14. ENERGY FLOW AND PRODUCTIVITY IN THE OCEANS

R. E. ULANOWICZ

Chesapeake Biological Laboratory, University of Maryland, Solomons, MD 20688, USA

INTRODUCTION

The term 'ecosystem' carries epistemological implications that are often not well appreciated. While most ecologists are aware that the concept embraces both the living and the abiotic entities of ecological ensembles (Tansley 1935; Waring 1989), fewer realize that some systems scientists, for example Klir (1981), draw a sharp distinction between the physical object of study and the associated mental image that the observer creates of that object — this latter abstraction being considered that which is properly termed 'the system'.

If 'systems' are actually abstractions of reality, it naturally follows that there will exist wide ranges of opinion concerning both (i) the utility of such abstraction, and (ii) the type of abstraction that should be drawn. These two issues pervade the literature of science in general and, *a fortiori,* ecology in particular. But disagreement and debate are preconditions to scientific understanding, so it is often helpful to chronicle recent advances in a particular discipline against the background created by these broader questions.

Concerning the utility of systems abstraction, the debate on this point translates into the familiar dialogue of reductionism vs. holism. At one extreme stand the nominalists, who are inclined to regard only individual, real objects as worthy of consideration. To the arch-nominalist any collection of real objects, say organisms, into categories, such as populations, guilds or communities, is futile, if not downright puerile. Such categories are believed to exist in name alone. Perhaps a larger fraction of ecologists is willing to entertain simple aggregations, such as populations, but holds that the direction of causality behind biological phenomena is almost exclusively from objects and events at smaller scales toward perceived larger entities and processes. Properties of these larger ensembles are assumed to be either accidental or epiphenomenal.

Of an opposing opinion is the holist, who is willing to reify and to attribute 'active agency' to relational entities, such as demes or ecosystems.

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What happens at larger scales is believed to be independent to some degree of events transpiring at finer resolutions. Furthermore, the larger entities are thought to exert some influence upon what can occur among their parts. As I hope to demonstrate, investigators positioned all along the reductionist–holist axis have contributed toward a more quantitative marine ecology.

Given that some degree of system abstraction is both unavoidable and beneficial, there still remains an infinity of ways of forming a mental picture of the object of study, and the results are bound to differ markedly in nature and complexity among investigators. For example, Ashby (1953) pointed out that one's perception of the complexity of a sheep's brain depends upon whether one is a neurophysiologist or a butcher! The issue of how to abstract is understandably less general than the degree to which one should abstract, and the particular methods vary among the disciplines. In my opinion, two major schools of thought exist on how to form an image of an ecosystem in aquatic ecology and biological oceanography, partitioned loosely between British and American ecologists. The two schools are probably best associated with the names of Charles Elton and Raymond Lindeman respectively.

Charles Elton, emeritus of Oxford University, cast his descriptions of ecosystems primarily in terms of the numbers and sizes of organisms, as in his book of 1927. In particular, he noted that the animals doing the eating were usually larger than their prey. The prey were never so small that it took a long time for the predator to collect, nor were they so large that the prey were difficult to catch and overpower (Cousins 1985a). Although Elton was concerned mostly with terrestrial systems, the importance of body size to predator–prey relationships appears to be even stronger in the water, where, as the saying goes, 'Big fish eat little fish, eat smaller fish, etc.'

Raymond Lindeman's (1942) concept of ecosystem had an impact on American ecology that is out of all proportion to his tragically brief career. A graduate student of G. E. Hutchinson at Yale University, Lindeman advanced the notion of the ecosystem as a thermodynamical hierarchy, where plants occupy the lowest level and are fed upon by herbivores, who in turn are preyed upon by carnivores, and so on. The contents of the trophic levels are estimated in terms of material or energy; and, if in the latter, then the second law of thermodynamics dictates that progressively less energy is transferred to successively higher trophic levels in pyramidal fashion. Less well-known by those who have not read his original paper is the fact that Lindeman also connected the upper trophic levels with their base via a set of detrital feedbacks.

Number and size versus functional group and transformation—the two perspectives echo throughout contemporary ecology, and appear especially to structure dialogues among biological oceanographers. Whereas one might expect most Eltonian descriptions to be reductionistic and Lindemanian representations to be steeped in holism, one need not search long to discover significant exceptions. The interplay between factors in how one goes about abstracting from ecological collections into ecosystems is subtle and hinders the separation of projects into crisp epistemological categories. None the less, most advances in quantitative marine ecology do seem to be motivated (often unconsciously) by how the investigators stand in regard to these two issues. For this reason I have attempted to structure this review into four parts according to whether a particular project reflects more the approach of Elton or Lindeman, reductionism or holism.

ELTONIAN REDUCTIONISM

It is difficult to reconcile nominalism *ad extremum* with the larger thrust of science, replete as scientific thought is with laws and generalizations. But there do exist articulate prophets who journey the lecture circuit warning against unnecessary reification of higher-level abstractions. Simberloff (1983), for example, argues that species interactions are insignificant in comparison with the effects the physical environment has upon the fate of an organism, and foresees the time when community ecology should cease to exist. Lehman (1986) argues that classifying lakes according to their macroscopic properties (clarity, trophic status, mean temperature, etc.) is unlikely to yield robust prediction or understanding; the latter he feels is better sought by a clearer knowledge of the genetical properties of organisms. He allows, however, that integrating biological properties with food web dynamics does hold much promise. Others (Hughes 1985; Price 1986) do entertain the notion of an ecological community, but argue that the community can exhibit only mechanistic behaviour. They believe that the progressive elucidation of constituent mechanisms will eventually obviate any need to consider many-species phenomena, such as indirect effects (cf. also Schoener 1986).

Whilst many reductionist projects yield few quantitative results useful to others, there is one notable exception. If one focuses upon individual organisms, there is little left to quantify, save for an individual's size, behaviour and physiological rates. The Eltonian emphasis upon body size as the leading descriptor of an organism helped to initiate a search for allometric formulae that relate the rates of

processes such as respiration, generation time and productivity (in plants) to the characteristic dimensions of the organism in question (Platt 1985). Haldane (1928) had commented earlier on how body size reveals much information about an organism's physiology, but it was Kleiber (1947) and especially Hemmingsen (1960) who found great regularity among data on how respiration rates vary with body size. In particular, they found that respiration rates vary as a power function of the organism's size or weight, i.e.

$$R = \alpha W^{\gamma}$$

where R is the respiration rate, W is the organism's weight and α and γ are constants.

The marine ecologist Fenchel (1974) was able to generalize this allometric formula for respiration to apply to Elton's speculation that generation time is also a function of body size. Briefly, Fenchel discovered that generation time also can be described by the same form of allometric equation as applies to respiration; that the multiplicative factor varies across groups of species, their ecologies and the types of physiological rates being described; but that the power γ was relatively constant over all the data. This virtual constancy bespeaks an underlying principle, and Platt & Silvert (1981) argued that there exists a universal, size-related time-scale in organisms to which all processes that can be expressed in units of time are related in a simple way.

ELTONIAN COMMUNITIES

The results from allometry did not derive in any way from the notions of community or ecosystems. However, the robustness and generality of allometric relations were most attractive to those seeking to describe the marine pelagic community in quantitative fashion. If Elton and Haldane were correct in citing body size as the paramount characteristic of an organism, then an organism's size should overshadow even its taxonomic designation. Ecological communities are conventionally described in terms of their taxonomic parts. Given the advantages of dealing with body size, might not a more effective quantitative theory ensue from classifying organisms according to size? Such a shift in emphasis would also afford significant practical advantages to limnologists and biological oceanographers. By employing inductive counting devices (such as the Coulter counter) it is relatively easy to acquire data on particle size distributions (psds) of planktonic communities in the range from 2 to 250 μm.

Evidence accumulated that the psds of planktonic communities in the ocean were relatively flat and lacking in definite structure, as shown in Fig. 14.1, based on the work of Sheldon, Prakash & Sutcliffe (1972). Platt (1985) noted how this relative flatness is the consequence of a simple transformation of the Eltonian pyramid, and had already been anticipated by H. T. Odum (1971). Platt & Denman (1978), employing the results of Fenchel, calculated that the density of living particles should decrease slowly as the negative one-fifth power of their body sizes.

If an organism's physiological rates are tied to its body size, and the distribution of size classes in an ecosystem is known, then by integrating the allometric formulae over the range of all sizes one should be able to estimate community parameters, such as gross respiration or total primary and heterotrophic production — rates which are central to a thermodynamic analysis of the community (Platt, Lewis & Geider 1984; Paloheimo 1988). Of course, system indices are rarely sufficient to describe interactions at the compartment level, and Silvert & Platt (1978, 1980) have modelled the transfers among the various size categories within the psd. Their first effort accounted only for transfers from smaller to larger size classes. It predicted that any transient in the distribution would propagate up the length scale with weak attenuation and no change in shape. Later refinements were to include 'diffusion' (i.e. propagation backward as well as forward) and feedback to smaller-size classes. Cousins (1983, 1985b), an ardent admirer of Elton, feels that some distinction based on function should be made among the types of particles comprising a community. He advocates the estimation of separate psds for autotrophs, heterotrophs and detritus. Presumably, differences in the dynamics of particles within each of these three categories are small in comparison with the differences in behaviour between the categories. Peters (1983) is optimistic that allometric and particle-size models offer the best starting-point for a predictive ecology.

The interest in particle size distributions of marine organisms has catalysed a number of new discoveries and practical applications. Most advances stem from efforts to obtain better information on plankton below 2 μm in effective diameter. Pomeroy (1974) suggested the existence of a widespread and diverse community of picoplankton, and this was verified by Waterbury *et al.* (1979) and Johnson & Sieburth (1979). Platt, Subba Rao & Irwin (1983), citing allometric and thermodynamic relationships, estimated that about half of the productivity of the world's oceans was generated by these smallest of micro-organisms. Just how much this incremental autotrophy affects heterotrophic production at macroscropic scales remains at issue. Everyone seems to agree
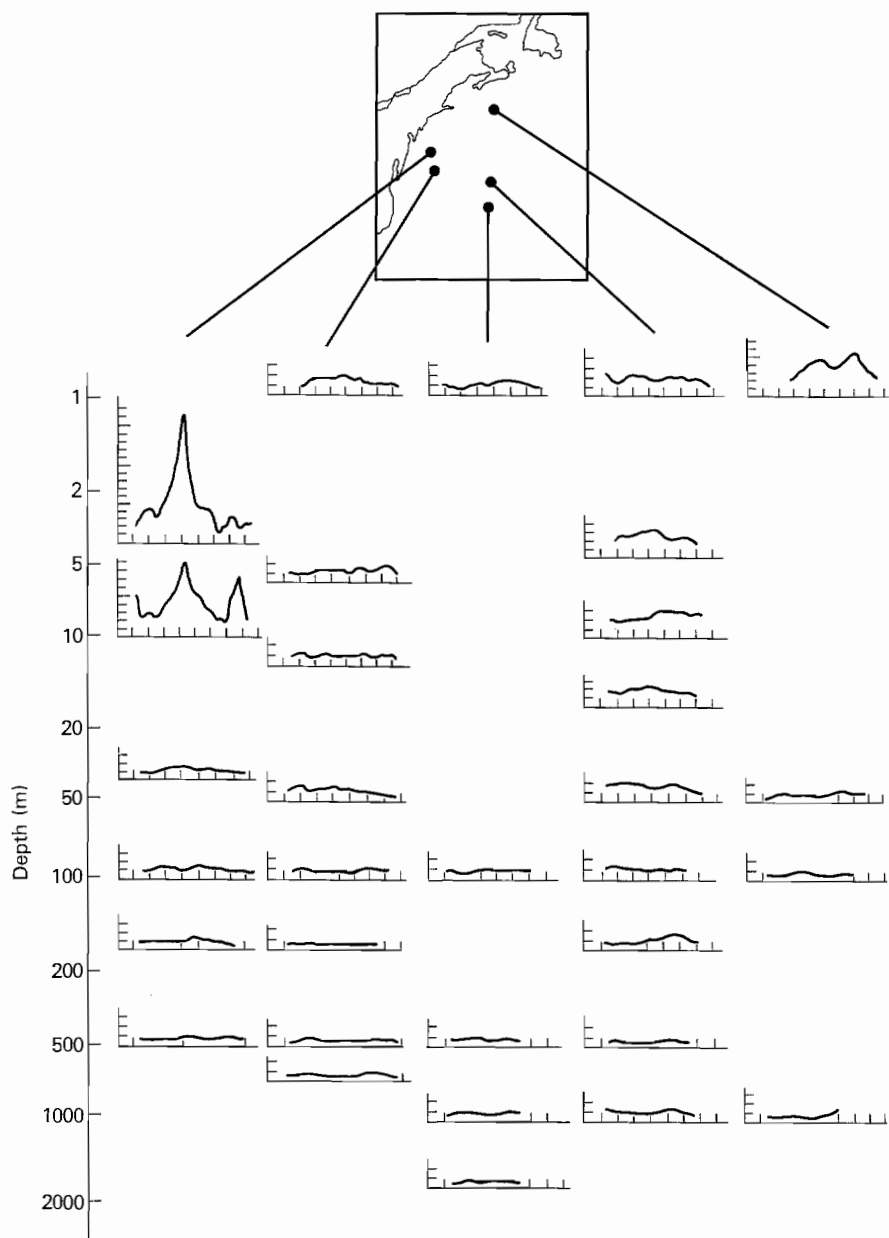
FIG 14.1   Size distributions of suspended particulate matter at various depths in the western North Atlantic (after Sheldon, Prakash & Sutcliffe 1972); in each graph the horizontal axis indicates particle diameter (with markers at 1, 2, 4, 8, 16, 32, 64 and 128 μm) and the vertical axis particle concentration by volume (ppm, with markers at intervals of 0.01).

there is a high degree of cycling and dissipation among the members of what has come to be known as the 'microbial loop' (Azam *et al.* 1983; Goldman 1984). Some, for example, Ducklow *et al.* (1986), argue that virtually all the picoplankton production is dissipated within the microbial loop, whereas others like Sherr, Sherr & Albright (1987) maintain that significant amounts are passed up the trophic web. In either event, it is highly probable that microbial metabolism is generating enormous quantities of dissolved organic carbon compounds (DOCs) within the upper layers of the world's oceans. New analytical methods point to DOC levels that are about four times those previously reported; the high levels result at least in part from the activity of the picoplankton (Sugimura & Suzuki 1988). The discovery of this new stock of organic carbon also ameliorates a previously disturbing imbalance in the global carbon cycle.

Knowledge about the nature of living particles below $2 \mu m$ in diameter is fast accruing now that the biomedical techniques of flow cytometry (Yentsch 1983) are being adapted for shipboard analysis of ocean plankton, pushing the limits of taxonomic detection down to 0.25 μm (Robertson & Button 1987) and possibly as low as 45 nm (Chisholm, Olson & Yentsch 1988). At the other end of the scale, side-scanning sonar appears to extend the acquisition of data on particle sizes well into the macroscopic ranges (Ehrenberg *et al.* 1981).

Paralleling the importance of organism size for ecosystem behaviour stands the possibility that physical phenomena of various characteristic scales also influence the make-up of the biotic community. That is, the measurements of spatial heterogeneities in physical variables, e.g. water movement, light and temperature, could be compared with the concomitant spatial structure of biotic distributions to investigate the potential coupling of physical and biological phenomena. To effect such a comparison marine ecologists have borrowed from their colleagues in physical oceanography, who are wont to represent their data on ocean currents in terms of 'power spectra'. Without going into the details of Fourier analysis, a power spectrum represents the aggregate amounts of kinetic power in fluid motions of successive characteristic lengths, e.g. the diameters of turbulent eddies. Typically, more kinetic energy is possessed by larger-scale currents, and this power is dissipated into heat as these motions degrade into smaller eddies. The same formal calculations can be applied to a temporal or spatial series of measurements on any other variable, such as chlorophyll concentration, to yield the 'power spectrum' of a biotic variable (Platt & Denman 1975).

It has been hypothesized by Okubo (1974) that when non-linear species interactions are affected by turbulent diffusion 'diffusive instab-

ilities' could result. These spatial structures are to some degree independent of the underlying fluid motions. Whenever the slopes of the power spectra for water flow and biotic concentration are parallel, one is safe in assuming that the biota are being passively dispersed by the currents in true planktonic fashion. A departure of the two spectra could be evidence of a biological dissipative structure. The occurrence of dissipative structures seems tied to the boundaries of the water body, because Powell *et al.* (1975) observed dissonance between the physical and phytoplankton spectra at lengths greater than 100 m, whereas Gower, Denman & Holyer (1980) concluded that phytoplankton are being passively dispersed by ocean currents on scales as large as 10–100 km.

NON-HOLISTIC LINDEMAN SYSTEMS

Whereas Elton tried to make sense out of complex ecosystems by concentrating on the numbers of organisms and their sizes, Lindeman paid scant attention to these attributes and focused instead upon the functional and relational attributes of the ecological ensemble. It should be noted that Lindeman's motivations for describing his senescent lake systems the way he did derived largely from the physical science of thermodynamics. He was inclined to describe the parts of the system in physical terms, such as the amounts of material or energy embodied in them, and the relationships among his system parts likewise were gauged by the magnitudes of the transfers of material between components. Classical thermodynamics can be regarded as a self-consistent theory of relationships among macroscopic properties. Reference to microscopic entities such as molecules is not necessary and is even scorned in certain thermodynamic circles: whence derives Lindeman's casual attitude toward attributes that Elton regarded as paramount. Lindeman's emphasis was more on describing the configuration of the entire ecosystem and upon the functions of its parts within the context of the whole.

Of course, Lindeman was not the first to treat ecosystems almost as physical entities. Among his predecessors Lotka (1922), an actuary from Baltimore, captured the attention of many with, among other things, his quantitative description of predator–prey relationships. His name is most often connected with that of Volterra to identify their model of the interaction of sharks and fishes in the Aegean. They represented this predator–prey relationship using two coupled, ordinary, non-linear differential equations. It is interesting to note that Lindeman did not attempt to portray the trophic dynamics of his lake system in terms of differential equations. Perhaps he was unfamiliar with this type of math-

ematics; but, even if he were not, it is unlikely that such a model would have helped his narrative to any significant extent. Known analytical solutions to non-linear differential equations are sparse.

It was advances in automated computation that revived interest in simulating ecological dynamics with differential equations. Analogue electrical circuitry could be quickly fashioned to integrate systems of coupled differential equations without recourse to analytical methods. H. T. Odum (1971), another student of G. E. Hutchinson, employed analogue computers to simulate ecosystem behaviour using data on aquatic communities collected in the style of Lindeman. Meanwhile, digital computers evolved during the late 1960s that were capable of integrating the numerical difference counterparts to differential equations with much greater ease and accuracy than had been available with analogue computers. It was then possible to 'solve' systems comprised of hundreds of coupled differential equations.

Because of the potential that multivariate simulation modelling held for quantitative ecology, it became a key task in the North American contribution to the International Biological Programme. Unfortunately, the full promise of large-scale simulation models in biological oceanography has not yet been fulfilled, and there are those who say it probably never will be. Nevertheless, praiseworthy attempts at simulating marine ecosystems do exist, for example those of Steele (1974), Kremer & Nixon (1978), Longhurst (1978) and Cushing (1981), that afford penetrating insights into ecosystem mechanics and dynamics. As will become apparent presently, the data amassed in the course of these exercises are beginning to pay dividends in another analytical context.

In 1977 the governing body of the Scientific Committee on Oceanic Research (SCOR) commissioned a working group to assess the value of mathematical models for biological oceanography (Platt, Mann & Ulanowicz 1981). The committee, under the chairmanship of K. H. Mann, cautioned against over-confidence in the results of simulations of many coupled biotic processes. They cited uncertainties in the data, the amplification of these errors during the simulation process, and the possibility of deterministic chaos as difficulties plaguing many-variable simulations. But their chief criticism was that, despite the avowed intention of modellers to treat the entire system, the simulation paradigm does not address the system *as a whole*. That is, systems of coupled difference equations are reductionistic in the mechanistic sense.

In the process of simulation modelling one normally begins by defining the parts of the system, then identifies the connections between the parts and proceeds to describe each bilateral interaction in terms of

some (usually fixed) mathematical function. Finally, these constitutive relations are incorporated into some balance scheme and numerically integrated. The dynamics of the ensemble of bilateral interactions is assumed to mimic the behaviour of the ecological community as a whole. Recent results from reconstructability analysis (Klir & Folger 1988) pin-point why such representation often fails: it does not take account of possible higher-order interactions or allow for the evolution of the system topology (the network of interactions) and constitutive relations.

These criticisms apply only to systems of coupled processes, and the SCOR committee commended the success of some models that treated only a single species or process, such as those of Paloheimo & Dickie (1966), Parsons, Lebrasseur & Fulton (1967) and Jassby & Platt (1976). Simple models of nutrient fluxes (Moloney *et al.* 1986), trophic interactions (Frost 1987) and primary productivity have been highly useful tools for understanding and measuring these processes. Platt & Sathyendran-ath (1988) have combined a single-process model that predicts phyto-plankton production from ambient light quality with several physical models of optics to infer the magnitude of primary production over large areas of the world's ocean from satellite data on ocean colour.

As for understanding the dynamics of the world's fisheries, single-process models have helped to structure dialogue for many years (Beverton & Holt 1957; Ricker 1975; Cushing & Horwood 1977), although most of these quantitative models belong more to the Eltonian school, cast as they are in terms of fish numbers and body lengths. Rothschild (1986) declared that 'A suitable formulation for linking whole ecosystem models with recruitment variability . . . is not yet available', due, in his opinion, to the exclusion of density dependence and amplifier effects in both ecosystem and recruitment models. He urged the incorporation of somatic/reproductive energetic ratios (a Lindeman–Elton hybrid) into recruitment models, and held some hope for an ecosystem approach to the problem of predicting fish population levels, because he felt that stock 'variability may arise as much from environmental variables as from biotic variables'.

This possibility that physical forces may dominate interbiotic effects in certain spatial domains makes feasible the prediction of biotic levels and distributions in these regions, providing of course that the driving physical forces are themselves known or predictable. Harris (1988), for example, documents the strong connection between phytoplankton ecology and physical driving forces. Nihoul (1986) presents examples of how the strong gradients in physical energies that exist near to physical

interfaces (e.g. air–water, water–sediment, water–ice, etc.) can radically alter the rates of biological processes, such as production.

WHOLE-SYSTEM ECOLOGY

If the simulation modelling of ecological communities is not a wholly satisfactory quantification of ecosystems, then whither should we direct our efforts? One possibility is to enclose subsystems of a biotic community to be used as microcosm (Giesy 1980) or mesocosm (Grice & Reeve 1982) analogue models of the prototype. There have been some ambitious efforts to construct mesocosms of marine ecosystems, notably the CEPEX enclosures of oceanic planktonic communities (Grice *et al.* 1980) and the MERL tanks (Nixon *et al.* 1984) containing both pelagic and benthic elements of an estuarine ecosystem, as well as more modest endeavours to contain natural communities and replicate their environments, e.g. those of Lane & Collins (1985) and Frost (1987).

If fidelity to the dynamics of the prototype community is the hallmark of an exact ecology, then mesocosms offer perhaps the best available method for predicting ecological behaviour. They are capable of yielding a cornucopia of data on coupled processes that are more reliable than anything issuing from approaches of a more a priori nature. The use of mesocosms as both a management and a research tool definitely should be encouraged. Such promise notwithstanding, mesocosms are not the panacea for biological oceanography. If the objective of our research is to gain some understanding about the workings of ecosystems, observing mesocosms still leaves us with the problem of how to abstract from the events transpiring in the container. Secondly, any mesocosm is by definition a subsystem of the prototype, and one still faces the problem associated with reconstructability.

One approach to interpreting mesocosm data is purely phenomenological and inductive in nature — akin to what Peters (1983, 1986) calls 'empirical limnology'. Synoptic time-series data on the principal biotic and physical elements in the mesocosm are accumulated and are then used as input to an algorithm that automatically parses the relationships among the variables (cf. Ulanowicz *et al.* 1978; Ivakhnenko, Krotov & Visotsky 1979; Klir 1981; Shaffer 1988; Vezina & Platt 1988). It is hoped that after a sufficient number of such exercises certain laws or principles of ecological behaviour will emerge, much in the way that the laws of thermodynamics evolved from quantitative observations on gases and steam engines.

Another direction toward understanding whole-systems behaviour has been promulgated by the SCOR Committee on Biological Modelling in the Oceans (Platt, Mann & Ulanowicz 1981). They urged that greater emphasis in biological oceanography be placed upon the elucidation and quantification of the flows of material and energy among the components of marine ecosystems. Three international workshops to foster interest in the topic of flows in marine ecosystems have been organized by members of the Committee (Fasham 1984a,b; Ulanowicz & Platt 1985; Wulff, Field & Mann 1989). Regardless of how it was prompted, there has recently been a distinct renewal of interest in quantifying fluxes of material and energy in marine systems (De Vries & Hopstaken 1984; Longhurst 1984; Fasham 1984a,b; Platt & Harrison 1985; Beddington 1986; Gordon *et al.* 1986; Sissenwine 1986; Peterson & Fry 1987; Cushing 1988; Baird & Ulanowicz 1989; Waring 1989). This renewal of interest builds upon an already interesting base of marine studies, for example those of Steele (1974), Jansson & Wulff (1976), Warwick, Joint & Radford (1979), Baird & Milne (1981) and Dame & Patten (1981). The monitoring of fluxes of carbon in the ocean has taken on a new urgency in the wake of ambiguities surrounding the global balance of this element. An international effort called the Joint Global Ocean Flux Study (JGOFS) has been mounted recently under the auspices of SCOR to 'determine and understand on a global scale the processes controlling the time-varying fluxes of carbon and associated biogenic elements in the ocean' (Brewer *et al.* 1986; JGOFS 1987).

A problem with the acquisition of flow data is that the resultant web of biotic and abiotic exchanges often becomes quite complicated. As an example, the flows of carbon among thirty-six major compartments of the ecosystem representing the mesohaline region of the Chesapeake estuary is shown in Fig. 14.2. The biomass values and flow magnitudes in this figure are averaged over the full extent of the mesohaline region. The annual flows are based on four separate seasonal networks estimated by Baird & Ulanowicz (in press). Spatial averaging was achieved by multiplying the rates for each exchange by that fraction of the mesohaline region over which the given transaction occurs. Temporal dynamics would be better resolved if data were available to represent the flow systems as twenty-six biweekly networks. Furthermore, it is likely that the ecosystems represented in the various tributaries and littoral zones and the channel region all differ in their network topologies, and comparisons among these should provide useful insights into the functioning of the larger mesohaline ensemble.
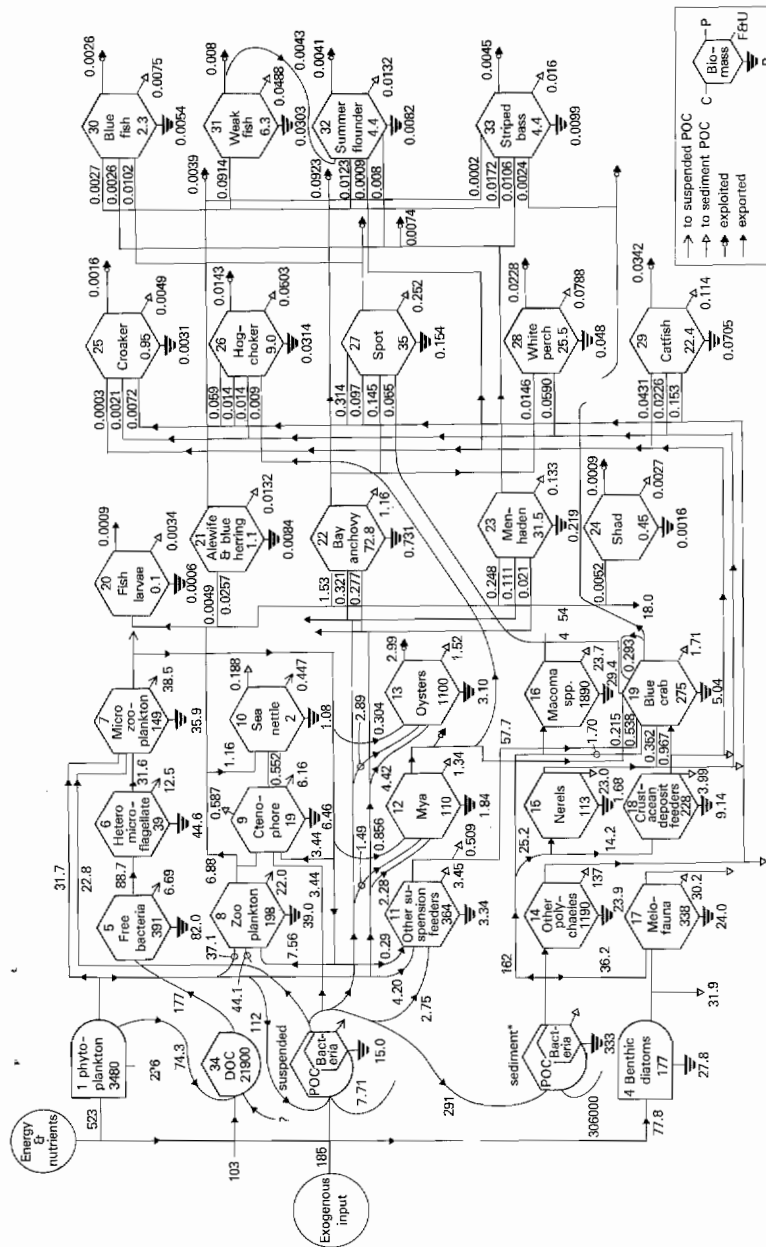
FIG 14.2 A schematic representation of the annual carbon flows among the principal components of the Chesapeake mesohaline ecosystem (based on Baird & Ulanowicz 1989). Standing crops of carbon are indicated within the compartments in mg m^{-2} and the indicated flows of carbon are in g m^{-2} year^{-1}.

Given such a confusing web of flows, it seems at first difficult to make definitive quantitative statements about its workings whilst keeping the number of a priori assumptions on the system to a minimum. However, the collection of exchanges can be viewed from several interesting perspectives, using what is coming to be known as 'ecological network analysis' (Wulff, Field & Mann 1989). The data on flows can be arrayed conveniently as the elements of an n-dimensional matrix, where n is the number of elements in the network. The rows of this matrix of transfers correspond to the donor compartments and its columns to the recipients. Exogenous transfers can be listed as n-dimensional vectors. It was discovered in economics (Leontief 1951) that, once such a matrix of flows is properly normalized, one can use matrix–vector operations to estimate the extent of *indirect* influences among compartments. In particular, the $i - j$th element of the mth algebraic power of the normalized flow matrix can be used to estimate the total amount flowing from i to j along *all* pathways of exactly m exchanges (Szyrmer & Ulanowicz 1987). Furthermore, the sum of all the positive integer powers of the normalized flow matrix forms an infinite series that converges to a finite limit. It happens that this limit can be calculated from the initial array using only two matrix operations — subtraction and inversion. The $i - j^{th}$ element of this limit matrix reveals the magnitude of the flow from i to j over all pathways of all lengths.

These economic analyses apply equally well to ecological networks (Hannon 1973; Patten *et al.* 1976; Szyrmer & Ulanowicz 1987). For example, striped bass and bluefish are two pelagic top carnivores in Chesapeake Bay. There are not many obvious differences in their feeding behaviours, although their diets differ somewhat. However, the indirect resources supporting the two fishes can be shown to differ markedly. Over 65% of the striped bass diet once was in the form of mesozooplankton, but only 29% of the bluefish diet passed through the same compartment. In contrast, only 2% of the striped bass intake of carbon was formerly incorporated into polychaetes, but this latter item supports 48% of the bluefish diet. One concludes, therefore that the striped bass is sustained mostly by the pelagic grazing chain, whilst the bluefish depends mostly upon the benthic detrital chain.

The estimation of indirect influence had been limited previously to 'vertical' trophic transfers of material and energy, but Ulanowicz & Puccia (unpublished) have recently reformulated the analysis to reveal 'horizontal' competitive relationships as well. The methodology now exists to gauge all *non-proximate* interactions occurring in the trophic network. Most exciting is the observation that indirect influences are

sometimes greater in magnitude and even opposite in character to direct interactions (Higashi & Patten, in press). Hence, observations made of direct effects should be interpreted only in the full context in which they occur.

Lindeman's idea of assigning each taxon to a distinct trophic compartment certainly would fail to apply to the network in Fig. 14.2, where numerous heterotrophs feed along multiple pathways of differing trophic lengths (Cousins 1985b). However, if one is willing to consider a distributed mapping of species to trophic levels, difficulties quickly fade. For example, if a given taxon were to obtain 20% of its intake along trophic pathways one step removed from the autotrophs, 70% along pathways two steps removed and 10% along sequences three steps distant, then the activities and biomass of that taxon would be assigned in those given proportions to the herbivore, carnivore and top carnivore levels, respectively. The mechanics for mapping a complex web of ecosystem feeding relations into a straight chain of trophic transfers were developed by Ulanowicz & Kemp (1979). Recently it has become possible to add the abiotic detrital recycling pathways to the analysis (Ulanowicz, in press). Thus, one can now reconfigure the most complicated webs of trophic interactions into Lindeman-style trophic chains with detrital feedbacks.

The trophic level reformulation of the Chesapeake network is depicted in Fig. 14.3 and reveals several interesting features. Trophic pathways at least eight steps long are apparent among the Chesapeake biota; however, the amounts passing through the top three levels are vanishingly small. In fact, when the average levels at which each compartment feeds are calculated, they all fall below five — a limit discussed elsewhere (Slobodkin 1961; Pimm & Lawton 1977). Secondly, it is clear that production at higher levels is significantly dependent upon the recycling of carbon (and some of its chemically bound energy) through the non-living elements of the system. Detritivory exceeds herbivory by a ratio of more than 10:1, and 70% of all the inputs to the detrital pool derive from recycling. Finally, there is a trend (not without exception) for successively higher trophic levels to *decrease* in efficiency, contradicting what Lindeman (1942) had expected.

As cycling is such an important element of most systems, it should be helpful to analyse the pathways for cycling in greater detail. Elsewhere (Ulanowicz 1983) I have outlined methods both for enumerating all biogeochemical cycles and for extracting those feedbacks from their supporting web of dissipative transfers. Cycling of material usually indicates cybernetic control at work in the system (Odum 1971;
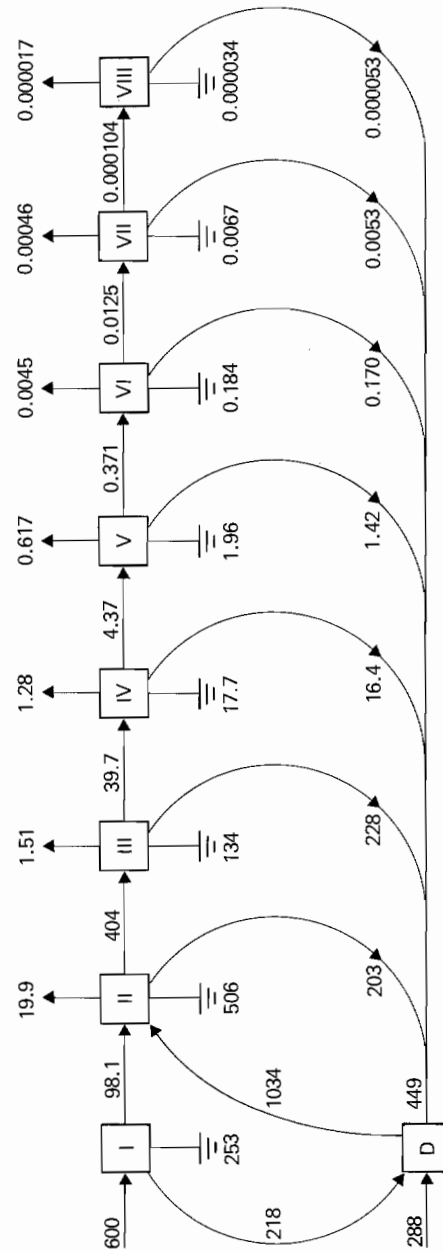
FIG 14.3 The aggregation of the flow web in Fig. 14.2 into a concatonated chain of transfers through eight trophic levels. Recycling of non-living material is through compartment D. Flows of carbon are in g m^{-2} year^{-1}.

Ulanowicz 1986), and the pattern of such recycling can help to define the function of a compartment in the context of the ecosystem.

For example, the cycles present in the Chesapeake network number only sixty-one. When properly weighted and aggregated they form the pattern shown in Fig. 14.4. The bipartite configuration of the cycles is surprising and suggests that control among the planktonic community is largely decoupled from that among the benthos and nekton. It is also interesting to note that fourteen of the compartments do not engage in any cycling of carbon. Eight of these non-participants are filter-feeding benthos or finfish. They may be regarded as 'boundary' populations, whose function is to shunt material and energy from the planktonic domain into the benthic-nektonic realm of control. Curiously, three elements of the microbial 'loop' also do not engage in any cycling. As regards carbon, the term 'loop' appears to be a misnomer. The microbiota function more to shunt excess primary production out of the ecosystem via their own respiration (Ducklow *et al.* 1986).

Indirect flow, trophic and cycle analyses address how a subsystem of a given ecological network can impose itself as a unit upon its constituent parts. But, if one's goal is to quantify the process of ecological succession, it becomes necessary to characterize the status of the ecosystem as a whole. E. P. Odum (1969) cited twenty-four community properties that he felt reflected the succession toward a more mature community. Most of Odum's system-level indices can be calculated from the same data used to create flow networks, e.g. overall $P:B$, $P:R$ or $R:B$ ratios. Others, such as nutrient retention time, require analytical interpretation (Hannon 1979), whilst those remaining, such as body size and life-cycle, are better included in Eltonian projects.

I have argued (Ulanowicz 1986) that all of the Lindemanian measures that appear on Odum's list are particular facets of a more general index called the network ascendancy. Ascendacy is a product of two factors, one quantifying the total activity of the system and the other specifying the level of organization inherent in the network structure. By organization is meant here the average degree of stenotrophic behaviour, or the extent to which those pathways of higher throughput efficiency dominate their more numerous, but less effective counterparts. The quantity 'average mutual information' as defined in information theory can be adapted to serve as the factor representing the organizational level of a given network (Rutledge, Basorre & Mulholland 1976). Any increase in the network ascendancy is presumed to mirror the growth and/or development of the whole system.
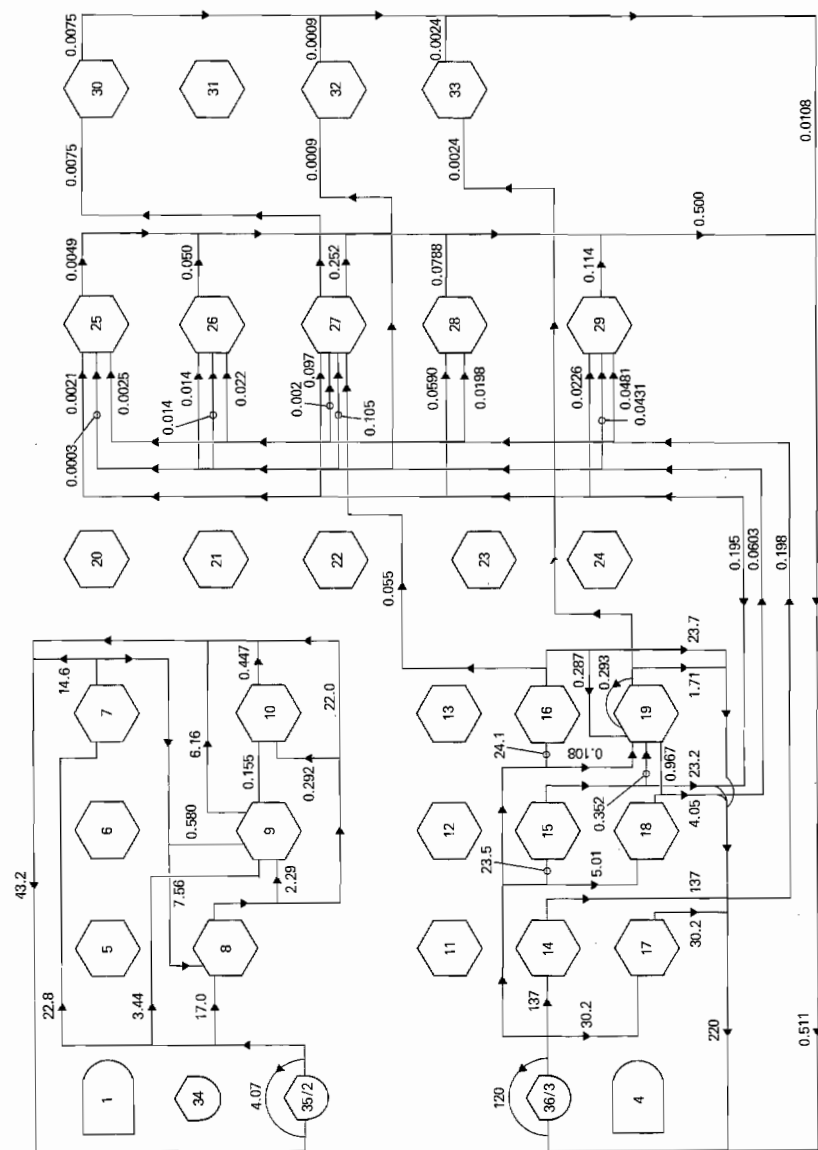
FIG 14.4   The composite cycling of carbon that occurs in the flow diagram in Fig. 14.2. Units of flow and numbering of the compartments are the same as in Fig. 14.2.

A remaining issue is whether systems-level organization, as quantified by ascendancy or any similar whole-system index, is purely epiphenomenal or results from an autonomous higher-level process. I have argued (Ulanowicz 1989) that autopoietic cycles as may exist in ecosystems characteristically endure longer than their components, and, more importantly, that the make-up of the autocatalytic cycle exerts a degree of selection upon its replacement parts. Hence, I regard cybernetic feedback in ecosystems as one of the origins of formal causes, *sensu* Artistotle, that effect the organization of ecosystems.

FUTURE DIRECTIONS

Left to the realm of academic speculation, opinions on how to abstract ecosystems are likely to continue to diverge. There are countervailing pressures favouring a more accommodating dialogue, however, as the world and its oceans are beset by a host of environmental problems. Humanity looks increasingly to ecologists to forecast future conditions, and offer suggestions on how to ameliorate the consequences of impacts on the biosphere. Those able to influence societal behaviour need to know what will be the effects of a slight rise in oceanic temperature, how low concentrations of pollutants might affect oceanic resources, or which biota will suffer as a consequence of a modest rise in sea-level.

It is unlikely that any of the avenues of research discussed in this paper would alone be sufficient to provide reliable answers to such questions. Simulation modelling *per se* is too mechanical an analogue ever to yield reliable predictions. Likewise, network analysis remains largely descriptive, providing only suggestions about ecosystem behaviour.

Until the advent of some radically new methodology, our present best hope for understanding ecodynamics and forecasting impacts would seem to lie in research on possible hybrids of existing tools. For example, Field, Moloney & Attwood (1989) have created a particle-size-based model simulating the evolution of a plankton community following an upwelling event astride the Banguella current off south-western Africa. The authors use their package to compute a temporal series of flow networks, each of which becomes the subject of network analysis. Thereby the authors are able to trace the course of ecosystem-level properties over time.

Although the efforts of Field, Moloney & Attwood (1989) combine most of the tools discussed in this review, even further amalgamation of methods is both feasible and desirable. Their system attributes result strictly from the characteristics of the driving model, whereas a realistic

portrayal of events might arise through allowing feedback to occur between the ecosystems being simulated and elements at adjacent hierarchical levels. For example, the integration of the model could be interrupted at convenient intervals, and changed by stochastic influences emanating from the system's infrastructure (Allen & McGlade 1987). At somewhat longer intervals the status of the ecosystem flow network could be evaluated, and these results used to alter the dynamical structure of the model so as to follow more closely those system-level trends most commonly observed in nature (Cheung 1985; T. F. Fontaine, personal communication).

The oceans that gave birth to life continue to sustain it today. They also provide the background to one of the most challenging and promising of contemporary scientific endeavours.

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