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Productivity, trophic structure, and energy flow in the steady-state ecosystems of Silver Springs, Florida

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1. Introduction

To a very large extent modern understanding of aquatic ecosystems has been shaped by concepts of energy flow, food webs, and trophic levels (e.g., Odum, 1971; Pomeroy and Alberts, 1988). The origins of these concepts date back perhaps to a nineteenth century essay that qualitatively described the interconnections among organisms through feeding relationships (Forbes, 1887). These ideas were later quantified as trophic pyramids of organism abundance (Elton, 1927) and as generalized trophic levels (Lindeman, 1942). For shallow aquatic environments where pelagic and benthic habits are both important, the ability to partition flows of energy and organic matter quantitatively through the biological community was limited in the early part of the twentieth century by two factors. The first problem was the absence of adequate methods for measuring the total economy (inputs and outputs) of organic matter for aquatic ecosystems (Odum, 1968), while the second problem was the absence of a method for placing organisms into discrete trophic levels given the complex dietary habits characterizing most aquatic animals (Rigler, 1975). On the other hand, there was a strong motivation for continued quantitative study of energy flow and trophic interactions provided by broad theories suggesting that ecosystem succession and community survival were regulated in natural ecosystems by energetic controls (Lotka, 1925).

This was the backdrop for H.T. Odum's widely cited investigation of north Florida's Silver Springs ecosystem conducted in the mid-1950s. In this review, we explain how Odum's modification and application of the diel oxygen method for measuring total ecosystem primary production and respiration provided constraints (i.e., total inputs and outputs of biological energy) for a quantitative description of energy flow through this ecosystem. We briefly describe the ambitious data collection program Odum developed to quantify trophic energy flows in this ecosystem, as well as his clever methods used for quantitatively assigning biomass of omnivorous animals to more than one trophic level. We argue that the publication of the Silver Springs monograph in 1957 represents the first in a series of H.T. Odum's ecosystem studies motivated by interest in testing the Lotka "maximum power theorem" and its associated theory of power-efficiency balance (Odum and Pinkerton, 1955). We then describe the enormous impact that this study had both on Odum's career and on the field of aquatic ecology for decades to follow.

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2. Background for study

The Silver Springs ecosystem had attracted the attention of native Americans, Spanish explorers, early naturalists, and many other impressionable visitors for decades and centuries prior to the initiation of this study (Odum, 1957a,b). By 1955, Silver Springs had already become an exotic stopping point for North American tourists, and the facility's *Ross Allen Reptile Institute* had developed into a well-known locus of popular science involving alligators and venomous snakes. Following his arrival at the University of Florida in the early 1970s, Odum incorporated a field trip to Silver Springs as part of his *Systems Ecology* course, which occasioned our first experience with this amazing place. We quickly assimilated Odum's sense of enthusiasm and reverence for this complex ecosystem through his elegant integrated portrayal delivered to the class with his characteristic exuberance.

The Silver Springs study was initiated in 1951 and continued into 1956, with most of the work completed during 1953–1955. The studies were supported by both the Office of Naval Research and the University of Florida. Odum began his first of two stints at the University of Florida in 1950 as Assistant Professor in the Department of Biology. This was the beginning of an extraordinarily important period of ecological thought and measurement in Odum's career. During this period Odum published, in addition to the Silver Springs monograph (Odum, 1957a): (1) an explication of the theoretical foundations for his career (Odum and Pinkerton, 1955), (2) an award-winning (ESA's *George Mercer Award*) description of a coral reef ecosystem's trophic structure and energy flow (Odum and Odum, 1955), (3) a synthesis of his method for measuring integrated aquatic ecosystem metabolism (Odum, 1956a,b), (4) a comparative analysis of ecosystem metabolism in Florida springs (Odum, 1957b), and (5) a pioneering microcosm study of stream ecosystems (Odum and Hoskins, 1957). This productivity is impressive given the fact that he also taught courses, wrote proposals and was actively engaged in fieldwork during this time. Odum noted that "since Silver Springs was located 40 miles from the laboratory, the work at times took on the characteristics of expeditions." In many ways, H.T. Odum's entire career could be described as a series of fast-moving expeditions.

3. The Silver Springs study

Silver Springs is the largest and best known of the springs of north-central Florida, with an average discharge of some 80,000 $m^3 h^{-1}$. The primary area of the spring and river examined in Odum's study included the main boil (area of upwelling spring water) and the initial 0.75 miles of the narrow (∼20–30 m) outflow stream. Although much of the sampling focused in the area of this main boil, measurements were also made at downstream stations and side-boils. The small size of this study area was not unlike the dimensions of other well-studied experimental systems used by aquatic ecologists (e.g., G.E. Hutchinson's Lindsey Pond).

The motivation for H.T. Odum's Florida Springs Study was compelling and clearly stated (Odum, 1957a,b): "because of their special properties, these springs are collectively a giant constant temperature laboratory." Furthermore, because each spring is maintained by a constant flow, "it is possible to compare whole communities in a ready made experimental design." The broad purpose of this effort was "to study the basic workings of stream ecosystems and factors controlling individual, population, and community productivity." Major objectives were stated as follows: (1) to examine relationships between power output (productivity) and efficiencies at the ecosystem level, (2) to quantify relationships between organism biomass and productivity, (3) to test effects of water movement as an auxiliary energy source enhancing primary production, (4) to measure and compare ratios of primary production to respiration (P/R) for Silver Springs and other aquatic ecosystems and relate these to measurements of community structure.

3.1. Trophic energy flow in aquatic ecosystems

The primary focus of the Silver Springs study was to quantify the trophic energy structure, function and efficiencies of this chemostatic, steady-state ecosystem. Although a few earlier papers had described aquatic ecosystems in terms of their annual energy budgets and integrated trophic flows (Juday, 1940; Lindeman, 1942; Clarke, 1946; Dineen, 1953), the Silver Springs study was by far the most detailed and thorough such analysis to that date. The amount and diversity of data collected and experiments conducted during this study were unprecedented, with measurements of more than 40 chemical constituent concentrations at several spring boils and stations along the river course. Abundance and biomass measurements were made for some 70 plant and algal species and more than 125 animal species or separate taxonomic groups. Great care was taken in this study to convert organism counts and size measurements into comparable energy units normalized per unit water volume or surface area, and details of each calculation were provided. Ecological rate measurements, including photosynthesis, respiration and growth as well as nutrient uptake and recycling, were made for individual taxa and habitats as well as for the entire ecosystem, often employing clever new approaches that exploited the most sophisticated methods available at the time.

Although it appears that most of the measurements reported in this paper were done directly by Odum and his technical assistants, this was in fact a large collaborative study that also involved other colleagues (at least five) at the University of Florida. Additional scientific inputs for methods and analyses of chemical constituents and for taxonomic identification were also provided by numerous (>20) collaborators, and the study generated an assortment of publications by other investigators, many of which are cited in this paper. Thus, the Silver Springs study represents an early prototype for the large multi-investigator ecosystem projects that were popularized decades later with the International Biological Program (IBP, Neuhold, 1975) and for the many multi-disciplinary ecosystem investigations that have followed in programs such as NSF's Long-Term Ecosystem Research studies (LTER, Callahan, 1984).

Odum's characterization of Silver Springs as a steady-state ecosystem with inputs of constant temperature, flow and chemical composition is fundamental to his study design and interpretation of research results. Odum quips that this steady-state nature is symbolically reflected in the question of an old boat captain/guide who asked if the waving grass ever grew because to him it always seemed the same. This view is also reflected in Odum's own comment that it is "most terrible and healthy for the poor ecologist . . . that anyone can check his field work at any later time." Although this steady-state nature minimized the need for synoptic sampling, seasonal variations in incident sunlight produced strong cycles of primary production and other measured ecological features. Odum's steady-state conceptualization of the Silver Springs ecosystem with constant inputs of inorganic nutrients converted to relatively invariant biomass and export of organic matter is depicted in his energy flow diagram (Fig. 1). Here the distribution of trophic flows from sunlight through producers to top carnivores and decomposers are quantitatively described. The vast majority (>85%) of photosynthetically fixed biological energy is lost to community respiration, while a residual portion (12%) is transported downstream.

Odum argues that the long-term steady-state characteristic of Silver Springs has afforded sufficient time for the ecosystem to adjust to its physical and biological conditions so as to achieve the "optimum efficiency" associated with maximum power output. Although it is difficult to imagine a direct empirical test of the Lotka (1925) "maximum power hypothesis," measured rates of gross primary production here were indeed high relative to other stream ecosystems. Rates were substantially lower in a poorly circulated side-boil, which did not benefit from the "auxiliary energy" subsidy of water movement. In any case, Odum seems to infer (p. 106) that the relatively low efficiency measured for production per unit sunlight input (5.3%) was consistent with the hypothesis that power maximization requires moderate-to-low efficiency (Odum and Pinkerton, 1955). It is perhaps no coincidence that over the course of his career, Odum conducted similar comprehensive ecosystem studies in two other prototypic steady-state biomes, a coral reef (Odum and Odum, 1955) and a tropical rain forest (Odum and Pigeon, 1970). Although he later conducted similar trophic energy flow analyses in highly variable estuarine ecosystems (Odum, 1967, 1989), we speculate that Odum was initially drawn to these steady-state ecosystems as testing grounds for the "maximum power hypothesis."

The abundances of individual organisms sampled in this ecosystem were converted into equivalent biomass values based on direct measurements, allometric relationships and chemical conversions. Rates of organic consumption, respiration and production were also estimated from direct measurements of temporal changes in oxygen and organic matter and from published turnover rates. The sums of these rates were constrained by the direct measurements of total ecosystem production and respiration. Biomass and

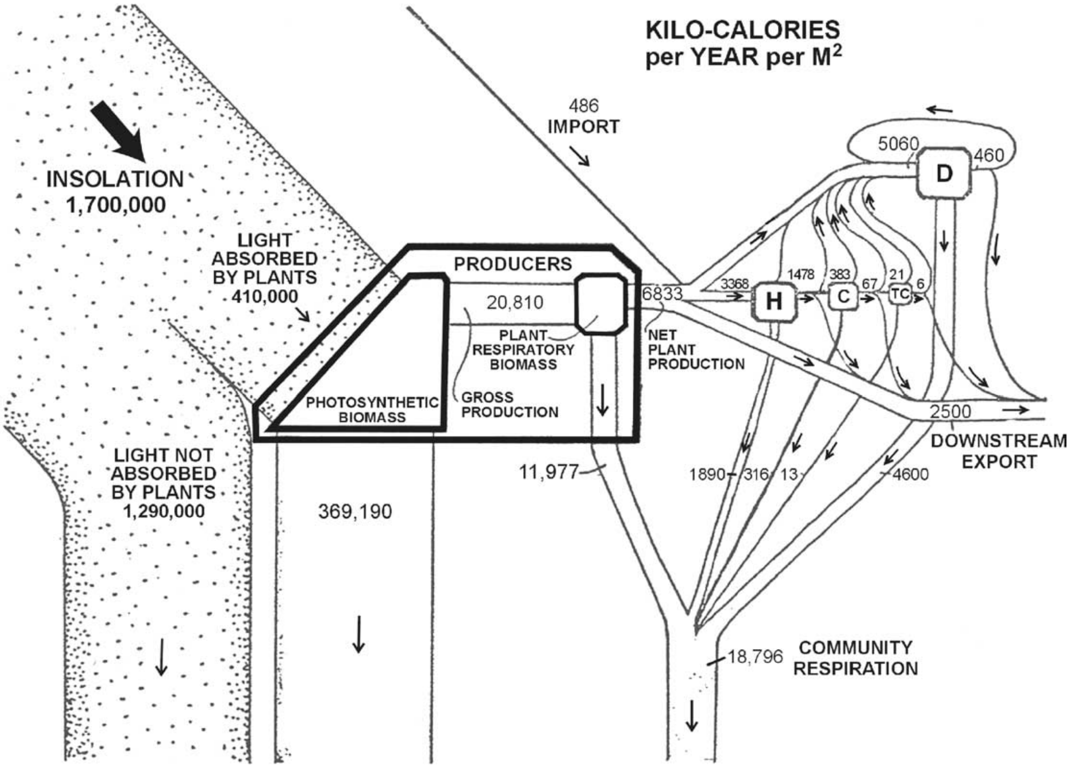

Fig. 1. A reproduction of the energy flow diagram that appeared as Fig. 7 in the Silver Springs paper (p. 61). All flows are expressed in units of kcal m^{-2} per year. The abbreviations H, C, TC, and D refer to herbivores, carnivores, top carnivores, and detritus, respectively.

metabolic rates of individual populations were then placed into five general trophic levels or categories (producers, herbivores, carnivores, top carnivores, decomposers) based on their food habits. In some cases, the biomass and metabolic rates of omnivorous animals (e.g., “stumpknockers”) were partitioned into more than one trophic level based on the proportion of their diet conforming to that trophic group. This approach allowed development of a robust trophic pyramid of biomass (Fig. 2). Odum reasoned that the shape and proportions of this pyramid may be broadly applicable because of the steady-state nature of Silver Springs. A similar approach for partitioning organisms into different trophic levels was applied in a study of a very small (0.6 m^3 volume) spring ecosystem published later in the same year (Teal, 1957). Although the feeding habits of animals included in these early analyses were probably too broadly defined, this novel approach provided the seeds for more rigorous quantitative partitioning of organism biomass and rates into trophic levels using matrix algebraic methods (e.g., Ulanowicz and Kemp, 1979; Pauly et al., 2000).

3.2. Ecosystem production and respiration

Another important focus of the Silver Springs study was the integrated measurement of ecosystem primary production (*P*) and respiration (*R*) rates. As indicated above, these measurements of *P* and *R* provided input/output constraints for assessing energy flow in the ecosystem. The addition of rigorous independent measurements of ecosystem *P* and *R* provided boundary conditions for trophic energy flow calculations made for each organism group. In this case, measurements of ecosystem-level *P* and *R* provided targets for rates estimated by summing measurements for individual organisms or habitats, thereby reducing potential problems with propagating errors. Estimates of trophic energy flow in earlier studies not supported by measurements of ecosystem total *P* and *R* may have suffered

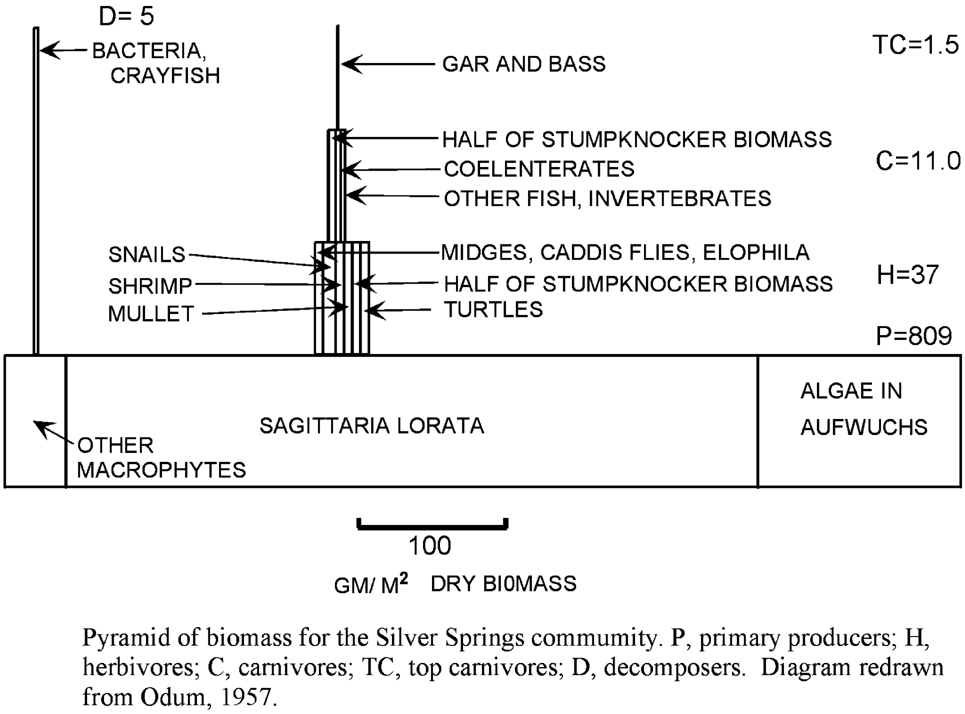

Fig. 2. A reproduction of the biomass pyramid for the Silver Springs community that appeared as Fig. 21 in the Silver Springs paper (p. 84) in Odum (1957a). Abbreviations P, H, C, TC, and D refer to primary producers, herbivores, carnivores, top carnivores, and decomposers. Numbers in the figure have units of dry biomass ($g\,m^{-2}$).

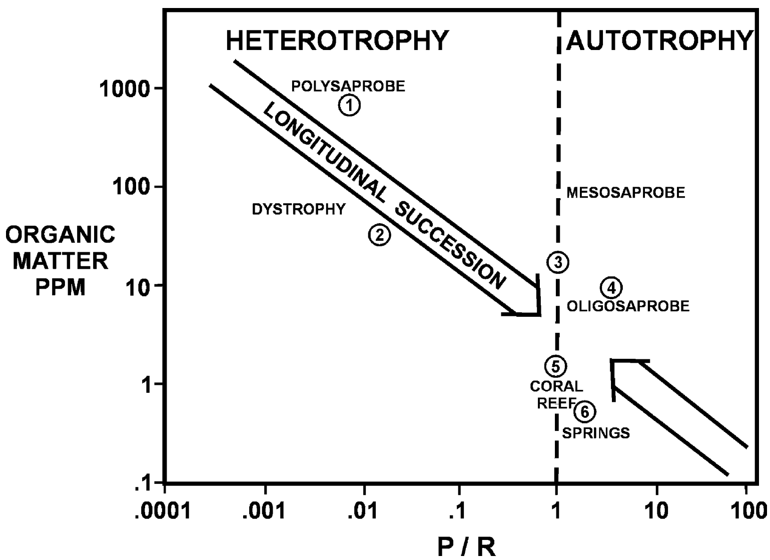

Fig. 3. A reproduction of the synthesis diagram relating longitudinal succession, total organic matter, and the relative balance of autotrophic and heterotrophic metabolism that appeared as Fig. 7 (p. 114) in Odum (1956a).

from large errors accumulating in summation of rates (e.g., Tilly, 1968). Thus, measurements of *P* and *R* provide a solid foundation from which the trophic structure could be quantified in terms of the transfer and partitioning of primary production inputs from producers and losses associated with respiration of all organisms. In addition, through comparative analysis of many measurements of ecosystem *P* and *R*, Odum was able to categorize aquatic ecosystems according to their *P*/*R* balance, efficiency of conversion of sunlight and presence of organic matter (Fig. 3, Odum, 1956a,b, 1957b). The inclusion of independent measurements of total ecosystem *P* and *R* became a fundamental element of most later ecosystem studies including those in the IBP and LTER programs. Odum's approach has also been extrapolated for estimating global scale terrestrial *P* and *R* (e.g., Hall et al., 1975; Keeling and Chin, 1996), where marked increases in global *P* and *R* have been demonstrated since the early 1970s.

4. Scientific legacy of the Silver Springs study

In the decades since the Silver Springs study, measurement of ecosystem level *P* and *R* has been adopted as a fundamental component for studies of trophic energy flow in stream (e.g., Hall, 1972; Fisher and Likens, 1973), lake (Cole et al., 2000), estuarine (Kemp and Boynton, 1980; Kenney et al., 1988), and continental shelf (DeGrandpre et al., 1997) ecosystems. In clear-water oceanic ecosystems, where diel changes in oxygen and carbon dioxide are damped by deep euphotic zones, researchers have developed related methods tracking seasonal and annual variations in metabolic gases in large water masses (e.g., Lee, 2001). Typically, measurements of ecosystem-scale rates of *P* and *R* are requisite elements of large-scale multi-disciplinary studies of oceanographic ecosystems, such as the Joint Global Ocean Flux project. In fact, there has been a growing interest over recent years in understanding the carbon balance and fluxes in the world's oceans (e.g., Williams, 1998; Duarte et al., 2001), for example, using Odum's concept of *P*/*R* ratios to estimate potential export of organic matter from the photic zone to deep regions of the oceans (Eppley and Peterson, 1979; Quiñones and Platt, 1991).

It is clearly evident in the Silver Springs monograph that Odum's thinking resonated with the idea that the springs' chemostatic nature rendered them a "ready-made natural laboratory" for studying the many factors potentially controlling productivity and trophic energy flow. In a companion paper, Odum and Johnson (1955) referred to Silver Springs as a "giant aquarium" and used results of this study to explain how organic matter production and consumption could be balanced easily in common household aquaria. In the same year that the Silver Springs study was published, Odum and Hoskins (1957) illustrated how an experimental stream microcosm could be constructed to test responses of whole ecosystems to variations in factors such as nutrients, organic matter, light, and temperature. Although microcosms and mesocosms have evolved to become standard research tools in aquatic ecology (e.g., Gardner et al., 2001), Odum seems to have valued these enclosed experimental systems as much for their often unique features as for their ability to mimic and replicate natural ecosystems (e.g., Odum et al., 1963). In any case, one can easily argue that origins for modern use of microcosms as tools for aquatic ecosystem research (e.g., Beyers and Odum, 1993) lie in the Silver Springs study.

In conclusion, we believe that H.T. Odum's Silver Springs study was a pioneering research project that sowed many seeds from which numerous areas of modern ecosystem science have developed. Present international focus on the net carbon balance for ecosystems, biomes and the whole biosphere clearly evolved from Odum's study of these small streams. Current techniques and concepts for analyzing and understanding trophic structure and energy flow also derive from the Silver Springs ecosystem study. Judging by the number and diversity of investigators and collaborators ultimately involved, this study was a prototype for modern multi-disciplinary approaches for study of large complex ecosystems. Finally, the roots for current routine use of experimental aquatic systems as tools for ecosystem research can be found in Silver Springs. This study was the first in a series that directed Odum's career toward testing and refining his hypothesis that competitive forces tend to direct systems to maximize output of useful work while maintaining sub-maximal levels of work efficiency. Clearly, the Silver Springs study had a profound impact in shaping both H.T. Odum's career and the evolution of modern ecosystem ecology.

References

Beyers, R.J., Odum, H.T., 1993. Ecological Microcosms. Springer-Verlag, New York.

Callahan, J.J., 1984. Long-term ecological research. Bioscience 34, 363–367.

Clarke, G.L., 1946. Dynamics of production in a marine area. Ecol. Monogr. 16, 321–335.

Cole, J.J., Pace, M., Carpenter, S., Kitchell, J., 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnol. Oceanogr. 45, 1718–1730.

DeGrandpre, M.D., Hammar, T., Wallace, D., Wirick, C., 1997. Simultaneous mooring-based measurements of seawater CO_2 and O_2 off Cape Hatteras, North Carolina. Limnol. Oceanogr. 42, 21–28.

Dineen, C.F., 1953. An ecological study of a Minnesota pond. Am. Midl. Nat. 50, 349–376.

Duarte, C., Agusti, S., Aristegui, J., Gonzalez, N., Anadon, R., 2001. Evidence for a heterotrophic subtropical northeast Atlantic. Limnol. Oceanogr. 46, 425–428.

Elton, C., 1927. Animal Ecology. The Macmillan Co., New York.

Eppley, R.W., Peterson, B.J., 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282, 677–680.

Fisher, S.G., Likens, G.E., 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43, 421–439.

Forbes, C.A., 1887. The lake as a microcosm. Illinois Natl. Hist. Surv. Bull. 15, 537–550 (republished 1925).

Gardner, R., Kemp, W.M., Petersen, J., Kennedy, V. (Eds.), 2001. Scaling Relations in Experimental Ecology. Columbia University Press, New York.

Hall, C.A.S., 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53, 585–604.

Hall, C.A.S., Ekdahl, C., Wartenberg, D., 1975. A fifteen-year record of biotic metabolism in the northern hemisphere. Nature 255, 136–138.

Juday, C., 1940. The annual energy budget of an inland lake. Ecology 21, 438–450.

Keeling, C.D., Chin, J.F.S., 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. Nature 382, 146–149.

Kemp, W.M., Boynton, W.R., 1980. Influence of biological and physical factors on dissolved oxygen dynamics in an estuarine system: implications for measurement of community metabolism. Estuar. Coast. Mar. Sci. 11, 407–431.

Kenney, B., Litaker, W., Duke, C., Ramus, J., 1988. Community oxygen metabolism in a shallow tidal estuary. Estuar. Coast. Shelf Sci. 27, 33–43.

Lee, K., 2001. Global net community production estimated from the annual cycle of surface water total dissolved inorganic carbon. Limnol. Oceanogr. 46, 1287–1297.

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

Lotka, A.J., 1925. Elements of Physical Biology. Williams and Wilkins, Baltimore.

Neuhold, J.M., 1975. Introduction to modeling in the biomes. In: Patten, B.C. (Ed.), Systems Analysis and Simulation in Ecology, vol. III. Academic Press, New York, pp. 7–12.

Odum, E.P., 1968. Energy flow in ecosystems: a historical review. Am. Zool. 8, 11–18.

Odum, E.P., 1971. Fundamentals of Ecology. Saunders, Philadelphia.

Odum, H.T., 1956a. Primary production in flowing waters. Limnol. Oceanogr. 1, 102–117.

Odum, H.T., 1956b. Efficiency, size of organisms, and community structure. Ecology 37, 592–597.

Odum, H.T., 1957a. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr. 27, 55–112.

Odum, H.T., 1957b. Primary production measurements in eleven Florida springs and a marine turtle grass community. Limnol. Oceanogr. 2, 85–97.

Odum, H.T., 1967. Biological circuits and the marine systems of Texas. In: Olson, T.A., Burgess, F.J., (Eds.), Pollution and Marine Ecology. Wiley, New York, pp. 99–157.

Odum, H.T., 1989. Experimental study of self-organization in estuarine ponds. In: Mitsch, W.J., Jorgensen, S.E. (Eds.), Ecological Engineering: An Introduction to Ecotechnology. Wiley, New York, pp. 291–340.

Odum, H.T., Johnson, J., 1955. Silver Springs and the balanced aquarium controversy. Sci. Counsel. 18, 128–130.

Odum, H.T., Pinkerton, R.C., 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. Am. Sci. 43, 331–343.

Odum, H.T., Odum, E.P., 1955. Trophic structure and productivity of a windward coral reef at Eniwetok Atoll, Marshall Islands. Ecol. Monogr. 25, 291–320.

Odum, H.T., Hoskins, C.M., 1957. Metabolism of a laboratory stream microcosm. Publ. Inst. Mar. Sci. Univ. Texas 4, 115–133.

Odum, H.T., Siler, W., Beyers, R., Armstrong, N., 1963. Experiments in engineering marine ecosystems. Publ. Inst. Mar. Sci. Univ. Texas 9, 373–404.

Odum, H.T., Pigeon, R.F. (Eds.), 1970. A tropical rain forest. US Atomic Energy Commun. Publ. Div. Technol. Inf. Washington, DC.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57, 697–706.

Pomeroy, L.R., Alberts, J.J. (Eds.), 1988. Concepts of Ecosystem Ecology: A Comparative View. Springer-Verlag, New York.

Quiñones, R., Platt, T., 1991. The relationship between the f-ratio and the P:R ratio in the pelagic ecosystem. Limnol. Oceanogr. 36, 211–213.

Rigler, F.H., 1975. The concept of energy flow and nutrient flow between trophic levels. In: van Dobben, W.H., Lowe-McConnell, R.H. (Eds.), Unifying Concepts in Ecology. Dr. W. Junk B. V. Publishers, The Hague, pp. 15–26.

Teal, J.M., 1957. Community metabolism in a temperate cold spring. Ecol. Monogr. 27, 282–302.

Tilly, L.J., 1968. The structure and dynamics of Cone Spring. Ecol. Monogr. 38, 169–197.

Ulanowicz, R.E., Kemp, W.M., 1979. Towards canonical trophic aggregations. Am. Nat. 114, 871–883.

Williams, P.J.leB., 1998. The balance of respiration and photosynthesis in the open oceans. Nature 394, 55–57.