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Short communication

Comments on “Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll” [Ecological Monographs 25 (3) (1955) 291–320]

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1. Odum and Odum in a novel ecosystem

The image of Howard and Eugene Odum snorkeling in a back reef lagoon peering through the crystal clear waters of the Pacific Eniwetok Atoll (now “Enewetak”) is the epitome of my image of the emerging science of “ecosystems ecology” during the middle of the past century. Ecosystems ecology was a new way of looking at natural systems, a view from “outside the box” that considered the flows of materials, energy and information, into, out of, and within, instead of merely considering the components “inside” the box. H.T. was certainly moving from box to box, at this point—from coastal seagrass systems to tropical rainforests and now to a coral reef. Most certainly, Enewetak Atoll in the Marshall Islands of the northwestern Pacific was a far cry from Silver Springs, Florida or Sapelo Island, Georgia, and the spirit of the Odums’ foray onto this Pacific paradise is evident throughout the manuscript. Like Silver Springs, the warm “gin clear” waters of Enewetak afforded an easy opportunity to study the shallow benthic communities as evidenced by the comment: “*It must be realized that the great clarity of water permits face mask work with as great visual intimacy as on a terrestrial quadrat.*” Further charm follows in the text: “*Two individuals of the poisonous stone fish [Scorpaena gibbosa] were found resting on the top of dead portions of [coral] heads when quadrat C was being mapped. So well did these fish blend with the background that one was at first sketched in as part of the reef structure before disturbance caused it to change it’s position!*”

An inter-island reef on a remote Pacific Atoll is certainly a classic system to study, within a small spatial scale, the order of a biological community, and the inherent and predictable physical forces that influence (energetically) the biological design of reef systems. The Odums noted:

> “*Save for fluctuations the reef seems unchanged year after year . . . for millions of years. With such long periods of time, adjustments in organismal components have produced a biota with successful competitive adjustment . . . famous for its immense concentrations of life and its complexity.*” They further reflected on the contrasting image of more recent human designed systems: “*Perhaps in the structure of organization of this relatively isolated system man can learn about optima for utilizing sunlight and raw materials, for man-kind’s great civilization is not in steady state and its relationship with nature seems to fluctuate erratically and dangerously.*”

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In contrast to the inefficiency of human's community designs, their reference to the persistence and complexity of perhaps the oldest ecosystems on the planet remaining relatively unchanged over 50 million years, is haunting. Coral reef biomes, such as the Great Barrier Reef, are the largest biologically constructed structures on the planet, and can be discriminated from space at a scale where the human equivalent, concrete and steel structured edifices, cannot. The novelty of these biologically complex coral reefs thriving in oligotrophic (nutrient-poor) tropical waters was noted by Charles Darwin during the "Voyage of the Beagle" (1842) and became known as "Darwin's Paradox." Likewise, it was H.T.' s mentor, G.E. Hutchinson, who later characterized the irony of high species diversity in nutrient-limited open ocean systems as "the paradox of the plankton".

H.T. and Eugene, like Hutchinson before them, were no doubt intrigued by this oasis of species diversity and productivity located in a virtual biological desert of the tropical Pacific. Work in aquatic systems was not foreign to the brothers; in fact, the prevailing uni-directional flow of currents over the windward reef at Enewetak provided the conditions for productivity measurements comparable to previous work done by H.T. in the constant-temperature riverine environment at Silver Springs, FL. These conditions allowed measurement of upstream and downstream oxygen conditions to enable the measurement of "whole-ecosystem" productivity, respiration, and their ratio. A case has been made by Scott Nixon that experiments of this type were also the predecessors to more recent mesocosm (or microcosm) approaches, where natural conditions and their inherent fluxes are simulated and manipulated. A more recent coral reef mesocosm experiment, included in the Biosphere II project, represents an intensive, albeit controversial, effort to simulate reef systems.

By all accounts, the Odums' work, performed in about six weeks, was an astonishing accomplishment in light of the rudimentary techniques and equipment available at Enewetak, in a remote site far from established supply networks that usually support scientific research. Their study was guided by several well-known coral reef scientists of the time, including F.M. Bayer, M. Doty, C.E. Cuttress, R. Hiatt, and A. Weylander. These reef experts contributed to the Odums' evaluation of taxonomic composition and biomass estimates of the reef community, including "a rough estimate of shark biomass" that was obtained by observing "the time sharks were in view during the 15 min underwater walk to and from the area across the back reef zone." Largely as a result of their inexperience in working on coral reefs, their work was immediately scrutinized as "controversial." One of the more spirited critiques can be found in J. Hedgepeth's 1957 Chapter on "Concepts of Marine Ecology" in the double volume *Treatise on Marine Ecology and Paleoecology*. In comparison to Cushing's (1955) work on pelagic production, Hedgepath noted:

> "*Such a cautious attempt to strike a marine balance sheet is in contrast to that produced by* Odum and Odum (1955) *for a coral reef at Enewetak after 6 weeks of field work . . . . This tour de force will probably excite comment for some years, and it will be of particular interest to have the experiment repeated several times as well as to test some of the assumptions on which the measurements were made . . . . As imperfect as our understanding of the trophic structure of the sea may be, such efforts to strike a balance sheet are steps in the right direction and may be expected to become one of the principal procedures in marine ecology*." Indeed it has!

The motivation supporting this study was the result of the Atomic Energy Commission's (AEC) interest in discerning the impacts of nearby nuclear explosions and subsequent fission products (radiation) on *whole populations and entire ecological systems in the field*. Clearly, the Odums were prepared to go beyond simple radio-ecological assays to determine baseline information on a reef "which as yet had been little affected by nuclear explosions." They were interested in gaining fundamental knowledge on total coral reef ecosystem function, which would serve a purpose beyond the value of a comparative baseline to adjacent U.S. military nuclear testing trials. Nearby sites were subjected to a hydrogen bomb and several atomic explosions, making the study site one of the locations most exposed to nuclear test trials on the planet. Ironically the Odums' gave us a description of a reef, before the most sinister assault on the health of the world's coral reefs . . . the human population bomb. Since the Odums' report, the human population has more than doubled (2.8 to 6.2 billion people), and reefs appear to be one of the best ecological indicators for anthropogenically induced global environmental change. As a community having evolved in the relatively stable tropical environment for nearly 50 million years, they are extremely sensitive to slight changes in sea surface temperature, carbon dioxide saturation, and nitrogen availability.

2. Contributions from the Enewetak report

2.1. Calculating productivity of coral reef communities

The Odums' measurement of "whole ecosystem metabolism" was not the first attempt of its kind on a coral reef, but certainly more comprehensive than previous investigations. Their work followed the productivity analyses of M.C. Sargent and T.S. Austin (1949, 1954) who utilized oxygen measurements to construct diel curves of production versus respiration. However, the Odums' report, by constructing quantitatively calibrated trophic pyramids of community composition, was the first to estimate metabolic efficiency, and specific productivity (turnover rate of the standing crop). Clearly, this was the first significant attempt at measuring, collectively, these linkages between trophic structure and community metabolism on a coral reef community. The fact that only a relatively small amount of energy was derived from the "upstream" open ocean (which had low plankton biomass and low nutrient concentrations) made the implications of the high gross productivity of this isolated ecosystem very compelling. Indeed, many of the questions raised in their assessment were pursued by coral reef investigators for decades to come.

Nearly a dozen subsequent studies have utilized "whole ecosystem" metabolism measurements on reefs with similar unidirectional currents. Seventeen years after the Odums' study, the next generation of coral reef scientists, led by University of Georgia chief scientist R.E. Johannes, (including UGA colleagues L.R. Pomeroy, and W. Wiebe, post-docs J. Alberts and R.A. Kinzie, and students C. D'Elia and W. Sottile), aboard the R/V *Alpha Helix* on the *Project Symbios* expedition, revisited the Odums' community metabolism study site at Enewetak (see Johannes et al., 1972). An objective of their study was to assess the accuracy of the Odum's approach. For example, classic ecosystem productivity techniques, such as those used originally by the Odums for community metabolism, suffer from the following limitations: (1) oxygen readily exchanges between the water column and the atmosphere at the sea surface, and (2) oxygen concentration measurements may not directly reflect the amount of CO_2 fixed by photosynthesis, or consumed in respiration (Barnes et al., 1986). Yet, one compelling finding from this expedition, and later reported by Smith and Marsh (1973), was the verification that the oxygen measurements reported by Odum and Odum (1955) did, indeed, accurately reflect community carbon production. In addition to measuring changes in oxygen (see Marsh, 1974) these investigators calculated carbon fixation by measuring pH and alkalinity changes (the "alkalinity anomaly technique") near the original Odum & Odum transect and discriminated CO_2 changes between calcification versus organic carbon production (see Smith, 1973). Their results indicated that changes in gross production (ΔO_2) equaled non-calcification ΔCO_2 over a 24 h period. This finding was significant, because of the recognition by Ryther (1956) that the photosynthetic quotient for carbon production relative to oxygen production is 1.2 ($PQ = {}^{-}\Delta O_2 : \Delta CO_2$) for other productive oceanic systems, as corrected for greater atmospheric gas exchange of O_2 versus CO_2. Thus it can be concluded that despite obvious methodological limitations, the Odums' estimate of generalized equity in production versus respiration (i.e., P to R ratio) on coral reefs has largely been upheld in the coral reef literature, after some sixty or so published reports of primary productivity in reef areas (Kinsey, 1985; Hatcher, 1988, 1990, see Table 1).

The Odums recognized that the high gross productivity of the Enewetak reefs rivaled that of modern agriculture systems and was higher than that of nutrient-rich lentic systems in the southeastern United States, such as Silver Springs. However, they later realized these rates were typical of other coastal marine ecosystems such as seagrass beds (see Odum et al., 1959). More interesting, though was their recognition that production was not homogenous among the distinct zones of the reef ecosystem. Indeed, they recognized that the general equality of P and R included portions of the reef that were net autotrophic while other portions were net heterotrophic. These differences, dependant on the zonation of dominant benthic

Table 1
Some "community metabolism*" measurements of productivity and respiration (g C m^{-2} h^{-1}), and P:R ratios for coral reef communities between sites and seasons

Reference	Site	Community	P_{Net}	R	P:R
Sargent and Austin (1949, 1954)	Rongelap Atoll	Coral/algal	0.33	0.30	1.1
Odum and Odum (1955)	Enewetak Atoll	Coral/algal	0.80	0.80	1.0
Smith and Marsh (1973)	Enewetak Atoll	Coral/algal	0.50	0.50	1.0
Smith and Marsh (1973)	Enewetak Atoll (transect II)	Algal	0.97	0.50	1.9
Marsh (1974)	Guam	Coral/algal	0.32	0.26	1.1
Kinsey (1985)	Davies Reef, GBR	Coral/algae	0.26	0.31	0.8
Kinsey (1985)	Rib Reef (July)	Coral/algae	0.22	0.15	1.4
Kinsey (1985)	Rib Reef (September)	Coral/algae	0.16	0.15	1.1
Kinsey (1985)	Myrmidon Reef (July)	Coral/algae	0.30	0.37	0.8
Kinsey (1985)	Myrmidon Reef (September)	Coral/algae	0.25	0.20	1.2

*Although over 100 published values are now available on specific reef zones and biota, fewer consider changes over entire reefs (see Hatcher, 1990).

biota of a particular reef, apparently balanced out when the whole system was considered collectively. Their results suggested that organic productivity was largely the result of endolithic and exolithic coral reef algae (see next section), after determining that photosynthesis of the corals per se (i.e., coral-algal symbiosis) did not exceed respiration, a finding later verified by Smith and Marsh (1973) and subject to much investigation since. Indeed, the *Project Symbios* team determined that gross productivity on an adjacent algal-dominated transect was twice as high (10 g C m^{-2} day^{-1} versus 4 g C m^{-2} day^{-1}) than their measurement at the original Odum and Odum transect. Further, this algal dominated reef had a P:R ~ 2, denoting high net autotrophy and subsequent energetic export. Estimates for gross P:R on other reefs around the tropics have likewise varied relative to the mean community estimate of Odum and Odum, depending on the relative dominance of corals versus epilithic macroalgae in the respective ecosystems (see Table 1).

The Odums also marveled at the 5.8% efficiency of primary production to available solar energy input as evidenced by the following statement:

> *Here is an ecosystem which has had millions of years to evolve an effective composition, which is built for a low efficiency. This may be support for the hypothesis (*Odum and Pinkerton, 1955*) that there is an optimum but relatively low efficiency that produces the most effective trophic structure whose survival is based on a high primary productivity.*

2.2. Productivity of endolithic versus exolithic algae

Through the examination of cross-sections of major coral species, the Odums noted the high biomass of filamentous algae living within the carbonate framework ≥ 1 cm below the coral polyp/zooxanthellae veneer that covers live corals. They estimated the biomass of this endolithic flora to be sixteen-times that of the zooxanthellae in overlying coral tissues, although the importance of this biomass appears to have been anomalous when compared to coral heads reported at other locations since that time (Schlichter et al., 1997). The Odums' estimate of the trophic importance (i.e., biomass estimates) of the endoliths relative to more recent estimates of symbiotic zooxanthellae productivity was not supported in reviews by Lewis (1977), Jaques and Pilson (1980), Larkum (1983), and Schlichter et al. (1997). The latter review by Schlichter et al. (1997) estimated the productivity of the filamentous endoliths to be merely 6–7% of the overlying zooxanthellae in the same coral species, despite higher biomass of these endoliths. This may be a result of the discrepancy of the Odums more empirical measurement of productivity, versus the more refined techniques now utilized for measuring productivity of coral endosymbiotic zooxanthellae. Regardless of this revised estimate, the Odums marveled at the apparent low irradiance available to these filaments (4–6% of the surface irradiance) that creates a critical compensation point within the coral head, consequently constraining the endolith's boring depth (Highsmith, 1981). The Odums were correct in suggesting that the endolithic algae were important in the overall energetics of the coral itself by supplying photoassimilates to the coral that would also be transferred to reef grazers. Schlichter et al. (1995) using ^{14}C tracer techniques showed that up to 27% of the algal metabolites were incorporated into the overlying coral tissue; which, in contrast with the widely known facultative symbiosis with zooxanthellae, constitutes some kind of mutualistic ectosymbiosis (Schlichter et al., 1997). Ferrer and Szmant (1988) confirmed the presence of elevated nutrient concentrations in coral skeleton that may be available to both the endoliths and zooxanthellae.

In recognizing that the coral/zooxanthellae symbioses contributed little (and probably were a deficit) to overall P:R of the reef community, H.T. and Eugene quickly came to the conclusion that the majority of excess production was performed by “free-living” or exolithic algae. Their trophic pyramid, based on biomass estimates at Enewetak, indicated that the reef was composed of ∼85% algae. This recognition of “the predominance of plant protoplasm” preceded the more recently accepted concept that coral reefs should be more appropriately known as “algal reefs” if one considered this dominant component as a function of either biomass or production (see Hillis-Colinvaux, 1986; Adey, 1998). In fact, the dominant calcifiers (calcium carbonate producers) on reefs are not the corals themselves, but more likely the segmented macroalga from the genus *Halimeda* (Adey, 1998), known to form monotypic bioherms on shelf slopes. In fact, large portions of reef formations, including the “windward” fore-reef portion of Enewetak that the Odum’s observed, are accreted by coralline algae, which not only produce reef framework, but are important “cementers” that infill crevices and fragments of the framework itself (Bjork et al., 1995). Thus, recent recognition of the importance of algae on coral reefs have supported the original observations of the Odums.

2.3. *Nutrient availability and energy flux*

Although the Odums’ recognized the efficiency of phosphorus recycling across the Enewetak reef (and later confirmed by Smith and Marsh, 1973; Pilson and Betzer, 1973), the availability of nitrogen proved to be an enigma in their energy budgets. Clearly, there was an imbalance in the flux and uptake of nitrogen from the particulate and dissolved sources entering the reef via oceanic currents versus the nitrogen content of the reef algae and its specific productivity. Their estimate of the ratio of nitrogen to organic matter content calculated for algal production (thus preceding the widely recognized Redfield ratio” (C:N:P) of organic matter in the oceans, published in 1958) rates indicated that nitrogen was indeed limiting, with respect to phosphorus, and some “new” nitrogen must be produced on the reef. Odum and Odum stated: “It seems equally likely that there is cyclic re-use of nitrogen along with some nitrogen fixation by the abundant blue-greens of the front reef.” Indeed, they postulated that nitrogen-fixation may be important for nitrogen supply on coral reefs before detailed N budgets were calculated. The *Project Symbios*’ analysis of nitrogen cycling (see Webb et al., 1975; Wiebe et al., 1975) calculated that C:N of oceanic water decreased from 15 to 7 as the water flowed across the Enewetak lagoon, and their calculations suggested that “nitrogen-fixation rates must have been occurring at rates of the same high order as those reported for alfalfa fields in order to balance the observed export of fixed nitrogen (Johannes et al., 1972).” At these elevated rates, Smith (1984) later estimated that N-fixation may provide 31–127% of a reef’s N budget. A further observation by Webb et al. (1975) is that Enewetak exports about 20% more nitrogen than is imported by inflowing oceanic seawater, and may be important in the development of the “island effect” of enriching downstream communities. This example of “open” nitrogen cycling may be a typical feature of most reefs, as dissolved inorganic nitrogen concentrations are commonly elevated in back-reef lagoons as compared to fore-reef or upstream offshore communities (D’Elia and Wiebe, 1990). This evidence conflicts with the classic view, dating back to Darwin, that coral reef are efficient, categorically, at nutrient cycling. It is apparent that of the major macro-nutrients, nitrogen, at least, does not follow this rule.

3. Summary

Despite the controversial nature of this paper at the time, it remains one of the seminal manuscripts in ecology, not to mention marine ecology and coral reef science. It is clear that for six weeks in the early 1950s H.T. and E.P. Odum looked at coral reefs in a way not done so before. Although they were not experts on the biology of reefs per se, they taught us much about how reef metabolism is regulated relative to the specific biota of the system. Many of the topics they reported on, such as the importance of endolithic algae, have been subject to major revision. The finding of general equivalence of production to respiration on coral reef communities, have held, and have become the accepted dogma. Many of the questions raised in this paper, such as the suspected importance of nitrogen fixation, provided the intellectual fodder for several generations of coral reef scientists to follow. Like many others, I am honored to address questions on the ecology of coral reefs, many of which were inspired by the Odums' study at Enewetak. My work, specifically, is focused on how coral reefs are changing in the present-day advent of human-induced biogeochemical alteration of the biosphere (Barile, 2001). Baseline information on the dynamics and metabolism of the relatively pristine reefs of Enewetak in the early 1950s (albeit for a few nearby atomic bomb craters), make compelling comparisons to present day human-dominated coral reefs such as those on the Florida Reef Tract of the Florida Keys (see Lapointe et al., 2002). We are just two generations removed, academically, from the work of the Odums. Ironically, the low efficiency of man's management of the biosphere, as H.T. and Eugene noted in their 1955 manuscript, has since contributed to the demise of 25% of the world's coral reefs, with 70% of the remaining reefs presently threatened by human activities.

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