



Sunlight and water transparency: cornerstones in coral research

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Abstract

Reef-building corals throughout the world are considered endangered. The evidence is a decline in coral health and reduced coral cover. Competing hypotheses for the cause of coral loss include removal of grazers, nutrient enrichment, disease, coral bleaching, increase in temperature, and excess light/ultraviolet exposure. We suggest that light limitation as a second order effect of anthropogenic activity (e.g. sediment resuspension and nutrient enrichment) is a valid and tractable hypothesis. This experimental field and laboratory study demonstrates that corals of the Florida reefs are functioning close to the compensation point where respiration (of coral polyp plus zooxanthellae) consumes the products of photosynthesis of the zooxanthellae, with little if any remaining for growth. We extend this work into an optical nomograph that is useful for predicting coral loss and recovery. The nomograph is designed to elucidate compensation depth for waters of various transparencies. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Practically every book that includes the subject of corals starts with “corals thrive in clear water;” yet it is difficult to pinpoint what “clear” means. On the other hand, there is

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a strong record of optical studies and primary productivity that shows a close relationship to relatively small changes in water transparency, expressed as $K_{(PAR)}$, and phytoplankton growth. Throughout this manuscript we will refer to water transparency as K with the units (m^{-1}). Nearly 50 years ago, Ryther (1956) published a pioneering paper that focussed on phytoplankton growth in the sea. This model estimated seasonal change in gross photosynthesis as a consequence of seasonal change in solar radiation. In this model, net photosynthesis (resulting in growth) was estimated assuming ratios of maximum photosynthesis to respiration rates (P/R) measured in cultures of marine phytoplankton. Ryther used four values of P/R which covered a range of 20:1 to 5:1, a range of photosynthetic rate of 20–5 times the rate of respiration. The model demonstrates that at temperate latitudes if photosynthesis is twenty times respiration, there is net production throughout the year; if photosynthesis is five times respiration, net photosynthesis would be observed only for May, June, July and August.

Ryther's model demonstrated the importance of the combined effects of light and respiration on marine phytoplankton. There is no reason why these effects are confined to phytoplankton or to the temperate regions. One purpose of our study was to test the Ryther model in the semi-tropical region using data from zooxanthellae and the zooxanthellae–coral complex.

In spite of the importance of light for corals, studies bridging the disciplines between coral research and optics are rare. Most data sets in the literature are presented as percentage coral cover vs. depth. This is meaningful when the water transparency is high and relatively constant. However, as water transparency degrades, the utility of this relationship is lost. Tomascik et al. (1993) demonstrated that a more useful representation

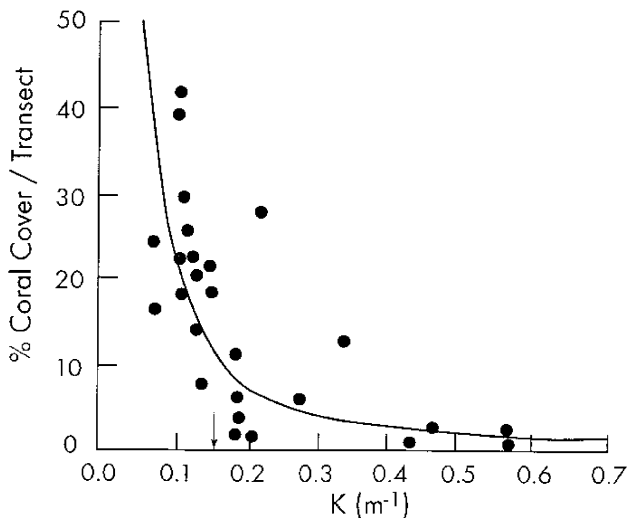


Fig. 1. The relationship between the maximum depth of a coral reef and water transparency, K (m^{-1}) as measured by Secchi depth, d (m), using the relationship $K = 1.5/d$. Data from UNESCO, 1986 as per Tomascik et al. (1993).

is the relationship between K and the percentage of coral cover at a given depth (Fig. 1). These data are values for the attenuation coefficient calculated from Secchi disk observations by the relationship $K=1.5/d$ where d is the depth in meters at which the disk disappears from view. This analysis has a reasonable correlation ($r^2=0.59$). The highest percent of coral cover, greater than 40%, occurred with highest transparency, $K=0.05-0.10\text{ m}^{-1}$, that of clearest oceanic waters. The relationship suggested that the percentage of coral cover decreased markedly with a relatively small change in K . The “Tomascik curve” is an apparent correlation and therefore could arise from causes other than changes in light reaching corals. There is no dimension of time associated with these data. Time could favor competing ecological interactions for coral decline. However, the coral reef history in Indonesia as described by Tomascik et al. (1993) is a documented example of the decline of reefs due to eutrophication.

2. Methods

2.1. Description of sites

The field studies were undertaken as a part of the ONR CoBOP program in the western most reefs of the Florida Keys and at Lee Stocking Island in the Bahamas. These two regions allowed comparative measurements in waters of two optical types. The Dry Tortugas of the Florida Reef System is surrounded by fringing and patch coral and algal reefs. The reef system off Key West is dominated by a spur and groove formation. Between this reef and the shore is a lagoon area with some coral and algal patch reefs. The reef off Lee Stocking Island is a fringing reef; however, throughout the region are shallow water and numerous patch reefs of mixed algae and corals. Many of our coral reef colleagues have observed that the percentage of coral cover is lower in the Dry Tortugas and higher in the waters of the Bahamas.

2.2. Optical and photosynthesis parameters

To estimate the influence of irradiance (E) and respiration (R) requires estimates of gross photosynthesis (P_{gross}) and net photosynthesis (P_{net}). P_{net} is P_{gross} minus R . The photosynthesis maximum to respiration ratio is P_{max}/R , see reviews by Yonge et al. (1932) and McCloskey et al. (1978). To estimate the relationship between irradiance and photosynthesis, the intercept between the light-limited and light-saturated portions of curve, E_k , is used. The function P vs. E used for our estimates is shown graphically in Fig. 2. The graphs are for six experiments performed at the Bermuda Biological Station using isolated zooxanthellae from cultured Cnidaria, *Aiptasia pallida*, (isolations according the methods of Cook et al., 1992; unpublished data from Cullen and Cook). These data represent two experiments each on three types of material: well fed, partially starved and starved). The zooxanthellae were exposed to 24 intensities of light at 22 °C in the presence of added carbon-14 for 30-min incubations in a photosynthetron (Lewis and Smith, 1983). We include this experimental work to emphasize that the curves shown in Fig. 2 in terms of carbon are in close agreement with the data obtained by changes in oxygen observed by

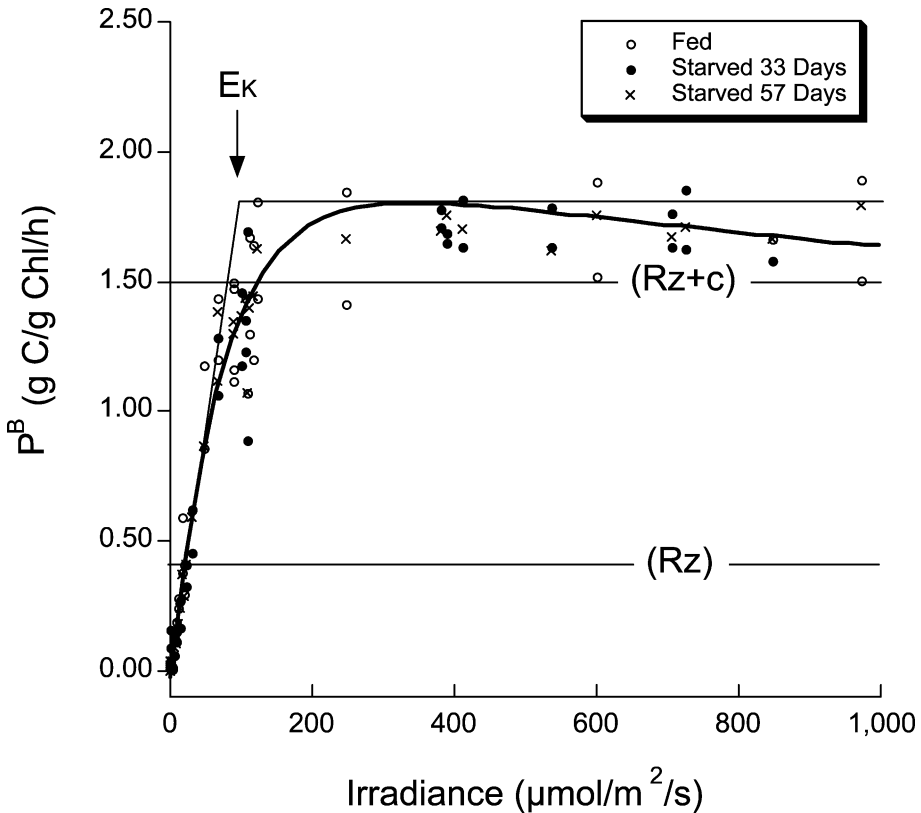


Fig. 2. Photosynthesis (C-14 uptake over 30 min) normalized to chlorophyll *a* (P^B , g C per g chlorophyll per h) for zooxanthellae isolated from cnidarian colonies. The horizontal lines are inferred rates of respiration for zooxanthellae alone (Rz) and for a zooxanthellae–coral complex (Rz+c). These results are for colonies subjected to three feeding regimes: continuous feeding (open circles), starved for 33 days (closed circles) and starved for 57 days (x). Results for the three treatments (48 points each; only results for $E \leq 1000 \mu\text{mol}/\text{m}^2/\text{s}$ are shown here) were statistically indistinguishable and curve represents the best fit for all points to the model of Platt et al. (1980). Saturation irradiance, E_k , is shown graphically (Cullen and Cook, unpublished).

Chalker (1981) for *Manicina areolata*, *Acropora cervicornis*, and *A. formosa*. Added to the carbon-14 data in Fig. 2 are the inferred respiration for zooxanthellae (Rz) and the zooxanthellae–coral complex (Rz+c). Little direct respiration data exists. Thus, the rate of respiration, unlikely to be constant day and night, represents an oversimplification. Respiration quotients and photosynthesis quotients of many associations under various environmental conditions are largely unknown. What is known is that different genotypes confer different tolerances to stress or physiological latitude to acclimatize to a range of environmental conditions.

Daily measurements of photosynthetically available radiation (PAR) were taken at the C-MAN observatory platform off the Dry Tortugas at latitude $24^{\circ}38' \text{N}$ and longitude

82°55' W. The platform is equipped to measure PAR at the surface and at 1-, 2- and 3-m depths. We have used the one-meter depth readings for this study. PAR at depth at all other locations was measured by lowering a LiCOR unit at 1-m intervals to a maximum of 10 m. K was calculated by fitting these data with a straight line and adjusted according to the

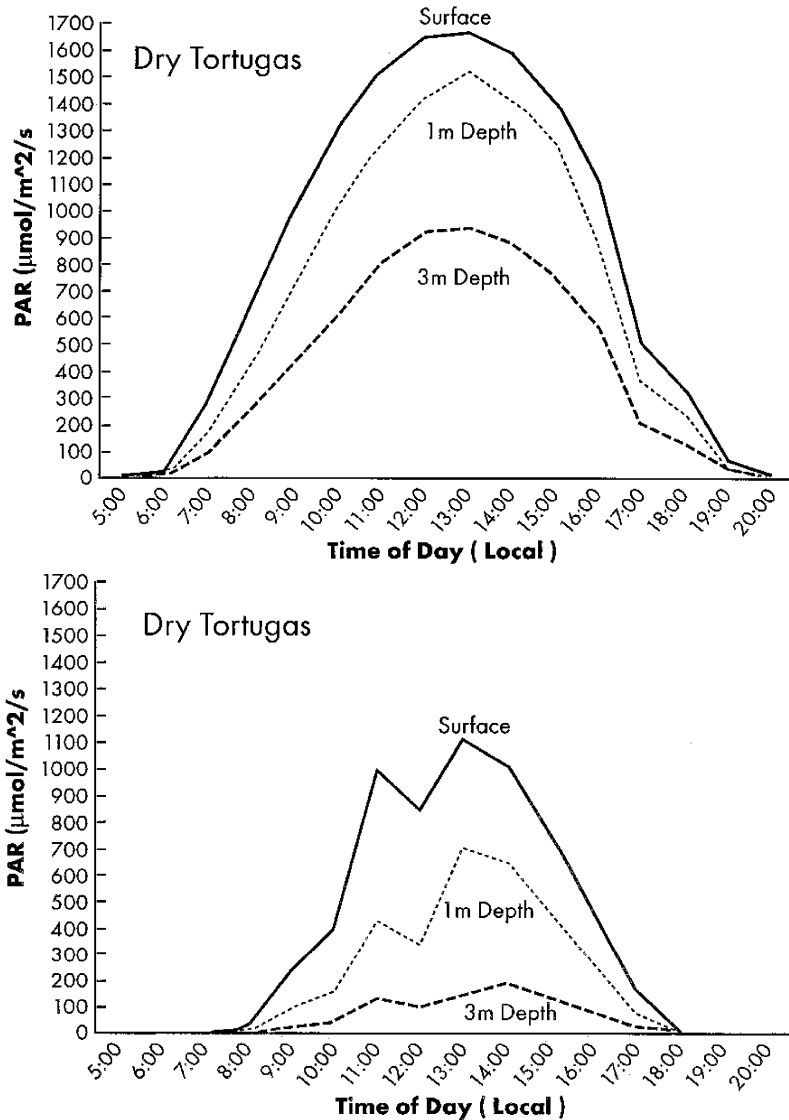


Fig. 3. Solar irradiance at the surface, 1 and 3m depth at the Dry Tortugas site. These data are from two time periods. The top is for a day in summer, the bottom is for a day in winter.

equation $K \text{ (m}^{-1}\text{)} = \ln E_o - \ln E_{\text{(depth)}}/\text{depth}$. The submersible LiCOR visible light detector is a flat response unit fitted with a cosine diffuser.

3. Results

3.1. Effect of variability in solar surface irradiance; sun angle and day length

3.1.1. Summer/winter irradiance levels

The maximum PAR during summer (mid-July) at the Dry Tortugas site was approximately $1700 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3, top). At 1 m, the value is $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. During winter (December), the solar radiation is reduced to about $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ maximum at the surface and 700 at 1 m (Fig. 3, bottom). In both cases, the highest irradiance values occur at midday. There is a marked difference in day length. The winter day is 10 h while the summer is close to 14 h.

3.1.2. Summer/winter difference in gross and net photosynthesis

Fig. 4 is the product of the function P vs. E (as in Fig. 2) and the irradiance at 1 m (as in Fig. 3, top and bottom). This represents the change in gross photosynthesis for the two seasonal extremes at the Dry Tortugas. The line connected by open circles is for summer and the line connected by x's is for winter. The maximum rate of photosynthesis

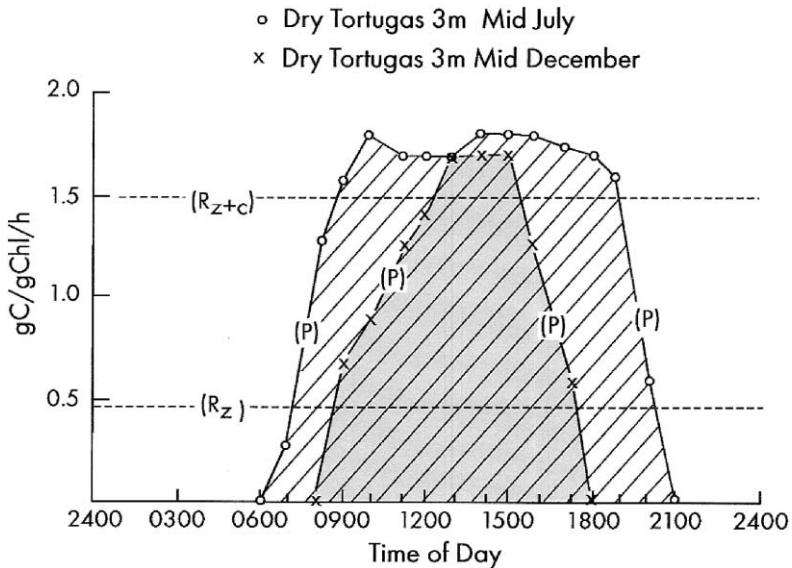


Fig. 4. Product of Figs. 2 and 3, therefore the photosynthesis (P) adjusted for light intensity at measured at Dry Tortugas at 1 m depth during mid-July and mid-December. R_z+c is the respiration quotients for the zooxanthellae–coral complex; R_z is the respiration quotient for the zooxanthellae alone.

(approximately 1.5–1.7 g C/g Chl/h) is observed at approximately the same hours for both cases. Moreover, the influence of the shorter day markedly affects the daily gross production.

The dashed lines on Fig. 4 represent the carbon loss due to respiration required to sustain the zooxanthellae (Rz) and the zooxanthellae–coral complex (Rz+c). For Rz, we used a P:R ratio of 4.0 (Chalker et al., 1983). For Rz+c we used the value of P/R as 1.3 (Chalker and Dunlap, 1983). Compensation ($P/R=1.0$) occurs for zooxanthellae at 0700 and 2000 during midsummer and 0830 and 1700 during midwinter. For the zooxanthellae–coral complex, compensation occurs at 0900 and 2000 in midsummer and 1200 and 1700 in midwinter. Net production values represent the carbon production above the two respiration levels. The day length has a significant effect on the net growth of coral. Adding the high respiratory demands of the coral symbiosis respiration (Rz+c) results in net carbon for growth occurring only about 3 h per day during winter irradiances, but between 12 and 13 h during summer irradiances.

3.2. Effect of water transparency variability

We believe that even in a region where seasonal change in solar input is usually high and relatively consistent, the importance of the attenuation coefficient, K , becomes paramount. To illustrate the effects of water transparency, we have focussed on the influence of changes in K on the depth of the compensation intensity (depth where $P/R=1.0$) or more simply, the depth of “no growth” by corals. The compensation intensity and compensation depth for corals have been measured and estimated by a number of researchers. Although some have not measured water transparency, there exists continuity among these observations.

The interplay of water transparency and coral bioenergetics can be demonstrated by examination of a nomograph or suite of curves for a range of attenuation values for ocean water masses (see Fig. 5). For the sake of simplicity, water masses are placed into two optical classifications, oceanic and coastal. The range shown for oceanic water is $K=0.04\text{--}0.18\text{ m}^{-1}$. The range shown for coastal waters is $K=0.18\text{--}0.51\text{ m}^{-1}$. Along the irradiance axis (x -axis, log scale) the values for 24-h compensation irradiance (E_c) are shown as three vertical lines for three examples of the zooxanthellae–coral complex. Follow each E_c vertically. At the points that E_c intercepts the irradiance curves, read the depth axis (y -axis, linear scale). This is the compensation depth. Moving from the most turbid coastal waters of $K=0.51\text{ m}^{-1}$ to the clear ocean water $K=0.04\text{ m}^{-1}$ the compensation depth changes from 4 to 5 m to slightly greater than 40 m during the summer months. A simple mathematical model of annual variability could extend this work.

In terms of regional variation, examples of water transparency (K) along the Florida Reef Tract were measured. The 25-km tract was from the Gulf of Mexico to slope waters of the Atlantic near the edge of the Gulf Stream (Table 1). The reefs in the system are adjacent to Sand Key at Eastern Dry Rocks. The range for stations along this transect is $K=0.04\text{--}1.15\text{ m}^{-1}$ and can be highly variable on short time scales. The clearest water was most often seaward of Sand Key. Most of the spring and summer values have the characteristics of turbid ocean water. Corals would not be expected to grow at

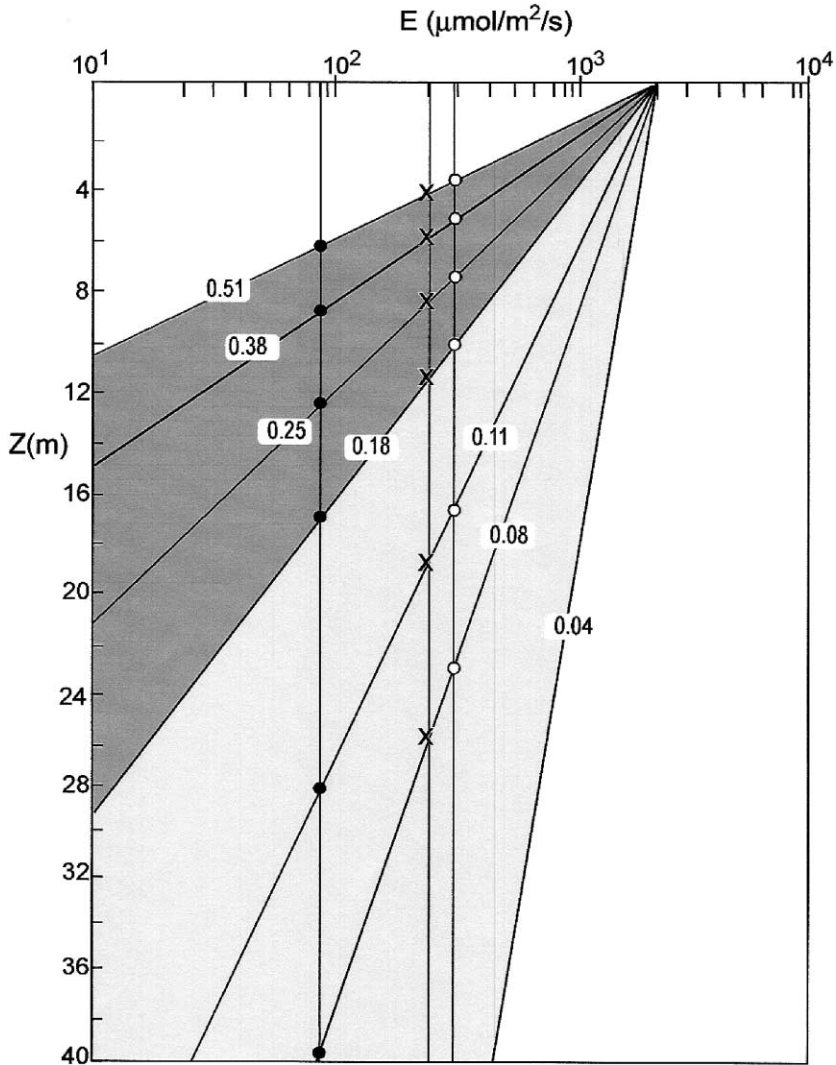


Fig. 5. Nomograph for the relationship of light irradiance (E in $\mu\text{mol}/\text{m}^2/\text{s}$) on a log scale vs. depth (Z in m) on a linear scale. So-called coastal waters are heavily shaded; so-called clear oceanic waters are lightly shaded. The lines for the amounts of irradiance at depth are fitted with values for attenuation for water types. The compensation intensity when extended with depth intersects water masses of different K values and defines the compensation depth. These depths are shown for zooxanthellae alone as black dots. Crosses and clear dots represent the observed compensation depths of Chalker (1981).

depths much greater than 15 m. Note that the seasonal condition depicted is for solar irradiance in summer. Lower irradiance during winter months and reduced day length will produce shallower compensation depths. To demonstrate the relationship between

Table 1

Attenuation K (m^{-1}) for stations off Key West, Florida, during May, June, July and August of 1999 measured using a Li-COR PAR sensor

Station	Gulf of Mexico I	Gulf of Mexico II	Harbor	The Boil	Hawk Channel	Sand Key Reef	Gulf Stream
Latitude	24 38'	24 36.5'	24 34'	24 32'	24 30'	24 27'	24 26.5'
Longitude	81 55'	81 51'	81 49'	81 47.5'	81 50'	81 52'	81 52'
K (m^{-1})							
May 7, 1999	0.1957	0.1541	0.2007	0.2744	0.2138	0.2231	0.0488
Jun 19, 1999	0.2324	0.6201	0.8406	0.6792	0.8747	1.1537	0.4076
Jul 27, 1999	0.3314	0.1497	0.2663	0.3389	0.0341	0.0931	0.1542
Aug 30, 1999	0.2107	0.2751	0.2218	0.3483	0.1953	0.2297	0.0197

compensation depth and coral cover, our data are superimposed on the Tomascik curve (Fig. 6).

4. Discussion

The final figure (Fig. 6) supports the Tomascik finding that water transparency and percent coral cover are closely related and are predictable in terms of optical phenomena. The message is clear: the lower the P/R of corals, the shallower the compensation depth. In

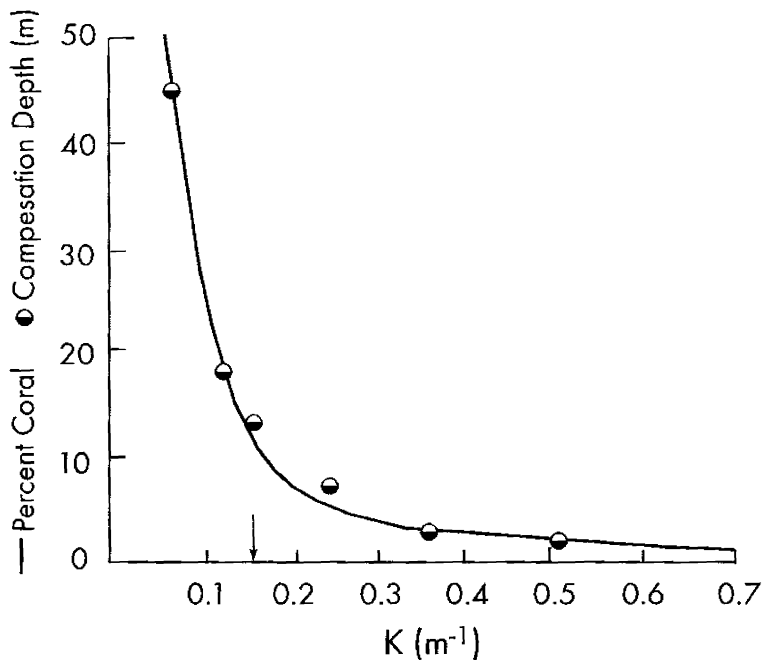


Fig. 6. The relationship between the percent coral cover (solid line from Tomascik curve as in Fig. 1) and calculated compensation depth (from nomograph in Fig. 5) vs. K (m^{-1}).

short, as water transparency decreases, corals are forced to grow in more shallow waters—yet the zooxanthellae are not free-living like phytoplankton, but anchored within the coral polyp and calcium-carbonate skeleton. Of note is that under reduced light conditions, corals produce fragile thin skeletons (Cook et al., 1997). Thin skeletons can be destroyed when subjected to the high-energy wave action breaking across the reefs. We conclude that some of the reefs off Florida are caught between two jaws of a vice: one, they cannot grow any deeper because of light limitation; two, in shallow regions, the high wave energy limits colonization of these organisms.

When comparing the rate of photosynthesis (P) for isolated zooxanthellae from Cnidaria to photosynthesis and respiration (R) measurements in the zooxanthellae–coral complex, the following points emphasize the differences: (1) the zooxanthellae–coral complex requires a major fraction of net production, and (2) the greater the fraction of net production required, the greater the compensation intensity and therefore the shallower the depth of growth or compensation depth.

There are two parameters responsible for the amount of light reaching corals and these should be measured as independent variables in all coral studies. The first is the amount of light entering the surface of the water column (E_0); the second is the transparency or clarity of the water expressed as attenuation coefficient per meter, K (m^{-1}). As anthropogenic effects increase (e.g. dredging, beach erosion, eutrophication), the trend will be reduction of water transparency and corals will be some of the first organisms to be influenced (Veron, 1995).

The value of measurement of zooxanthellae photosynthesis from isolates of a symbiotic animal is frequently questioned (Battey, 1992). In our case, we counter this argument by the close agreement of P/E curves obtained from whole corals (Chalker, 1981) to those of zooxanthellae isolates from various nutritional regimes. The interactive nature of zooxanthellae translocation to coral polyps (Muscatine and Cernichiaro, 1972) is beyond the scope of this paper.

Porter (1985) reported effects of day length on coral photosynthesis at Discovery Bay, Jamaica. The interpretation of photosynthesis with depth is augmented by photoacclimatization to low light by Dustan (1982), Chalker and Dunlap (1983), Chalker et al. (1983) and Dubinsky et al. (1984). Chalker and Dunlap (1983) observed that for the coral *Acropora* sp. photosynthesis rapidly declined below 35 m where photoacclimatization was unable to accommodate the decline. Lesser et al. (2000) demonstrate the importance of optics in the study of corals.

Baker (2001) recently reported measurements of genetic clades (surveys of restriction-fragment-length polymorphisms in genes encoding large sub-unit ribosomal RNA) of coral zooxanthellae show strong zonal patterns within their coral hosts. These clades correspond to light intensity (shallow is high light or sun algae, and deep is low light or shade algae). Baker demonstrates 'symbiosis recombination' in transplant experiments (Baker, 1999, 2001). This makes a case for the role of symbionts as adaptive agents.

Reef-building corals have a basis in geology, biology and climatology (Veron, 1995). Reefs develop three-dimensionally by extension to existing colonies. Growth is slow at rates of centimeters per year or meters per century. Coral health and percent coral cover is decreasing worldwide (Ginsburg, 1993) and at an alarming rate in the Florida Keys (Porter and Meier, 1992; Dustan, 1993; Dustan et al., 2000). The questions are: "What is the

cause of this decline?” and “How can this trend be reversed?” Competing hypotheses of the causes of coral loss include: removal of grazers (Hughes, 1994; Hughes et al., 1999), nutrient enrichment (Lapointe and Clark, 1992; Lapointe et al., 1997), both resulting in overgrowth by macroalgae and disease, and increase in temperature (Glynn, 1990) and/or excess light/ultraviolet exposure (Shick et al., 1996) which results in coral bleaching. In a few cases, reduced light reaching the coral reefs or coral transplants is suggested as a key factor (Tomascik et al., 1993; Cook et al., 1997) albeit a second order effect. There are two components contributing to light limitation: (1) solar irradiance at the surface influenced by seasonal sun angle and day length and (2) water transparency. The water transparency hypothesis is tractable; and because it is based on optical parameters, can prove useful for simple, inexpensive monitoring of reef decline and recovery. We contend that these two optical measurements are independent and both are necessary for an adequate understanding of the light/growth relationship of corals.

5. Conclusions

The data we present here argues that Florida's reefs are strongly stressed by seasonal change in solar input plus decreasing water transparency. The practical question is: why is this not being critically examined at the same degree as for other environmental factors (e.g. temperature, salinity, disease, etc.)? In discussing the light limitation problem with a noted coral biologist, the reply was “Why bother with the optical measurements? My reefs are all in clear water.” This may be so, but it is certainly not the case for most of the Florida reefs and some of those in the Caribbean. Hence, part of this human indifference is due to assumptions plus the fact that the human eye, looking downward at a body of water, is a poor instrument for assessment of small changes in transparency. The importance of these small decreases in transparency on the percentage of coral cover seem rarely understood except by those familiar with photoautotrophic coral kinetics and factors influencing downwelling irradiance of sunlight.

Those of us who regularly measure K in ocean waters are aware of the difficulties of measuring K in near-surface waters. The marked effects of changing transparency and changing photophysiology of these corals means that we must somehow monitor K as well as solar radiation coming into the system. This seems to be plausible for tower-mounted or buoy-mounted devices. These measurements are needed throughout the world's oceans, especially in the regions where reefs exist. These measurements are needed on a routine basis and with sufficient frequency so that we can make meaning of the time and space considerations of coral decline and recovery. It would seem important that in the near future we give serious attention to global change in water transparency and the causes of these changes.

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