton (the “microbial loop” of aquatic ecosystems) are widely recognized (Azam et al. 1983, Ducklow 1983) but poorly quantified. These organisms are ubiquitous in Chesapeake Bay waters (Tuttle et al. 1985, 1986, Sellner and Brownlee 1986). We have estimated that a relatively large fraction of the phytoplankton net production is utilized by free bacteria and microzooplankton. During summer, fall, winter, and spring the respective proportions of phytoplankton net production that are channeled through the microbial loop are  $\approx 50$ , 30, 28, and 25%.

The proportion of annual phytoplankton production consumed by herbivores in other ecosystems varies from 84% in Narragansett Bay (Kremer and Nixon 1978), to 40% along the Belgian coast (Joiris et al. 1982), to 28% in the Lynher estuary, Cornwall (Warwick et al. 1979). The cropping of phytoplankton in Chesapeake Bay will certainly be influenced by the seasonal abundance of herbivores. Consumption of phytoplankton is low during fall and winter when only 10–14% of net primary production is utilized. However, during spring, 36% of net phytoplankton production is grazed, mainly by zooplankton (32%). During summer about the same fraction is consumed (this time 25% of the grazers are microzooplankton).

The high rate of phytoplankton production during the summer coincides with a notably low zooplankton biomass, a phenomenon also observed by Hargrave et al. (1985) in St. Georges Bay, Gulf of St. Lawrence, and by Williams et al. (1968) in estuaries along the northeast coast of the United States. In Chesapeake Bay, predation on zooplankton by ctenophores, sea nettles, and fish is highest during summer and actually exceeds the zooplankton production thereby causing a decline in zooplankton standing stock. The production and biomass of zooplankton were much higher during spring (Table 2 and Figs. 2–5), concomitant with an increasing phytoplankton production and a dearth of major predators. Hence, it appears that predators control zooplankton and other herbivore populations during summer, thereby making more phytoplankton production available for consumption by bacteria and other protozoans. The evidence available to us supports previous suggestions that phytoplankton dynamics can be indirectly regulated by grazing pressure on zooplankton (Hargrave et al. 1985).

The decline in the biomass and heterotrophic productivity of macrobenthic invertebrate communities in Chesapeake Bay during late summer and fall is well documented. It can be attributed mainly to predation by crabs and nekton, and to the additional mortality caused by physical stresses, such as decreasing water temperature and low dissolved oxygen concentrations (Holland et al. 1977, 1980, Kemp and Boynton 1981, Holland 1985, Tuttle et al. 1985, 1986). Predators on the macrobenthos (mainly the blue crab and fish species, such as the hogchoker, spot, white perch, croaker, and

catfish) collectively remove 40% of the summer and 45% of the fall production of their prey. These ratios decline to 28% in winter and 17% in spring.

Trophic interactions among the various fish populations (Figs. 2–5) reveal that no less than six species of fish feed directly on the bay anchovy. Seasonally, piscivores consume 66, 80, 5, and 54% (summer through spring) of the anchovy's secondary production. The bay anchovy also comprises a significant fraction of the total energy intake by the truly carnivorous fish species (30–33), contributing 70, 90, and 60% to their diet during summer, fall, and spring, respectively (Figs. 2–5). In turn, the bay anchovy is a major consumer of zooplankton. It indeed occupies a key position in the food web, yet information on its general ecology remains scarce.

#### *Indirect influences*

While observations on the direct trophic interactions reveal much about the workings of the ecosystem, knowing virtually the full complement of biomasses and flows allows one to quantify all the indirect influences (i.e., the effects of serial trophic interactions) as well (Hannon 1973, Patten et al. 1976). More recently, Szyrmer and Ulanowicz (1987) have outlined how one can calculate the degree to which the diet of any particular species depends, directly and *indirectly*, upon the production of any other member of the ecosystem.

Without going into detail, the calculation of indirect dependencies is accomplished using the matrix of direct dietary coefficients, wherein the fractions by which each prey species (defining the rows) contributes to the diet of each predator population (listed down the columns) are arrayed. This matrix has the convenient property that when it is multiplied by itself (squared), the components of the product matrix represent the sources of input to each predator from all indirect prey sources one trophic link away. Similarly, the third power of the diet matrix yields the fractions by which all indirect prey two trophic steps removed contribute to the predators, etc. The sum of all the powers of the diet matrix forms an infinite series that can be shown in the limit to converge to a matrix akin to the matrix of total dependencies as defined by Szyrmer and Ulanowicz (1987).

The entire suite of such "total dependency coefficients" for the 36 compartments (expressed as percentages of total consumption) of the Chesapeake system are displayed in Table 4. The matrix reads from donors along the rows to recipients down the columns. For example, looking along row 8 will show the percentages of each species' total intake which has arrived at that compartment after passing through the mesozooplankton. Perhaps more interestingly, reading down any column defines the "extended diet" of that species. For example, reading down column 30 shows that 44% of the bluefish diet was once phytoplankton, 3.1% bac-

teria in suspended POC, 64% bacteria in sediment POC, etc. Because the same carbon may visit several compartments before it is consumed by a particular animal, the sum of the figures in any column will usually exceed 100%. In fact, the sum of any column is related to the trophic position of that species (cf. Levine 1980 and the analysis below).

Comparing the extended diets of two predators often will illuminate differences that are not apparent from contrasting their direct diets. For example, bluefish (30) and striped bass (33) are both pelagic piscivores, as may be seen in Figs. 2–5. However, their extended diets are not at all similar. The striped bass depend mainly on three components of the planktonic community—64% on phytoplankton, 12% on microzooplankton, and 66% on mesozooplankton. No benthic compartment accounts for >8% of its extended diet. Bluefish, on the other hand, rely strongly on material passing through benthic organisms. About 63% of bluefish prey was once benthic bacteria and 48% passed through polychaetes. Only 29% of bluefish food has passed through zooplankton. These results may help to explain why large residues of the pesticide Kepone appeared in the flesh of bluefish after the James River sediments were heavily contaminated by that toxin during the 1970s. No proportionate concentrations appeared in striped bass samples.

Bluefish appear to be the only piscivorous fishes that are strongly coupled to the benthos. The diet of weakfish (31) mirrors the extended diet of the striped bass rather closely, and that of the benthic-feeding flounder (32) resembles the striped bass more than it does the bluefish. The other carnivorous fishes (croaker, hogchoker, spot, white perch, and catfish) are all tied strongly to the benthos (as can be seen in the list of their direct prey). To no one's surprise suspension-feeding fish possess an indirect diet characteristic of a pelagic feeder. There is the hint of a pelagic trophic chain evident in the indirect diets of the series: free bacteria, microzooplankton, zooplankton, ctenophores, and sea nettle.

The diagonal elements of the total dependency matrix give the amounts by which each species is dependent upon its own kind via cyclic pathways. These diagonal fractions are generally quite low, with only three exceeding 10%. As might have been expected, the recycle through the benthic POC and its attached bacteria are the highest (both  $\approx 44\%$ ). Only one other component engages in a high degree of recycling. About 25% of polychaete consumption comes indirectly from its own production. This fraction is approximately five times the recycle exhibited by the meiofauna and *Nereis*. Such a fivefold difference seems puzzling at first in light of the observation that the fractional contributions from the compartment "other polychaetes" do not differ significantly from those of its coinhabitants of the benthos. We conclude that the high recycle through (14) is purely a consequence of scale and ag-



TABLE 4. Total Dependency Coefficients: the percentage of carbon arriving at the column designation that once passed through the row index. Compartment numbers are those shown in Figs. 2–6. Coefficients are calculated from the annual flows shown in Fig. 7.

Donor compartment	Recipient compartment																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	0.0	42.7	31.2	0.0	41.8	41.8	63.5	68.4	60.8	66.0	75.8	76.8	76.8	31.2	31.2	31.2	20.8	31.2
2	0.0	1.4	3.3	0.0	0.0	0.0	2.0	2.1	2.8	2.3	2.7	2.4	2.0	3.3	3.3	3.3	2.2	3.3
3	0.0	0.0	44.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0	100.0	66.7	100.0
4	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	10.0	10.0	40.0	10.0
5	0.0	9.7	6.8	0.0	0.0	100.0	39.3	8.1	16.3	10.8	5.2	5.2	5.2	6.8	6.8	6.8	4.6	6.8
6	0.0	7.8	5.5	0.0	0.0	0.0	38.8	7.2	15.2	9.8	4.5	4.5	4.5	5.5	5.5	5.5	3.7	5.5
7	0.0	11.4	8.2	0.0	0.0	0.0	3.0	14.2	34.9	20.9	8.2	8.3	8.3	8.2	8.2	8.2	5.4	8.2
8	0.0	6.8	5.1	0.0	0.0	0.0	1.8	3.6	52.2	84.6	2.6	2.7	2.7	5.1	5.1	5.1	3.4	5.1
9	0.0	1.7	1.4	0.0	0.0	0.0	0.5	0.9	1.0	32.9	0.7	0.7	0.7	1.4	1.4	1.4	0.9	1.4
10	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1
11	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.9	0.9	0.6	0.9
12	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.3	0.2	0.3
13	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.4	0.2	0.4
14	0.0	0.0	24.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.7	24.7	24.7	16.5	24.7
15	0.0	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	5.2	5.2	3.5	5.2
16	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.6	5.6	5.6	3.7	5.6
17	0.0	0.0	6.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9	6.9	6.9	4.6	6.9
18	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.7	1.0
19	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.4	0.3	0.4
20	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	0.0
21	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	0.0
22	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.3	0.2	0.3
23	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	0.0
24	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	0.0
25	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	0.0
26	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	0.0
27	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.1
28	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	0.0
29	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	0.0
30	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	0.0
31	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	0.0
32	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	0.0
33	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	0.0
34	0.0	9.7	6.8	0.0	100.0	100.0	39.3	8.1	16.3	10.8	5.2	5.2	5.2	6.8	6.8	6.8	4.6	6.8
35	0.0	100.0	70.3	0.0	0.0	0.0	26.4	51.9	57.6	53.7	38.6	39.0	39.1	70.3	70.3	70.3	46.8	70.3
36	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0	100.0	66.7	100.0

gregation. The “other polychaetes” component is by far the largest single contributor of detritus back into the benthic pool; hence, they also have the highest probability of capturing that material after its first pass through the sediment POC. Had compartment 14 been disaggregated into individual species, it is unlikely that any one of them would feed on itself to the extent of the aggregate. In interpreting the importance of recycle in a system one should constantly bear in mind that the perceived amount of recycle tends to rise as the degree of aggregation increases.

The indirect diets do not vary overwhelmingly on a seasonal basis. Most of the significant changes that do occur are the result of seasonal shifts that occur low in the planktonic food web. (Matrices of total dependencies for each of the four seasons are not presented here in the interest of conserving space.) As mentioned in the preliminary observations, there is a significant shift in the planktonic food chain between spring and summer. During spring there is a major zooplankton bloom that crops the phytoplankton. As spring progresses into

summer, the zooplankton population falls, presumably due to increased predation by ctenophores; however, the primary production continues at very high levels into summer, and the “excess” production is shunted into the components of the “microbial loop” (including the microzooplankton). This shift ramifies up the trophic web, and most of the significant seasonal changes observed in the extended diets of higher trophic level species can be traced to this change in the planktonic community. Some of the magnitudes of change are remarkable. On an annual basis the striped bass depends on the microzooplankton (e.g., ciliates) for  $\approx 12\%$  of its sustenance; however, most of that indirect flow occurs during summer, when the dependency reaches a surprising 30%. In general, the dependencies of all species upon members of the “microbial loop” are larger during the summer.

A secondary seasonal pattern in indirect flows appears to be a consequence of the relative shutdown of productivity by benthic diatoms during fall and winter seasons. Deposit feeders and their predators all register

TABLE 4. Continued.

Recipient compartment																	
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
35.2	68.4	68.4	68.7	62.6	68.4	31.2	35.4	32.3	34.8	31.2	43.7	68.7	65.4	63.9	41.8	42.7	31.2
3.2	2.1	2.1	2.3	3.1	2.1	3.3	3.2	3.3	3.2	3.3	3.1	2.3	2.6	2.7	0.0	1.4	3.3
79.5	0.0	0.0	0.0	0.0	0.0	100.0	90.6	97.0	90.2	100.0	63.8	0.0	3.5	6.3	0.0	0.0	44.1
9.1	0.0	0.0	0.0	0.0	0.0	10.0	9.1	9.7	9.0	10.0	6.4	0.0	0.4	0.7	0.0	0.0	10.0
6.7	8.1	8.1	7.3	8.1	8.1	6.8	6.7	6.9	6.9	6.8	7.2	7.3	7.6	7.6	0.0	9.7	6.8
5.4	7.2	7.2	6.3	7.0	7.2	5.5	5.4	5.6	5.6	5.5	5.9	6.3	6.5	6.5	0.0	7.8	5.5
8.2	14.2	14.2	11.9	12.6	14.2	8.2	8.2	8.3	8.5	8.2	9.6	11.9	12.0	11.9	0.0	11.4	8.2
4.9	100.0	100.0	73.0	67.3	100.0	5.1	4.9	7.2	11.8	5.1	28.7	73.0	68.8	65.8	0.0	6.8	5.1
1.3	0.9	0.9	0.9	1.1	0.9	1.4	1.3	1.4	1.3	1.4	1.2	0.9	1.0	1.0	0.0	1.7	1.4
0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	0.1	0.1
7.2	0.0	0.0	0.0	0.0	0.0	0.9	0.8	0.8	0.8	0.9	0.5	0.0	0.0	0.6	0.0	0.0	0.9
2.9	0.0	0.0	0.0	0.0	0.0	0.3	9.7	0.3	0.3	0.3	0.2	0.0	0.0	0.2	0.0	0.0	0.3
0.3	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.4	0.3	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.4
22.5	0.0	0.0	0.0	0.0	0.0	81.2	68.7	73.0	60.5	77.4	48.0	0.0	0.9	1.8	0.0	0.0	24.7
8.8	0.0	0.0	0.0	0.0	0.0	26.0	18.6	24.1	42.1	15.0	15.9	0.0	0.2	0.7	0.0	0.0	5.2
56.6	0.0	0.0	0.0	0.0	0.0	5.6	5.0	16.2	5.0	5.6	10.6	0.0	0.2	4.5	0.0	0.0	5.6
6.3	0.0	0.0	0.0	0.0	0.0	6.9	6.2	6.7	6.2	6.9	4.4	0.0	0.2	0.5	0.0	0.0	6.9
12.4	0.0	0.0	0.0	0.0	0.0	4.1	15.3	1.4	0.9	20.5	0.9	0.0	3.5	1.0	0.0	0.0	1.0
3.8	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.4	0.4	0.4	0.3	0.0	0.0	7.9	0.0	0.0	0.4
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	0.0
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	0.0
0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.3	3.3	10.0	0.3	19.6	100.0	65.1	56.6	0.0	0.0	0.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.8	0.0	31.4	34.9	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	0.0	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	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	0.0	0.0	0.0	0.0	0.0
0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	65.8	0.0	0.0	0.0	0.0	0.0	0.1
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	0.0
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	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	0.0	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	16.9	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	0.0	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	0.0	0.0	0.0	0.0	0.0
6.7	8.1	8.1	7.3	8.1	8.1	6.8	6.7	6.9	6.9	6.8	7.2	7.3	7.6	7.6	0.0	9.7	6.8
67.4	51.9	51.9	52.4	63.1	51.9	70.3	67.3	69.7	68.5	70.3	65.6	52.4	56.4	57.3	0.0	7.6	70.3
90.9	0.0	0.0	0.0	0.0	0.0	100.0	90.6	97.0	90.2	100.0	63.8	0.0	3.5	7.2	0.0	0.0	44.1

reduced dependencies on benthic primary production during colder months.

#### *Trophic structure*

Since its introduction by Lindeman (1942), the concept of a trophic chain has held great intuitive appeal for ecologists. Although the idea permeates ecological discourse, it remains difficult to speak about diets of omnivorous organisms in a rigorous, quantitative way. Until recently it has also been impossible to describe unambiguously the chain of trophic transfers thought by many to underlie any web of ecosystem feeding relations. But now methods exist to interpret quantified, directed networks of ecosystem transfers in terms used by Lindeman (Ulanowicz 1986). The results of such analysis afford new and unique insights into well-studied ecosystems, such as that of the Chesapeake Bay.

The problem with applying Lindeman's trophic level concept to real ecosystems is that heterotrophic species rarely can be assigned to single trophic levels. Cousins

(1985), for example, remarks that a hawk feeds at five different levels, and this circumstance bodes ill for the idea of a trophic pyramid.

However, there is no logical necessity that trophic levels be collections of discrete (whole) populations. If the hawk apportions its activity over five levels, then it is appropriate to define the trophic groupings to reflect the fact. The proportion of feeding activity by a particular population at each trophic level should be assigned to those respective levels (Wiegert and Owens 1971). If one knows the dietary rations of all the species in an ecosystem, matrix algebra will effect an apportionment of each species' activity to the various trophic levels (Ulanowicz and Kemp 1979). Thus, for example, if the microzooplankton receive 61.6% of their sustenance from primary producers, 1.6% of their food over pathways of two trophic transfers, and 36.8% over pathways of three transfers, then their activity should be apportioned to trophic levels II, III, and IV in those respective amounts.

The mathematics of the apportionment are unam-

biguous only when no cycles are present in the web of feeding relationships (i.e., any trophic pathway exclusively through living compartments will not contain any element more than once). Fortunately, this is usually the case in most real ecosystems (Pimm 1982, May 1983). When cycles among feeding organisms do exist, the amounts of energy and materials being circulated are usually very small, and the cycles can be subtracted from the web without appreciably affecting the structure of the network (Ulanowicz 1983). Hence, intuitively realistic trophic apportionments may be achieved by confining the trophic analysis strictly to living populations.

Significant cycling is interjected into the trophic analysis as soon as connections with detrital materials are included in the study, and the description of trophic dynamics would be quite incomplete were these important circulations somehow omitted. Wiegert and Owens (1971) and Patten and Higashi (*in press*) prefer to retain detrital pathways in their calculations of trophic levels. This leads to an infinite number of trophic levels, albeit with vanishingly small activities at higher levels. It also tends to inflate artificially the trophic values of the detritus and the detritivores. Our preference is to base the trophic calculations unambiguously on active feeding transfers and to superimpose the recycled detritus back on the resulting trophic chain. But the question remains as to what trophic status to give to the detrital material. Cousins (1985) points out that it became common practice during the International Biological Program to assign detritus entirely to the first trophic level. Thus, organisms eating living plant material and those feeding on the same material after it had died naturally would both be treated as belonging to the second trophic level. Detritus from nonplant sources is treated in the same manner, thereby ignoring any differences among the qualities of detritus from various sources. We adopt this convention strictly as a matter of mathematical convenience, because it then becomes routine algebraic bookkeeping to apportion the cycled flows among the trophic levels using the trophic assignments derived from feeding relationships alone. The full technical details of determining trophic assignments involving detritus are described by Ulanowicz (*in press*).

Finally, one may also use the trophic apportionments for a given species to calculate the average trophic position of that population (Levine 1980). For example, the aforementioned microzooplankton population would feed 61.6% of the time at level II, 1.6% at level III, and 36.8% at level IV. On the average it is feeding at the noninteger level  $2.75 (=0.616 \times 2 + 0.016 \times 3 + 0.368 \times 4)$ . The values and rankings of the average trophic positions of ecosystem elements often yield useful insights into trophic dynamics.

In order to keep the discussion of results to manageable proportions it becomes useful at this point to aggregate the four seasonal networks represented in

Figs. 2–5 into the single gridwork of annual flows shown in Fig. 7. Much of the discussion in the following two sections will center about this network of annual flows. Nonetheless, all of the seasonal networks were separately analyzed, and whenever seasonal differences prove to be significant or otherwise interesting, they will be interjected into the discussion.

As was the case with Figs. 2–5, the two particulate detrital compartments (labeled POC on Fig. 7) require further elaboration. The separation of the detritus from the attached bacteria (the annual summary of the details shown in Fig. 6) is depicted in Fig. 8. The arrows with dots represent the aggregated exchanges with the other 32 components of the ecosystem. The particular exchanges with each of the other species are detailed in Table 5.

During three seasons of the year trophic pathways of length eight are present in the ecosystem network. During winter the virtual absence of top carnivores reduces the length of the longest pathways by one. The annual apportionments of each species to the eight levels are given in Table 6. The effective trophic levels at which the various species feed are ranked in Table 7 in ascending order.

It is remarkable that, despite the existence of several long pathways in the system, the highest effective trophic level of any species is only 4.59 (bluefish). Looking at Table 6, one sees that, although bluefish and summer flounder do obtain some of their sustenance at the eighth trophic level, neither receives an appreciable amount over those long concatenations. In fact, none of the seven species that do any feeding at levels VII or VIII receives more than 5% of its total ingestion via these long series of transfers. Most of their feeding is occurring at levels IV or V, and enough is taken at even lower levels to make their average trophic positions fall short of 5.

That highest predators do not exceed, on average, the fifth trophic level accords with the observations of Hutchinson (1959) and others. Why such a limit should exist (see Odum and Pinkerton 1955, Slobodkin 1961, Pimm and Lawton 1977) cannot be resolved by the available data, although there may be a trend towards decreasing trophic efficiency at higher levels (further discussion at the end of this section). Suffice it here to say that feeding *does* take place at trophic levels greater than five, but that the magnitudes (not necessarily the consequences) of such high-level carnivory are insignificant.

Another surprising observation from Tables 6 and 7 concerns the trophic position of the sea nettle (*Chrysaora quinquecirrha*). Its small standing stock belies the fact that this species consists mostly of water, making the medusa stage of this animal very visibly abundant during most of the summer season. Remarkably, it feeds higher on the food chain than do many commercially important species, such as oysters, clams, menhaden, anchovy, herring, shad, and blue crabs. (The

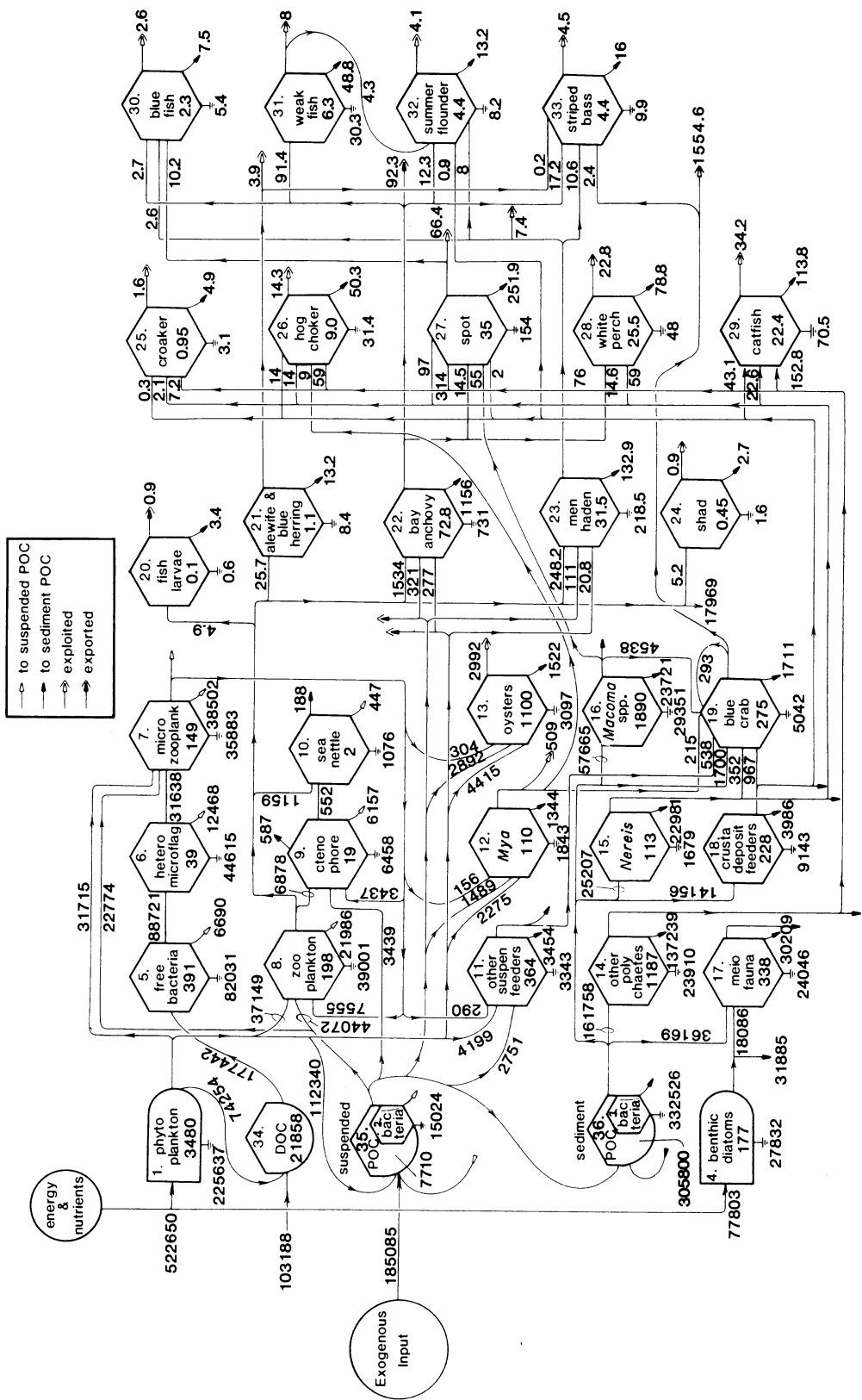


Fig. 7. Schematic representation of the annual carbon flows among the 34 principal components of the Chesapeake mesohaline ecosystem. Carbon standing crops are indicated within the compartments in  $\text{mg} \cdot \text{m}^{-2}$  and the indicated carbon flows are in  $\text{mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ .

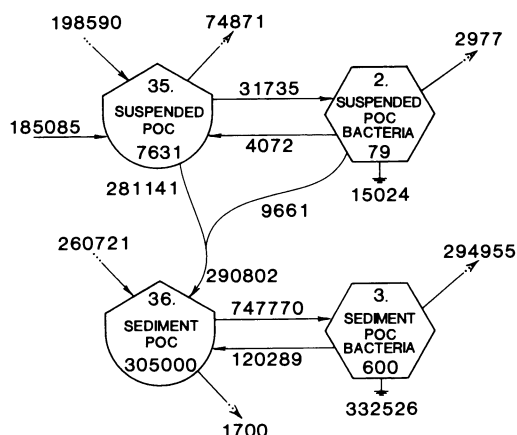


FIG. 8. Schematic representation of the conceptual separation of the living bacteria from the particulate detritus in components 2 and 3 of Fig. 7. Dotted arrows represent aggregated exchanges with the other 32 compartments. Units as in Fig. 7. (n. b., available data point to an annual deficit in sediment POC [particulate organic carbon].)

nettle actually ranks higher than the blue crab [3.58 vs. 3.51] during the summer—the only season during which medusae are abundant.) It will be shown in the next section that when these medusae are present in abundance, they also control the recycle of carbon among the members of the planktonic community. Thus, all signs point to this unimpressive animal as playing a significant role in the dynamics of the planktonic community. Practically all past research has centered on this organism as a pest, and pest it may be. However, the ecological impact of the sea nettle during the summer deserves more consideration than it has heretofore received.

For the most part, the effective trophic values of the various species vary little from season to season. The major exception is the shift of secondary production from zooplankton in spring to the microbial loop during summer. Microzooplankton, for example, feed at level 4.0 during spring, when they consume heterotrophic microflagellates. With the advent of summer, however, they rely mostly on copious phytoplankton and detritally attached bacteria, giving them an average trophic position of 2.58. The zooplankton actually increase their trophic status during summer and fall (2.34 and 2.42, respectively). During these seasons they must rely more on the ingestion of ciliates compared with their position during the spring (2.12), when they are busier cropping phytoplankton and bacteria. In contrast, there is a drop in the trophic status of ctenophores from spring to summer (3.32 vs. 3.08), apparently in response to the decrease in the trophic status of ciliates. This latter drop more than compensates for the concomitant rise in trophic status of the dominant ctenophore prey, the zooplankton. These changes ramify up the food web in ever-attenuating fashion, with secondary shifts most notable in the trophic indices of filter-feeding fish.

TABLE 5. Detailed listing of annual carbon exchanges from the two POC and two Bacteria compartments (see Fig. 8) to the remaining 32 compartments in Fig. 7. All values in  $\text{mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ .

Into 35		Into 36		From 2	
(1,35)	112 340	(4,36)	31 885	(2,7)	1 406
(5,35)	6 690	(9,36)	587	(2,8)	1 102
(6,35)	12 468	(10,36)	188	(2,9)	121
(7,35)	38 502	(11,36)	3 454	(2,11)	154
(8,35)	21 986	(12,36)	1 344	(2,12)	69
(9,35)	6 157	(13,36)	1 522	(2,13)	107
(10,35)	447	(14,36)	137 239	(2,22)	13
Total	198 590	(15,36)	22 981	(2,23)	5
		(16,36)	23 721	Total	2 977
		(17,36)	30 209		
		(18,36)	3 986	From 3	
		(19,36)	1 711	(3,14)	161 758
		(20,36)	3	(3,15)	25 207
		(21,36)	13	(3,16)	57 665
		(22,36)	1 156	(3,17)	36 169
		(23,36)	133	(3,18)	14 156
		(24,36)	3	Total	294 995
		(25,36)	5		
		(26,36)	50		
		(27,36)	252		
		(28,36)	79		
		(29,36)	114		
		(30,36)	8		
		(31,36)	49		
		(32,36)	13		
		(33,36)	16		
		Total	260 721		
From 35					
(35,7)	21 368				
(35,8)	42 970				
(35,9)	3 318				
(35,11)	2 597				
(35,12)	1 420				
(35,13)	2 784				
(35,22)	308				
(35,23)	106				
Total	74 871				
From 36					
(36,19)	1 700				
Total	1 700				

Results of the trophic aggregation are depicted schematically in Fig. 9, where the detrital pool is shown separately from primary producers. The productivity of higher trophic levels is overwhelmingly dependent upon the recycling of carbon and energy through the nonliving members of the ecosystem. (Energy may cycle in chemically bound form before it ultimately dissipates, or otherwise leaves the system.) Detritivory exceeds herbivory by a ratio of more than 10:1, and 70% of all the inputs to the detritus compartment derive from recycle. As might have been expected, the detritivory/herbivory ratio is lowest (9.65) during the spring bloom and highest (17.03) during the winter period of lower primary production.

In order to evaluate trophic efficiencies, it becomes necessary to merge the detrital pool with primary producers (Fig. 10). Without the combination of plants and detritus the amounts of carbon flowing down the trophic "spine" cannot be guaranteed to decrease in pyramidal fashion. Trophic efficiency (indicated as a percentage figure within each box) is defined as that fraction of the total carbon input to a trophic level which is transmitted to the next higher level. For example, of the 403 684  $\text{mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  cropped at the carnivore level (III), 39 733 units are transmitted to level IV, giving a trophic efficiency of 9.8%. With the exception of trophic level IV, trophic efficiencies also are seen to decrease as one ascends the trophic pyramid. (The trophic efficiency of the first compartment in the pyramid is inflated slightly by the deficit in sources of

TABLE 6. Annual apportionment of species among discrete Lindeman trophic levels.

Level	Phytoplankton	Susp. POC bacteria	Sed. POC bacteria	Benthic diatoms	Free bacteria			
I	1.000	0.0	0.0	1.000	0.0			
II	0.0	1.000	1.000	0.0	1.000			
Level	Hetero. microflag.	Ciliates	Zooplankton	Cteno- phores	Sea nettle	Misc. susp. feeders		
I	0.0	0.0	0.0	0.0	0.0	0.0		
II	0.0	0.616	0.902	0.241	0.0	0.939		
III	1.000	0.016	0.065	0.614	0.689	0.046		
IV	0.0	0.367	0.001	0.037	0.242	0.001		
V	0.0	0.0	0.031	0.093	0.013	0.015		
VI	0.0	0.0	0.0	0.016	0.051	0.0		
VII	0.0	0.0	0.0	0.0	0.005	0.0		
Level	<i>Mya arenaria</i>	Oysters	Misc. polychaetes	<i>Nereis</i>	<i>Macoma</i> spp.	Meiofauna	Crustacean deposit feeders	
I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
II	0.943	0.946	0.0	0.0	0.0	0.333	0.0	
III	0.042	0.039	1.000	1.000	1.000	0.667	1.000	
IV	0.001	0.001	0.0	0.0	0.0	0.0	0.0	
V	0.015	0.015	0.0	0.0	0.0	0.0	0.0	
Level	Blue crab	Fish larvae	Alewife and herring	Bay anchovy	Menhaden	Shad	Croaker	
I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
II	0.205	0.0	0.0	0.274	0.334	0.0	0.0	
III	0.085	0.902	0.902	0.655	0.603	0.902	0.0	
IV	0.709	0.065	0.065	0.047	0.042	0.065	1.000	
V	<0.001	0.001	0.001	0.001	0.001	0.001	0.0	
VI	0.001	0.031	0.031	0.023	0.020	0.031	0.0	
Level	Hogchocker	Spot	White perch	Catfish	Bluefish	Weak fish	Summer flounder	Striped bass
I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
III	0.088	0.008	0.027	0.0	0.104	0.274	0.237	0.288
IV	0.910	0.990	0.966	1.000	0.221	0.655	0.587	0.594
V	<0.001	0.001	0.005	0.0	0.666	0.047	0.146	0.098
VI	0.001	<0.001	<0.001	0.0	0.001	0.001	0.009	0.001
VII	0.0	0.001	0.002	0.0	0.007	0.023	0.017	0.020
VIII	0.0	0.0	0.0	0.0	<0.001	0.0	0.004	0.0

TABLE 7. Trophic rankings and average annual trophic levels of the major components of the Chesapeake mesohaline ecosystem. POC = particulate organic carbon.

Trophic ranking	Effective trophic level	Trophic ranking	Effective trophic level
1. Phytoplankton	1.00	19. <i>Nereis</i>	3.00
2. Dissolved organic carbon	1.00	20. <i>Macoma</i> spp.	3.00
3. Suspended POC	1.00	21. Crustacean deposit feeders	3.00
4. Sediment POC	1.00	22. Ctenophores	3.03
5. Benthic diatoms	1.00	23. Fish larvae	3.16
6. Suspended POC bacteria	2.00	24. Alewife and blue herring	3.16
7. Sediment POC bacteria	2.00	25. Shad	3.16
8. Free bacteria	2.00	26. Sea nettle	3.44
9. Oysters	2.08	27. Blue crab	3.51
10. <i>Mya arenaria</i>	2.09	28. Weakfish	3.84
11. Misc. suspension feeders	2.09	29. Striped bass	3.87
12. Zooplankton	2.16	30. Hogchoker	3.91
13. Meiofauna	2.67	31. White perch	3.98
14. Ciliates	2.75	32. Flounder	3.99
15. Menhaden	2.77	33. Spot	4.00
16. Bay anchovy	2.84	34. Croaker	4.00
17. Heterotrophic microflagellates	3.00	35. Catfish	4.00
18. Misc. polychaetes	3.00	36. Bluefish	4.59

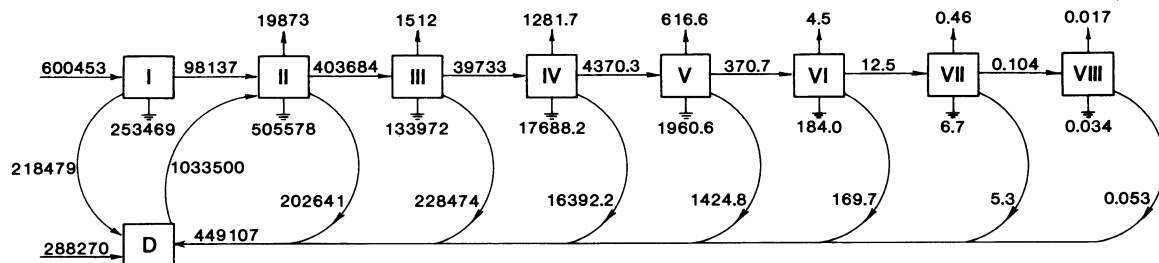


FIG. 9. The aggregation of the flow web in Figs. 7 and 8 into a concatenated chain of transfers through eight trophic levels. Flows out of the tops of levels II–VII represent exports. Recycle of nonliving material is through compartment D. Carbon flows in  $\text{mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ .

benthic POC that intentionally has been left unresolved. Correcting for this deficit reduces the efficiency of the combined compartment to 79.9%.) In a multiplicative chain of elements the average factor is calculated using either the geometric or the logarithmic mean. The logarithmic mean of the first seven efficiencies is 9.6%, coincidentally very close to the legendary 10% rule-of-thumb!

The almost uniform decrease of trophic efficiencies up the chain masks a considerable variation in these coefficients when calculated on a season-by-season basis (Table 8). For example, the trophic chain for the winter season shows a dramatic increase in efficiency at the fourth level. A survey of the apportionments of the winter species among the trophic levels (i.e., the seasonal analogies to the annual apportionments in Table 6) reveals two species that feed strongly at levels II and IV, but considerably less at level III. These components, the microzooplankton and the blue crab, might be termed “trophically bimodal” in what they consume. Ciliates (microzooplankton) act as herbivores in feeding on phytoplankton at the same time they are consuming a large fraction of the tertiary production of heterotrophic microflagellates. Among benthos, the blue crab is ingesting sediment POC in its role as a detritivore and is also preying upon various benthic invertebrates, which are mostly tertiary producers. However, crab production during winter is very small (occurring mostly at the extremes of the season) and does not pass much carbon up the web. Hence, it is the high efficiency of the microzooplankton, which pass on much of their ingestion to the larger zooplank-

ton, that accounts for the peak in trophic efficiency at level IV.

This peak at level IV persists into the spring, but during the summer it shifts up to level V. This is because microzooplankton appear to produce more than their predators can consume, and their trophic efficiency falls, as much of their production is recycled back to the suspended POC. Meanwhile, the mesozooplankton and the filter-feeding benthos that do prey on the ciliates and other microzooplankton are all transferring much of their intake farther up the food web at a reasonably high efficiency. Thus, one sees a smaller peak in trophic efficiency farther up the chain. Autumn appears to be a transitional period when efficiencies at both levels IV and V rise.

#### *The structure of recycling*

There are numerous pathways evident in Fig. 7 for carbon to recycle through the detritus. The presence of material cycling in an ecosystem is believed by many to be significant. Odum (1969) listed cycling as a major characteristic of more mature systems. Presumably, material cycling points to some form of homeostatic control working to retain materials in the system for reuse. Ulanowicz (1983) notes how material cycles can accompany autocatalytic configurations of processes that are capable of exerting selection pressure upon their participating components. One result of such autocatalytic agency is to amplify the activities of the participants relative to those of others, thereby culminating in a more “efficient” and streamlined network structure. Finally, as shown below, the overall

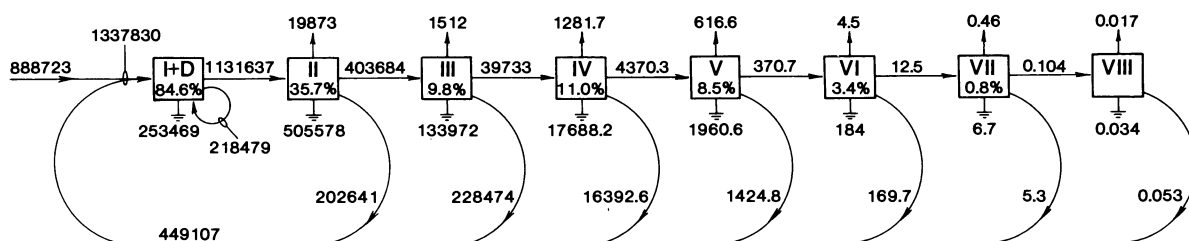


Fig. 10. The trophic chain of Fig. 9 with primary producers and detritus merged. The percentages in the boxes represent annual trophic efficiencies.

structure of recycle pathways can help to define the functions of individual components within the context of the operation of the whole system.

The methodology for analyzing the structure of cycling present in a network is covered in Ulanowicz (1983). Three major tasks are involved: (1) The identification and enumeration of all simple cycles. (Simple cycles have no repeated nodes.) (2) The collection of cycles into distinct subgroupings, called nexuses, wherein all cycles composing a particular nexus share the same limiting, or smallest link. (3) The successive removal of all nexuses from their supporting tree (a web without cycles) of dissipative transfers.

The analysis of the structure of cycling in the Chesapeake mesohaline ecosystem network yielded several surprises. The first was its simplicity. There are only 61 distinct cycles in the ecosystem network (Table 9). Furthermore, there was a preponderance of single-cycle nexuses (32 in all). There was a single nexus of planktonic organisms containing 11 cycles (one cycle therein was six elements in length), but the remaining nexuses contained few cycles (two nexuses with 4 cycles, one with 3, four with 2, while the remainder contained solitary cycles).

Of course, the networks pertaining to the individual seasons contained even fewer cycles. Almost all the annual cycles (58) appeared during the summer season, but significantly fewer (36, 31, 36) occurred in the other seasons (spring, fall, and winter, respectively). Despite the seasonal variation in the number of cycles and in the amounts flowing in those cycles, the ratio of the aggregate recycled flow to total activity (the Finn [1976] cycling index) remained remarkably stable. The annual value of the Finn index was high (23.2%, cf. Ulanowicz 1984) and did not deviate by >2% over the year!

The paucity of cycles and the brevity of the individual circuits coupled with a high Finn index bespeak a disturbed system. Ulanowicz (1984) compared the cycle structure of a polyhaline tidal marsh gut near Crystal River, Florida, with a nearby gut that had been thermally stressed. It was the large nexuses with many longer cycles that were missing from the stressed network, despite the fact that the stressed system had a higher Finn index. The nexuses of the impacted network consisted mostly of single cycles, as appears to be the case in the Chesapeake. What is not clear from this one-time assessment of the Chesapeake ecosystem is whether its simple configuration of cycles is the result of natural eutrophication (characteristic of even pristine estuaries), or whether a more "baroque" cycling structure had existed earlier and has since succumbed to the increase in nutrient loadings over the past several decades.

The list of cycles in Table 9 is split into two disjoint subgroups of cycles, one involving only planktonic compartments and another consisting of benthic and nektonic species. This bifurcation is more readily apparent in the schematic of composite cycling shown in

TABLE 8. Trophic efficiencies: Each datum is the percentage of all carbon flows into that level that is transmitted to the next higher level.

	Trophic level						
	I	II	III	IV	V	VI	VII
Spring	88.1	33.7	6.2	41.6	2.4	1.6	2.6
Summer	92.0	35.1	14.7	5.6	21.7	6.2	0.7
Fall	76.3	37.5	8.5	20.9	22.2	1.8	0.9
Winter	67.9	38.1	5.6	44.1	7.4	0.06	...

Fig. 11. What is also striking about Fig. 11 is that 14 of the compartments do not engage in any cycling whatsoever, and that eight of these isolated species occur along the trophic "boundaries" of the three major habitats.

Previous experience with the Crystal River comparisons (Ulanowicz 1984) revealed that control appears to exist in proportion to the trophic length of the cycles but seems to be inversely related to the magnitudes circulating around the loops. This observation is probably a result of predator control acting in the system, that is, populations with small biomasses exerting sufficient pressure upon their prey to depress prey populations significantly. The most striking example of such control acting in the Chesapeake ecosystems involves control of the numbers of crustacean zooplankton by their gelatinous predators during the summer season.

It may be possible to describe the nature of control in any cycle by the location of its critical, or least, arc. If the smallest arc in a cycle occurs as an input to an active predator, then it is likely either that the predator is not focusing the majority of its feeding on the cited prey, or else the predator is limited by the availability of that particular prey (prey limitation). When the critical arc connects the highest feeder in a cycle to the detritus, then it is a possible indication that the control by that top predator ramifies back down the pathway of that isolated cycle. Of course, the overlap of cycles in any real web might confuse the issue of system control, but it is often useful to mark the location of the critical arcs in the hope that a reasonably clear picture of control might emerge.

Referring to the planktonic loops in Table 9A, one's attention is immediately drawn to the 11-cycle nexus controlled by the return of carbon from the sea nettle (*Chrysaora quinquecirrha*, species 10) to the suspended detritus (35). Interestingly, this nexus involves all of the planktonic species that participate in cycling, and the critical arc occurs *after* the top predator. This configuration, especially when coupled with the high trophic status of the nettles mentioned earlier, points to the sea nettle as the key species in the control of the planktonic community during the summer season when it is abundant.

The cycling that occurs within the planktonic system during the spring and summer seasons is depicted in



TABLE 9. Enumeration of cycles, nexuses, and weak arcs. See Fig. 2 for identification of compartments.

No. cycles in nexus	Cycle no.	Compartments involved	Carbon flow (mg·m <sup>-2</sup> ·yr <sup>-1</sup> )	No. cycles in nexus	Cycle no.	Compartments involved	Carbon flow (mg·m <sup>-2</sup> ·yr <sup>-1</sup> )
A. Planktonic cycles							
2	1	Cycle nexus with weak arc (2,9) = 35-2-9-35	121.0	4	33	Cycle nexus with weak arc (19,33) = 36-19-33-36	2.4
	2	35-2-10-35			34	36-3-15-19-33-36	
11	3	Cycle nexus with weak arc (10,35) = 35-9-10-35	447.0		35	36-3-16-19-33-36	
	4	35-8-9-10-35		1	36	36-3-18-19-33-36	
	5	35-8-10-35			37	Cycle nexus with weak arc (25,36) = 36-3-14-25-36	4.9
	6	35-7-9-10-35		3	38	Cycle nexus with weak arc (30,36) = 36-3-14-27-30-36	7.5
	7	35-7-8-9-10-35			39	36-3-15-27-30-36	
	8	35-7-8-10-35			40	36-3-16-27-30-36	
	9	35-2-8-9-10-35		1	41	Cycle nexus with weak arc (15,26) = 36-3-15-26-36	14.0
	10	35-2-8-10-35		1	42	Cycle nexus with weak arc (18,26) = 36-3-18-26-36	14.0
	11	35-2-7-9-10-35		1	43	Cycle nexus with weak arc (15,29) = 36-3-15-29-36	22.6
	12	35-2-7-8-9-10-35		1	44	Cycle nexus with weak arc (18,29) = 36-3-18-29-36	43.1
	13	35-2-7-8-10-35		1	45	Cycle nexus with weak arc (26,36) = 36-3-14-26-36	50.3
2	14	Cycle nexus with weak arc (2,8) = 35-2-8-35	1102.0	1	46	Cycle nexus with weak arc (16,27) = 36-3-16-27-36	55.0
	15	35-2-8-9-35		1	47	Cycle nexus with weak arc (15,28) = 36-3-15-28-36	59.0
4	16	Cycle nexus with weak arc (2,7) = 35-2-7-35	1406.3	1	48	Cycle nexus with weak arc (14,28) = 36-3-14-28-36	76.0
	17	35-2-7-9-35		1	49	Cycle nexus with weak arc (15,27) = 36-3-15-27-36	97.0
	18	35-2-7-8-35		1	50	Cycle nexus with weak arc (29,36) = 36-3-14-29-36	113.8
	19	35-2-7-8-9-35		1	51	Cycle nexus with weak arc (27,36) = 36-3-14-27-36	251.9
1	20	Cycle nexus with weak arc (35,9) = 35-9-35	3318.0	1	52	Cycle nexus with weak arc (15,19) = 36-3-15-19-36	352.0
1	21	Cycle nexus with weak arc (7,9) = 35-7-9-35	3437.0	1	53	Cycle nexus with weak arc (18,19) = 36-3-18-19-36	967.0
1	22	Cycle nexus with weak arc (2,35) = 35-2-35	4072.0	1	54	Cycle nexus with weak arc (36,19) = 36-19-36	1700.0
2	23	Cycle nexus with weak arc (9,35) = 35-8-9-35	6157.0	1	55	Cycle nexus with weak arc (19,36) = 36-3-16-19-36	1711.0
	24	35-7-8-9-35		1	56	Cycle nexus with weak arc (18,36) = 36-3-18-36	3985.7
1	25	Cycle nexus with weak arc (7,8) = 35-7-8-35	7550.0	1	57	Cycle nexus with weak arc (15,36) = 36-3-15-36	22 981.3
1	26	Cycle nexus with weak arc (35,7) = 35-7-35	21 367.7	1	58	Cycle nexus with weak arc (16,36) = 36-3-16-36	23 721.0
1	27	Cycle nexus with weak arc (8,35) = 35-8-35	21 986.0	1	59	Cycle nexus with weak arc (17,36) = 36-3-17-36	30 209.0
				1	60	Cycle nexus with weak arc (3,36) = 36-3-36	120 289.0
				1	61	Cycle nexus with weak arc (14,36) = 36-3-14-36	137 239.0
B. Benthic-nektonic cycles							
1	28	Cycle nexus with weak arc (18,25) = 36-3-18-25-36	0.3				
1	29	Cycle nexus with weak arc (18,32) = 36-3-18-32-36	0.9				
2	30	Cycle nexus with weak arc (18,27) = 36-3-18-27-36	2.0				
	31	36-3-18-27-30-36					
1	32	Cycle nexus with weak arc (15,25) = 36-3-15-25-36	2.1				

Fig. 12a and b, respectively. The critical arcs are highlighted. Only six cycles are present during the spring season. The control status of the zooplankton (8) is ambiguous, as it has one controlling arc feeding into it and two exiting from it. However, the ctenophores (9) are definitely *not* in control, because both input arcs are critical, and no smallest arc exits from it. Hence, on balance, control of populations among the spring plankton is probably shared by the zooplankton and bacteria attached to the detritus.

Quite a different picture emerges during the summertime. Both inputs to the zooplankton and two of the three inputs to the ctenophores are critical, whereas neither of the inputs to the sea nettle appear to be controlling it. It appears that as the year progresses, control within the planktonic community shifts from the zooplankton in spring toward the nettle in mid-summer. By interpolation one might speculate that the ctenophores are dominant during some part of the interim.

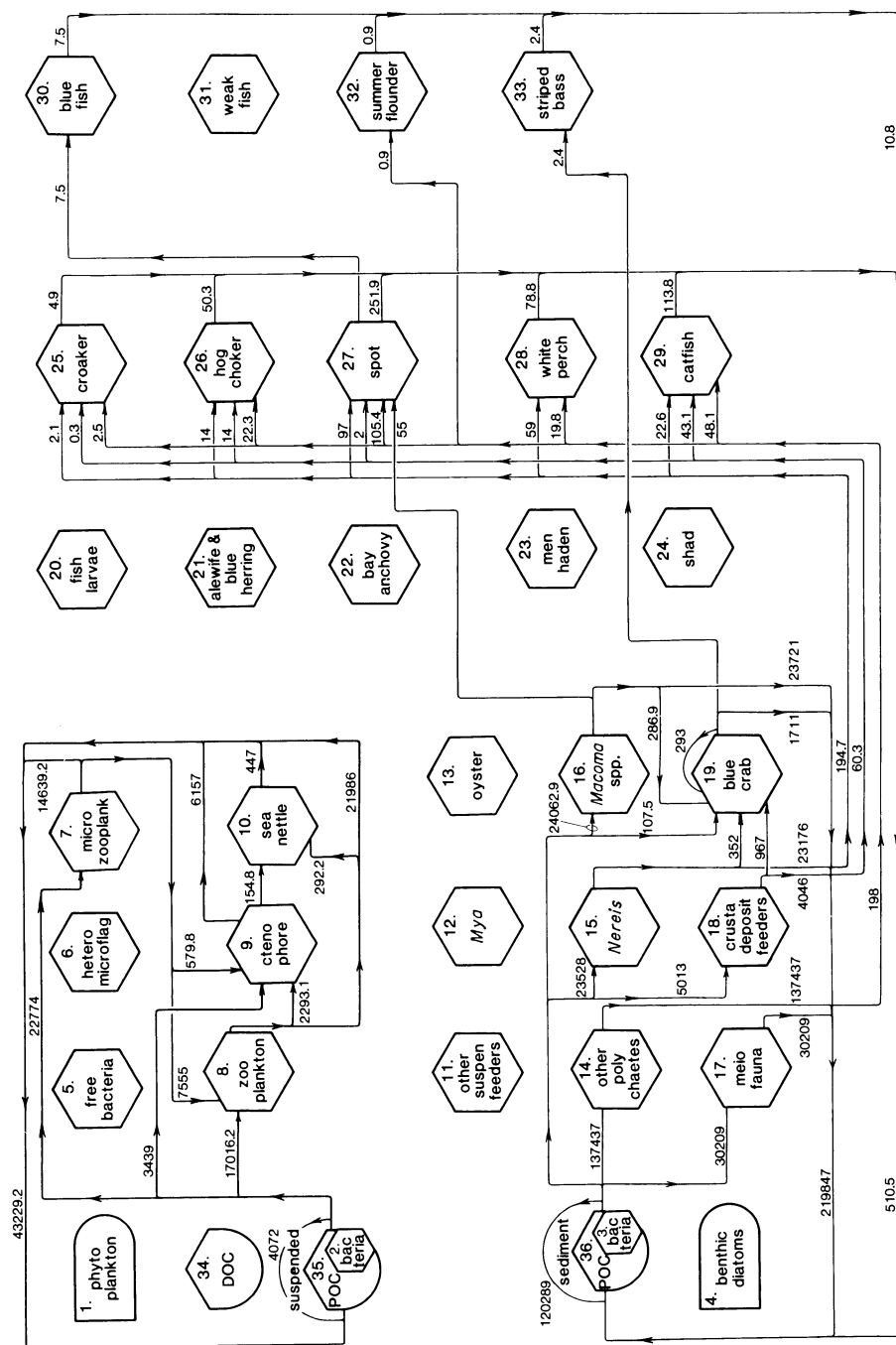


FIG. 11. The composite cycling of carbon that occurs in the flow diagram in Fig. 2. Units of flow and numbering of the compartments are the same as in Fig. 2.

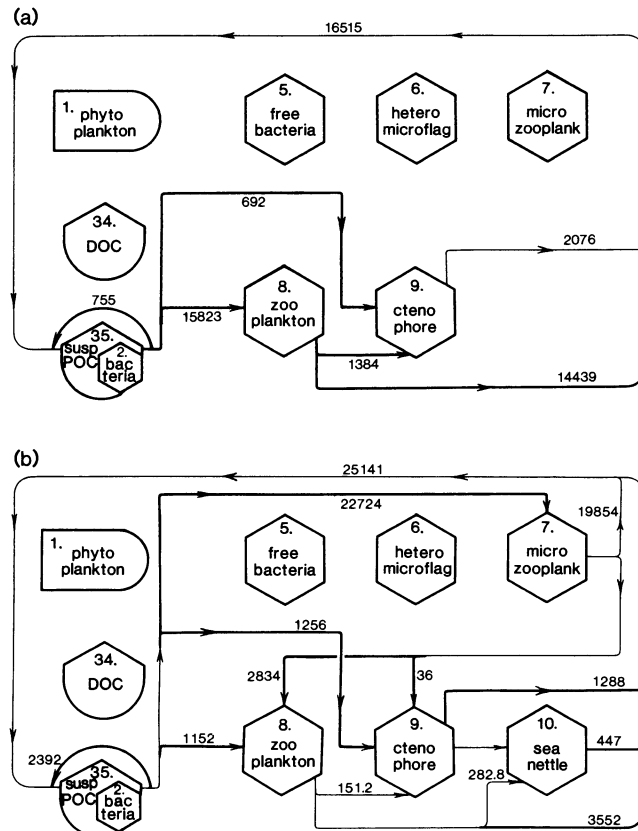


FIG. 12. (a) Detail of the recycling of carbon within the planktonic community during the spring. Units are  $\text{mg} \cdot \text{m}^{-2} \cdot (92\text{d})^{-1}$ . (b) Cycling among the same community during the summer. Critical arcs are denoted by dark lines.

What is also quite remarkable is the virtual absence of any recycle occurring through the DOC, free bacteria, and microheteroflagellates, key elements of the "microbial loop." One infers from this circumstance that, in the eutrophic waters of Chesapeake Bay at least, a microbial "loop" of carbon does not exist! These microbiota are functioning more to *shunt* carbon and energy out of the system, i.e., to dissipate the excess phytoplankton production.

By far the larger amount of recycled carbon is circulating among the benthic-nektonic communities. Again, control probably resides in the longer but less intense cycles having critical arcs that involve the nektonic predators. This comes as no surprise, as others have suspected that the benthic-feeding fish (26–33) dominate and order the benthos (Homer et al. 1981). The visual message of Fig. 3 is that the blue crab (*Callinectes sapidus*, species 19) is at the hub of benthic recycle. The largest nexus in Table 9B is controlled by striped bass (*Morone saxatilis*) predation upon the blue crab.

The bifurcation of the mesohaline ecosystem into separate domains of control appears to be the result of a virtual one-way flow of organic carbon from the plankton to the benthos. Most of this carbon flow occurs as the sedimentation of suspended detritus ( $281\,000 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ), but it is abetted by the action of the

filter feeders (components 11–13), which collectively ingest  $\approx 18\,800 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  annually. The resuspension of organic carbon from the sediments is negligible by comparison. Had there been a major route of organic carbon from the benthos back into the planktonic community, the cycling structure and routes of control would have been more complicated.

The benthic suspension feeders (11–13) are decoupled from the material feedback loops. Their primary function in the carbon system appears to be to shunt material and energy from the planktonic community into that of the benthos. Similarly, the grazing fish (20–24) transport planktonic material into the nekton (25–33).

#### System-level dynamics

Most analytical results up to this point have pertained to only parts of the whole network. Notable exceptions have been the large seasonal variation in system productivity and the contrasting homeostasis of the fraction of total activity devoted to aggregate recycling (the Finn index).

Another quantitative descriptor of system-level activity related to the system productivity is the total system throughput (Hannon 1973), the sum of all the flows occurring in the system. The largest component of the total throughput is the total system output (i.e.,

TABLE 10. Seasonal trends in the measures of system organization. All absolute values have the units of carbon flow ( $\text{kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) times "bits" of information. Normalized capacities given in bits (values in parentheses under "Capacity"). All other component fractions (in parentheses) are dimensionless.\*

Season	Capacity	Ascendency	Overhead			
			Inputs	Exports	Dissipation	Redundancy
Spring	4.37 (3.35)	2.74 (0.626)	0.08 (0.018)	0.010 (0.002)	0.74 (0.170)	0.80 (0.183)
Summer	5.88 (3.51)	3.62 (0.615)	0.09 (0.015)	0.004 (0.001)	1.15 (0.195)	1.03 (0.175)
Fall	2.46 (3.19)	1.59 (0.646)	0.05 (0.021)	0.002 (0.001)	0.39 (0.160)	0.43 (0.173)
Winter	1.83 (3.05)	1.22 (0.666)	0.03 (0.015)	0.001 (0.001)	0.28 (0.154)	0.30 (0.164)

\* The *capacity* of a network is taken to be its total activity,  $T$ , multiplied by the diversity of its constituent exchanges. It can be decomposed into five separate components (Ulanowicz 1986): The *ascendency* represents the amount of capacity that appears as coherent structure. The remaining four terms together comprise the *overhead*, or that amount of capacity encumbered from contributing network structure. *Inputs*, *exports*, and *dissipation* all generate overhead, as does the multiplicity, or *redundancy* of pathways between components. The fractions of each seasonal capacity comprising the ascendency and the four overhead terms appear in parentheses following the absolute values of each component. The number in parentheses after each capacity is the value obtained when each capacity has been normalized by  $T$ .

The magnitude of the network and its distribution among the five components profile the developmental status of the corresponding ecosystem.

aggregate final demands), which takes the forms of the gross national product in economic systems. The total annual activity level for the Chesapeake ecosystem in carbon units is  $\approx 4.35 \text{ kg/m}^2$ , of which the spring season comprises  $1.30 \text{ kg/m}^2$  (or 30%). Activity rises during the summer to  $1.68 \text{ kg/m}^2$  (or 39%), but falls back in the autumn and winter to  $0.77$  (18%) and  $0.60$  (14%)  $\text{kg/m}^2$ , respectively.

The question remains as to whether there exist other useful indices that characterize the "maturational" status, or degree of development of the whole network in terms of one or a few numbers. Ulanowicz (1986), for example, has theorized that one may describe the developmental status of an ecosystem network using a suite of whole-system indices derived through the application of information theory to the flow structure. In particular, he defines a system index called the ascendency, which is intended to encapsulate into one measure the attributes of system "size" and organization. Size appears as a scaling factor, which is set equal to the total system throughput just discussed. Ulanowicz argues that organization in ecosystems is intimately coupled with the average degree of trophic specialization. Such "stenotrophy" can be estimated through the application of information theory to ecological networks (Rutledge et al. 1976).

Of course, no system can be perfectly organized, and the complement to ascendency is what Ulanowicz calls the overhead. Overhead is generated by structural ambiguities deriving from multiplicities in the system inputs, exports, dissipations (respirations), and internal exchanges, or functional "redundancy." The ascendency and overhead taken together constitute the system's "capacity" for development. The seasonal values of the Chesapeake ecosystem's development capacity, ascendency, and overhead terms are listed in Table 10. It is quite apparent that the magnitudes of the various components are all strongly correlated with the seasonal changes in activity (total system throughput). For this reason it is more interesting to compare values of the components after division by the throughput (the

numbers given in parentheses after each absolute value). For example, normalized development capacity ranges from a high of 3.51 (dimensionless) in the summer to a low of 3.05 in the winter. It is obvious that the diversity of system flows does not change radically from season to season. In the remaining columns of Table 10 are listed the seasonal ascendencies and the various components of the overhead along with their normalized values (the number in parentheses).

The fraction of the capacity expressed as structure (ascendency) is highest in winter (0.666) and lowest in summer (0.615). This is in stark contrast to the corresponding activity levels, which behave conversely. This summer-winter difference in the ascendency component can be attributed mainly to elevated dissipation and redundancy during the summer months. These quantitative results recapitulate the intuitive notion that the carbon flow dynamics in Chesapeake Bay during the summer are both more dissipative and less organized than those during the less active, cooler seasons.

Slight seasonal differences in structure notwithstanding, the emerging picture of the Chesapeake ecosystem is one in which the community maintains essentially the same topological structure throughout the cycle of seasons, despite large changes in its level of activity over the course of the year.

## CONCLUSIONS

The chief qualitative change in the seasonal dynamics of the Chesapeake ecosystem that became apparent before any of these quantitative analyses had been initiated on the network of flows was the evolution during late spring of predator control by ctenophores upon the numbers of mesozooplankton. This shift was reflected in all further analysis. It probably increases the dominance of benthic and detrital pathways over the water-column grazing routes.

It appears that species such as bluefish that indirectly rely on benthic productivity will be favored over species

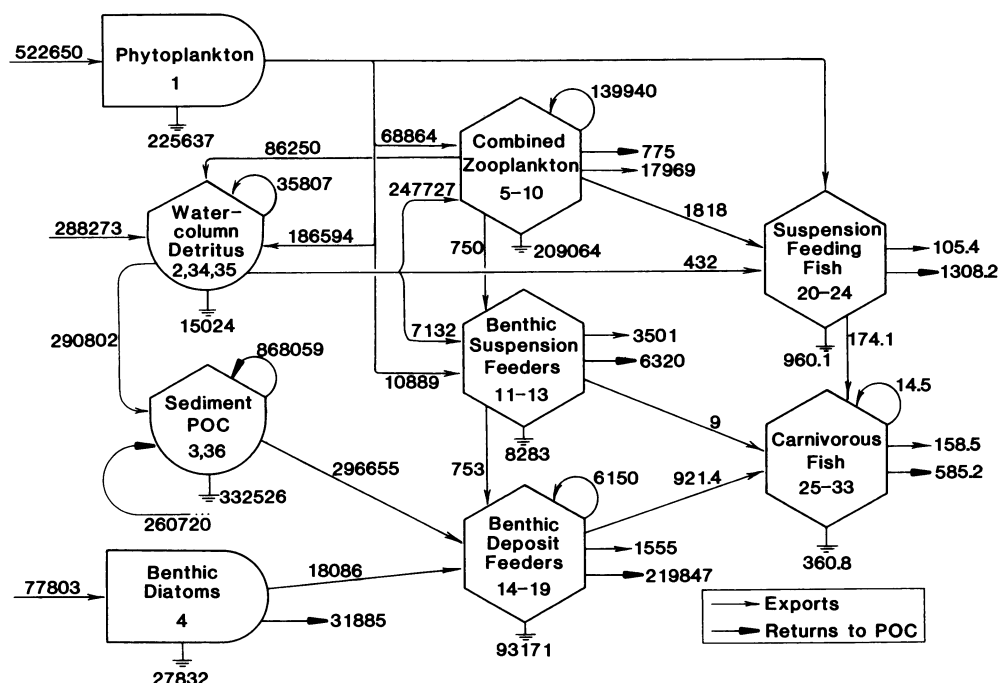


FIG. 13. A condensed representation of the flows among the heterotrophic compartments of the Chesapeake mesohaline ecosystem. Units are the same as in Fig. 7.

like the striped bass, which receive most of their sustenance over pelagic trophic pathways. The analysis of the underlying trophic dynamics of the Chesapeake ecosystem highlights certain heretofore unheralded species as playing significant roles in the transfers of material and energy to higher predators. For example, the microheterotrophs (mostly ciliates) provide a highly efficient route of carbon to higher levels during the winter and spring. At the other extreme stands the abundant, but largely ignored sea nettle. It passes on very little to the nektonic predators, but its high trophic status and potentially controlling role are only now being revealed.

In some ways the present analysis recapitulates earlier generalizations about trophic dynamics. The overall trophic efficiency of the system is surprisingly close to 10%, even though this often-cited value was never arbitrarily applied to any species or group of organisms. The proverbial upper limit of 5 on the trophic status of any organism appears to hold in the Chesapeake ecosystem, despite the presence of some trophic pathways as great as eight transfers in length. This limit may be the consequence of the observed tendency of trophic efficiencies to decrease as one ascends the trophic chain. However, this trend begins to appear uniform only after one has averaged over a sufficiently long interval (1 yr in this case).

It has long been known that estuarine ecosystems rely strongly on detritivory and recycle. Just how much the detritivory exceeds herbivory in the estuary has been vividly portrayed by the trophic aggregation. The Lindeman scheme for representing the processing of

energy and material by an ecosystem as a concatenation of transfers appears to afford a way to compare disparate ecosystems. Feeding webs of almost arbitrary complexity may be mapped into this standard network topology for the purpose of comparing corresponding aggregated elements (functions in the ecological sense of the word).

Delimiting the structure of recycle within a network of ecosystem flows provides a number of clues as to the identity of the organisms and processes that control the dynamics of the medium in question. This was most apparent when the cycle analysis and the trophic computations both pointed to the significant role of the sea nettle in structuring the plankton community during summer. By virtue of their nonparticipation in cycling, other species are presumed to play the role of conduits of material and energy between active domains of control. In the Chesapeake ecosystem, filter feeders constitute bridges between the planktonic community and the benthic-nektonic complex. The planktonic microbiota chiefly dissipate the excess summer phytoplankton production.

These observations on cycling allow one to aggregate the network in Fig. 7 into a nine-compartment ecosystem wherein each compartment represents a species or a group of species playing roughly the same ecological role. In the condensed network (Fig. 13) the primary producers and detrital compartments are the same as they were in Fig. 7, except that the DOC and suspended POC have been combined. The major simplification results from combining the 29 heterotrophic species into five functional compartments: planktonic

heterotrophs, benthic suspension feeders, deposit feeders, suspension-feeding fish, and carnivorous fish. The resulting aggregated network is a compact description of carbon flows in the Chesapeake mesohaline ecosystem.

With regard to seasonal changes in the overall system structure, it seems that the ecosystem exhibits a large interannual variation in the level of overall activity, but at the same time it undergoes little change in the topology of its trophic interactions. The single relevant exception to this pattern is the shift in the fate of much of the summertime primary production away from the pelagic grazing chain and into the microbial loop and the benthos. To recapitulate: high summer primary production combines with strong predator control upon the mesozooplankton to yield a degree of "excess" productivity that is either dissipated in the water by the very active microbial community or settles to the bottom and fuels benthic deposit feeders.

Apropos this last point, we end this narrative with a final observation and a question. The deposit-feeding organisms seem to heavily dominate the bottom-dwelling community in Chesapeake Bay. Was this always the case? Certainly the shellfish catch records indicate that a much denser filter-feeding community covered the bottom of the Bay in decades past. Water clarity, which is also abetted by large populations of filtering organisms, has diminished over the same interval. Missing are data on the levels of zooplankton, ctenophores, and benthic fauna over this period. Has there been a shift in the quality of the phytoplankton present during the summer or some other significant change that could have initiated this trophic restructuring, changing the appearance, utility, and functioning of this most valuable of estuarine ecosystems?

#### ACKNOWLEDGMENTS

The authors would like to thank the following persons for providing them with unpublished data and manuscripts, and extremely useful advice during the course of this study: Drs. Jon Tuttle, Edward Houde, Edward Chesney, Eileen Setzler-Hamilton, Roger Dawson, David Cargo, Cluney Stagg, and Christopher D'Elia, all of the Chesapeake Biological Laboratory, University of Maryland; Drs. Michael Roman and William Boicourt of the Horn Point Laboratory, University of Maryland; Drs. Kevin Sellner and David Brownlee of the Benedict Estuarine Laboratory, Benedict; Drs. Fred Holland and Fred Jacobs, Martin Marietta Environmental Systems, Columbia, Maryland; Dr. Steven Jordan and Mr. Harry Hornick of the Tidewater Administration, Department of Natural Resources, Maryland. Special thanks go to Dr. Walter Boynton for his critical reviews and many useful suggestions; to Dr. Kenneth Tenore, Head of CBL who provided laboratory facilities and support during this study, to Dr. Eric Schneider for his enthusiastic support; to Ms. Toni Heimer and Mrs. Jeri Pharis for typing and to Mrs. Francis Younger for the artwork. Drs. Stuart Fisher and Charles A. S. Hall suggested numerous helpful revisions to earlier drafts of this monograph. This research was supported by a grant from the Department of Natural Resources, Maryland (C-11-86-023) and supplemented by funds from the Department of the Navy (N00024-86-C-5188).

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## APPENDIX

Scientific names of species whose common names are used in the text.

Common name	Scientific name
Alewife	<i>Alosa pseudoharengus</i>
Atlantic croaker	<i>Micropogonius undulatus</i>
Bay anchovy	<i>Anchoa mitchilli</i>
Blue crabs	<i>Callinectes sapidus</i>
Bluefish	<i>Pomatomus saltatrix</i>
Sea catfish	<i>Arius felis</i>
Clam, soft shell	<i>Mya arenaria</i>
Herrings	Clupeidae (family)
Hogchoker	<i>Trinectes maculatus</i>
Atlantic menhaden	<i>Brevoortia tyrannus</i>
Oyster, American	<i>Crassostrea virginica</i>
Perch	Percidae (family)
Seanettle	<i>Chrysaora quinquecirrha</i>
Shad, American	<i>Alosa sapidissima</i>
Striped bass	<i>Morone saxatilis</i>
Summer flounder	<i>Paralichthys dentatus</i>
Spot	<i>Leiostomus xanthurus</i>
Weakfish	<i>Cynoscion regalis</i>
White perch	<i>Morone americana</i>