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Ecological Modelling 178 (2004) 59–63

ECOLOGICAL MODELLING

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Review

Odum in Texas: a brief review of H.T. Odum's Texas Bays studies

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> Each day as the sun rises and retires the beautiful green bays like great creatures breathe in and out.
>
> —opening line of Odum and Hoskin (1958)

From 1956 to 1964, Howard Odum served as the third Director of the University of Texas Institute of Marine Science at Port Aransas (L. DeHart, Librarian, Institute of Marine Science, personal communication). His enduring influence can be seen readily by the physical structures that were built while he was Director and by the contents of the Publications of the Institute of Marine Science of the University of Texas (published once or twice a year, and renamed "Contributions in Marine Science" in 1967), which increased in breadth (literally and figuratively!) while he was director. Reading over the list of investigators whose names are associated with the Institute we were impressed at how many relatively "big names" there were in ecology, geology and meteorology (for an exhaustive list of titles in the series, see http://www.lib.utexas.edu/msl/PublContents.html). Whether such names are characteristically associated with the station or whether Odum was a magnet we are not in a position to say, but the Institute must have been a pretty interesting place during his tenure, and today is a modern, multifunctional marine research facility (http://www.utmsi.utexas.edu/index.htm).

While Odum was Director, the papers within the "Publications" ranged all over more-or-less traditional biology and ecology and focused mostly on taxonomy, life history, fish and fisheries, including their economic significance, and impacts of disturbances such as pollution or dredging. As we reviewed some of these volumes in preparation for this assessment we were rather amazed that a lot of the papers seemed very thorough and well done, on for example, red drum life history, which we found very interesting to read today. There are a number of classics, some of which we have found especially useful for our own research, e.g. Hellier's (1958) paper on fish population estimates using a drop net, and some of the earliest whole ecosystem metabolism estimates for estuarine systems and microcosms (Odum and Hoskin, 1957, 1958). Odum and Hoskin (1958) lays out in careful detail the basic procedure for estimating metabolism using diel oxygen measurements. Odum et al. (1958) examined the density of chlorophyll a in communities and found that there could be as much chlorophyll and primary production packed into 1 cm of blue green algae mat as there was in 100 m of Sargasso Sea. Utilizing the analogy of a "cannonball catcher" with an adjustable number of arms, Odum argued that ecosystems adapted their structure to the available input energy to capture such energy as was possible, so that the productivity of all ecosystems of the world, or at

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doi:10.1016/j.ecolmodel.2003.12.031

least those that received a reasonable amount of input light (and had sufficient water and soil), were not so terribly different, something that we later confirmed (Boynton et al., 1982).

Howard Odum's own contributions in the "Publications," and in other journals and proceedings volumes, focused mostly on attempting to measure and characterize whole ecosystem metabolism for various different ecosystems, including the dominant marine and estuarine systems in the vicinity of Port Aransas. This work seems to be an obvious outgrowth of his earlier work measuring whole ecosystem metabolism (and other properties) at Eniwetok and Silver Springs (Odum and Odum, 1955; Odum, 1956; Odum, 1957). While several of the papers are relatively well-known (including those cited above), we consider the conclusions of a paper written for a proceedings volume (Odum, 1960) to be representative of the entire body of work, including the results of some previous studies published during the "Port Aransas period" and earlier, including Odum (1956); Odum and Hoskin (1958); Park et al. (1958); and Beyers and Odum (1959, 1960). The findings of these papers are summarized in 11 points, which collectively serve as a compendium of useful facts for those interested in O_2 or CO_2-based estimates of ecosystem metabolism (we chose to quote exactly those passages which we found particularly succinct, or especially characteristic of Odum's phrasing; our comments are in parentheses):

(1) Gross photosynthesis and total community respiration range from 1 to 60 g O_2 m^{-2} per day. (This relatively large range reflects responses to variable light conditions more than differences in community structure.)
(2) In systems <3 m depth, benthic respiration is generally greater than the plankton respiration in the water column. In very shallow waters (<0.5 m), benthic metabolism may exceed water column metabolism by 100 times.
(3) "High metabolic rates are associated with high circulation rates."
(4) The reaeration constant for estuaries and streams is ~1–2 g O_2 m^{-2} h^{-1} for a saturation deficit of 0.2 atm (i.e. at 80% saturation). Higher values are found in circumstances of strong currents or wave action. (It is unclear to us whether Odum means the reaeration constant (which is the gas transfer rate at 100% saturation deficit), or the typical gas transfer rate typical of 80% saturation.)
(5) In some environments, CO_2-based metabolism estimates are much greater than those based on diurnal DO curves. He suggests that the difference may be due to "nighttime anaerobic metabolism followed by aerobic daytime recovery."
(6) Because of the small partial pressure of atmospheric CO_2 (0.0003 atm), diffusion from the atmosphere into water is very slow. However, diffusion of CO_2 from water to the atmosphere from supersaturated systems may be as rapid as O_2 diffusion, so diurnal fluctuations from supersaturated conditions to undersaturation may pump out CO_2.
(7) The annual cycle of total community respiration follows closely that of total photosynthesis in "stabilized systems." "Consumers are regulated so that their life cycles and energy requirements are in phase with the pulse of energy from the sun or from import."
(8) Streams and estuaries receiving large river flow have an excess of respiration over photosynthesis apparently due to the rate of import of organic matter from the land runoff. Loss of photosynthesis with increasing turbidity of systems receiving runoff is partly compensated for by extra importations of organic matter associated with turbidity. Systems with large import may have higher total respiratory metabolism than fertile photosynthetic systems."
(9) Coral reefs and shallow grass flats are among the most fertile marine communities.
(10) Diurnal free water measurements are preferable to bottle-based measurements of metabolism because of bottle artifacts (e.g. they do not reflect the large role of current and bottom metabolism) in estuaries.
(11) The diurnal curve method cannot be easily used in many estuaries where there are complexities of vertical stratification and changing tidal currents, which prevent the observer from readily obtaining average values for whole water masses. Many estimates of metabolic rate from diurnal curves tend to be underestimates.

Students of estuarine metabolism will recognize several observations which have been repeatedly "rediscovered" in the period since this work was published (cf. Boynton et al., 1982; Kemp et al., 1997; Swaney et al., 1999).

At the end of the paper, Odum summarizes data (presenting only the metabolic rates) from a few other net-heterotrophic, polluted estuaries, including a marine bay (Clear Lake on Galveston Bay) and the Mission River at Copano Bay, which is subject to the impact of brines released from oil wells (bleedwater) and other effluents. He also reports on Hoskin's (1959) results from the Neuse River and 1957 results from a swamp in Singletary Lake, North Carolina. In all of these systems, respiration exceeded photosynthesis, and Odum remarks that "Such patterns are not unusual where there are land drainages," echoing point 8 in his summary of previous work.

As an example of the enormous amount of effort expended on free water estimates of estuarine metabolism by Odum and his Texas colleagues, we must mention Odum and Wilson (1962), a paper describing the results of a collection of 129 diurnal oxygen curves collected during the period 1958–1960 which characterize the ecosystem metabolism of Texas Bays ranging from the Lower Laguna Madre in the south to Sabine Bay in the north. The authors note that ecosystem metabolism had not been estimated on nine of the bays, and that all the bays appeared to be vertically well-mixed. A few new observations were made, and some refinements of conclusions of earlier work were attempted. The authors again note the dominance of respiration over photosynthesis for bays receiving surface runoff. They observed a positive relation between the area-based reaeration constant and water depth, and also a two-fold increase of volume-based reaeration rates over the range of observed windspeeds. Turbidity is repeatedly mentioned as a limiting factor for photosynthesis, especially in response to wind-driven stirring of the water column, or dredging. The impact of variation in light intensity associated with cloudiness is also mentioned. The highest values of system metabolism—"as great as in tropical reefs with photosynthetic efficiencies as high as other aquatic communities of maximum fertility on earth"—were observed in grass flat systems. Finally, the authors suggest management guidelines for maintaining maximum total photosynthetic production, including reducing turbidity and irregular flushing of flood waters, developing grass bottoms, retaining wind-driven circulation, and "adjusting water depths of shallow and deep areas towards an average depth of 0.5 m."

It is worth noting that many of Odum's studies on estimating whole ecosystem metabolism focused on improvements in estimating the diffusion constant, also called the reaeration coefficient, i.e. the coefficient which determines, along with the saturation deficit, the rate of oxygen diffusion from the atmosphere across a square meter of water surface in an hour at 100% saturation deficit (i.e. when the oxygen value of the water is zero. It is expressed either as rate per area, or dividing by the local water depth, per volume). Since the rate of diffusion (by Fick's law) is proportional to the difference in partial pressure between air and water when the water is at 50% saturation the diffusion then will be half that coefficient, and when the water is 90% saturated, 10%, and so on. Calculating the degree that water is saturated (which depends mostly on temperature and salinity) is easy, but getting the reaeration coefficient is not. As Odum noted repeatedly, it changes as a function of water movement (it is very high in a waterfall) and wind velocity (Liss and Slater, 1974; Liss and Merlivat, 1986; Kicklighter, 1987; Marino and Howarth, 1993; Wanninkhof, 1992; Raymond and Cole, 2001). Odum (1956) devised a clever technique to get this value empirically using data from two nighttime sample points of a diel sampling schedule. The saturation deficits of the water just before sunrise and just after sunset tended to be quite different, and the component of the rate of change of oxygen due to reaeration is proportional to these values and the reaeration coefficients. Assuming that the rates of change of oxygen and the saturation deficits are both measured, and that respiration is constant, the oxygen mass-balance equations can be rearranged to give the (average) diffusion constant. Odum and Hoskin (1958) examined the effect of relaxing the assumption of constant respiration and concluded that the reaeration coefficient determined this way was almost certainly an upper limit.

We can speculate about how Odum would have extended these studies with high-frequency DO sampling probes available today. A logical extension of Odum's procedure to estimate the diffusion constant, but requiring more than two sample times, would be to use linear regression to estimate simultaneously the (average) diffusion constant and nighttime respiration (or metabolism) rate by regressing the measured nighttime DO rates of change at times t, $q(t)$, against the corresponding measured saturation deficits $S(t)$:

$$q(t) = k\frac{S(t)}{100} - R$$

The regression parameters k_{est} (the reaeration constant) and R_{est} (the nighttime respiration rate—assumed constant) are given by the slope and intercept of the regression line:

$$R_{\text{est}} = k_{\text{est}}\frac{\bar{S}}{100} - \bar{q}$$

$$k_{\text{est}} = 100\frac{\sum(S(t) - \bar{S})(q(t) - \bar{q})}{\sum(S(t) - \bar{S})^2}$$

where the overbars denote the averages of the respective quantities.

Odum and Hoskins' (1958) paper examines the metabolism of very many marine and aquatic ecosystem types and we conclude from the figures that respiration in most of these ecosystems depended principally on that day's photosynthesis (implying that the local plants and microbes are the most important users of production), that respiration and photosynthesis tend to be very similar on a given day, that daily and especially seasonal changes in temperature and especially incoming sunlight are generally more important than ecosystem type in terms of metabolism per square meter, and that suspended sediments (as from dredging and intensive local agriculture) reduced photosynthesis more than did at least some oil residues. The paper ended with a statement that these marine bays were more productive than adjacent dry farm lands and should serve as a laboratory for global application of understanding the value and food production possibilities these coastal areas. These statements preceded the national interest in preserving and protecting coastal areas which really took off in the late 1960s and 1970s with, for example, the Hatch Act in Massachusetts. Most of this legislation was based on brother Eugene Odum's paper (Gosselink et al., 1974) which was extraordinarily influential in protecting coastal areas. We can only assume that Eugene was influenced by H.T.'s Texas Bays studies as well as his own in Georgia, all of which showed the tremendous importance of coastal productivity. The Texas Bays studies served as an example and starting point for our own research on coastal ecosystems (and that of most of H.T.'s other students). They remain a gold mine of information for those interested in estuarine ecosystem metabolism.

Acknowledgements

Thanks to Liz DeHart, Head Librarian at the Texas Institute of Marine Science, for her help with research.

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