

Littler M. M. & Littler D. S.

2005. A proposed sustainable coral-reef management model. *In*: Krupnick G. A. and Kress W. J. eds. *Plant conservation: a natural history approach*, pp. 262-269. University of Chicago Press, Chicago.

12.2 A PROPOSED SUSTAINABLE CORAL-REEF MANAGEMENT MODEL

Mark M. Littler and Diane S. Littler

DUE TO THE GROWING problems associated with coastal eutrophication and destructive fishing along tropical and subtropical shores, the responses of coral reefs and macroalgae to both nutrient enrichment and release from predation have been repeatedly cited as priority areas in need of intense management. The relative dominance model (RDM) proposed here suggests a useful perspective to resource managers attempting to protect coral reefs and similar coastal systems from eutrophication, destructive fishing, and initiation of harmful algal blooms. Thus, this approach is timely in proposing a framework and guidelines for improved understanding and sustainable management of critical reef ecosystems. Unfortunately, the recurrent role of modern humankind on coral reefs has been to decrease herbivorous fishes (Littler et al. 1991; Littler et al. 1993; Hughes 1994) through trapping, netting, poisoning, and dynamiting, while simultaneously adding nutrients via sewage and agricultural eutrophication (Littler et al. 1991; Littler et al. 1993; Goreau et al. 1997; Lapointe et al. 1997). Unless these anthropogenic effects are curbed, induced shifts from coral to fleshy-algal domination are anticipated to expand geographically at an accelerated pace (Nixon 1995).

COMPLEXITY

Because of the long history of environmental stability within tropical zones, coral reefs have evolved astounding levels of complexity and biological diversity. This complex nature of tropical reef ecosystems makes identifying causative factors difficult and has contributed to the considerable controversy concerning the roles of herbivory (top-down factors) versus nutrients (bottom-up factors). Turbulent water motion and the many uniquely specialized benthic algae and photosynthetic

symbionts dominating tropical reefs are responsible for some of the most productive natural ecosystems known. Four groups of benthic primary producers are responsible for the bulk of coral-reef productivity: cnidarian corals (containing symbiotic algae), crustose coralline algae, algal turfs, and frondose macroalgae. Of these, photosynthetic corals create much of the structural complexity and, with coralline algae, are primarily responsible for accretion of calcium carbonate (CaCO_3) into the reef matrix, making them the most desirable functional groups from a management perspective.

TOP-DOWN AND BOTTOM-UP CONTROLS

A basic objective in plant ecology is to understand the mechanisms by which natural and anthropogenic factors may maintain or alter structure and interactions in biotic communities. Anthropogenic eutrophication and destructive fishing are the most frequently cited factors correlated with the marked global decline in tropical-reef communities over the past two decades (see reviews in Ginsberg 1993; Birkeland 1997; papers in Szmant 2001). The concepts "top-down" and "bottom-up" controls have been used (e.g., Atkinson and Grigg 1984; Carpenter et al. 1985) to describe mechanisms where either the actions of predators or resource availability regulate the structure of aquatic communities. These factors provide a useful perspective to assess and manage the interactive mechanisms controlling stable states and phase shifts among the dominant functional groups of primary producers on tropical reefs.

In healthy tropical reefs, nutrient concentrations are extremely low, and attachment space is preempted by a broad diversity of epilithic organisms. Given these conditions, the major tenets of the RDM are (1) that competition for space and light is important in determining the relative abundances of major benthic photosynthetic organisms, and (2) that the outcome of competition for these resources is most often controlled by the complex interactions of biological factors and environmental factors. As proposed by Grime (1979) for terrestrial plants and expanded for marine macroalgae (Littler and Littler 1984a; Steneck and Dethier 1994), primary-producer abundances and evolutionary strategies are controlled by physical disturbances (i.e., factors that remove biomass) coupled with physiological stresses (i.e., factors that limit metabolic production). In the conceptual RDM (fig. 12.1), grazing (top-down) physically reduces biomass of fleshy algae, and nutrients (bottom-up) control production. The complex interactions between herbivory and nutrients are most dramatically impacted by large-scale disturbances such as tropical storms (e.g., Done 1992a), warming events (e.g., Macintyre and Glynn 1990; Lough 1994), diseases (e.g., Santavy and Peters 1997; Bruno et al. 2003), and predator outbreaks (e.g., Cameron 1977); however, these accelerate the ultimate long-term phase shifts postulated in the RDM. Such stochastic events selectively eliminate the longer-lived organisms in favor of fast-growing early-successional macroalgae, which are competitively superior following disturbances.

On undisturbed oligotrophic coral-reef habitats, the effects of top-down physi-

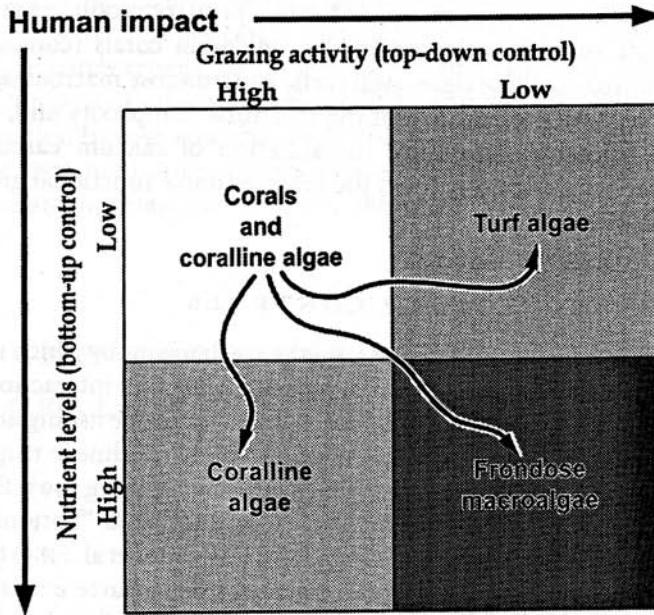


Figure 12.1 The competition-based relative dominance model (RDM) modified from Littler and Littler 1984a. All of the functional indicator groups are present all of the time on coral reefs, but dominate most often under the interacting conditions indicated by the four compartments. The complex interacting vectors of long-term eutrophication and declining herbivory (either naturally or anthropogenically derived) are postulated to produce competitive shifts (arrows) away from coral and coralline domination on pristine reefs toward various phases of algal dominance. Hypothetically, one vector can partially offset the other (e.g., high herbivory may delay the impact of elevated nutrients, or low nutrients may offset the impact of reduced herbivory). Latent trajectories are most often catalyzed or accelerated by large-scale stochastic disturbances such as tropical storms, warming events, diseases, and predator outbreaks. Degree of desirability, from a management perspective, is shown by light to dark shading.

cal controls via intense herbivory prevail, resulting in overcompensation by grazers; whereas bottom-up stimulation of productivity is minimal, due to lack of nutrient availability. Under persistent elevated nutrients, however, consistent coral declines can occur, concomitant with algal increases that may lead to profound long-term effects throughout all combinations of herbivory. Changes in bottom-up controls and their interactions not only alter the dominance patterns of primary-producer groups, but also can have even longer-term consequences mediated through structural transformations and chemical modifications to reef systems and their resident fish populations. In other words, excessive nutrient enrichment not only increases the productivity and biomass of weedy macroalgae, but, over the long term, may lead to coral habitat degradation through reduced spatial heterogeneity by overgrowth and nighttime anoxic conditions.

The proposed management model addresses the considerable complexity of coral-reef systems. Much of the overall diversity at the primary-producer level is

afforded by the interaction of opposing herbivory and nutrient controls. Because of the sensitive nature of direct and indirect interacting factors, coral reefs are particularly vulnerable to anthropogenic reversal effects that decrease top-down controls and increase bottom-up controls, dramatically altering community dynamics. For example, insufficient nutrients may act directly to limit fleshy-algal domination; conversely, abundant nutrients enhance fleshy-algal growth, with the opposite effect on reef-building corals. Furthermore, the effects of controls can be indirect by influencing competition. Competition between algae and corals can be direct (e.g., overgrowth) or indirect (e.g., preemption of substrate). Low nutrients and high herbivory also act indirectly on fleshy algae through reduced competitive abilities, whereas lowered herbivory and elevated nutrients also indirectly affect corals and coralline algae by favoring fleshy-algal competition. Other ecologically important bottom-up factors, such as light regime, abrasion, allelopathy, and sediment smothering, also can be indirect side effects of algal competition.

STATUS OF KNOWLEDGE

The relevant data on top-down versus bottom-up controls consist of short-term caging or feeding experiments, as well as circumstantial evidence (e.g., Hallock et al. 1993), correlative biogeography surveys (e.g., Littler et al. 1991; Verheij 1993), physiological assays (e.g., Littler and Littler 1990; Lapointe et al. 1997), and long-term manipulative studies. Top-down control by abundant populations of large mobile herbivores is particularly well studied for coral reefs, beginning over four decades ago with the caging study of Stephenson and Searles (1960). As examples, Sammarco et al. (1974), Ogden and Lobel (1978), Sammarco (1980), Carpenter (1986), Lewis (1986), Morrisson (1988), and numerous other workers (see review by McCook 2001) have all demonstrated that lowering herbivory without changing nutrient inputs most often results in rapid increases in algal turfs. Such low mats are unique in containing an abundance of nitrogen-fixing blue-green algae (Cyanobacteria) that can enrich other low-growing members of the turf community (Adey and Goertemiller 1987; Adey 1998). A sequence of phase shifts in algal form groups (from crustose corallines to algal turfs and, finally, to frondose macroalgae) as a function of declining herbivory was noted by Steneck (1989), who also pointed out that the biomass of an alga or functional group is ultimately the result of its rate of productivity relative to the rate at which it is removed by herbivores (see also Hatcher and Larkum 1983; Carpenter 1986; Russ 1987).

Although nutrient data are usually lacking in coral-reef field herbivory studies, natural background levels in conjunction with ample water motion are often assumed to exceed levels limiting to macroalgal growth. As pointed out by Lewis (1986), large frondose macroalgae do occur in oligotrophic reef areas of low herbivory (see also Littler et al. 1986; McCook 2001); however, many of these perennating forms occupy microhabitats that generate increased current acceleration, such as the reef crest and tops of patch-reef rocks, implicating higher nutrient fluxes (Atkinson et al. 2001). Also, some of the large perennial macroalgae are relatively

slow growing and, therefore, can maintain large biomass under low nutrient concentrations. A further consideration is the presence of substantial anthropogenic nitrogen sources in rainfall worldwide (Vitousek et al. 1997a). The decrease in coral cover (Pollock 1928), and associated rise in frondose algae (Doty 1971) and coralline algae (Littler 1971), on the reef flat at Waikiki, Hawaii, was the first phase shift from coral to macroalgal domination that was postulated to result from increases in eutrophication (Littler 1973). Spatial and temporal patterns of nutrients also have been shown to covary with algal biomass (Adey et al. 1977; Hatcher and Hatcher 1981; Hatcher and Larkum 1983). The primary production and growth of algal turfs (Hatcher and Larkum 1983; Williams and Carpenter 1988), frondose macroalgae (Lapointe 1987; Littler et al. 1991), and coralline algae (Littler 1973) generally increase with higher nutrient availability on undisturbed reef systems, suggesting limitation by nutrients.

Shifts from coral dominance to algal dominance that indicate linkages with chronic nutrient loading are exemplified by case studies worldwide (e.g., Littler 1973; Banner 1974; Weiss and Goddard 1977; Mergener 1981; Tomascik and Sander 1985, 1987; Cuet et al. 1988; Lapointe and O'Connell 1989; Bell 1992; Littler et al. 1993; Lapointe et al. 1994, 1997; Goreau et al. 1997; Bruno et al. 2003). Other coral to algal phase shifts on various types of degraded reefs have also been reviewed (Marszalek 1981; McClanahan and Shafir 1990; Done 1992b; Knowlton 1992; Hallock et al. 1993; Gardner et al. 2003).

Herbivory patterns, like nutrient levels, alone do not always explain the distributions and abundances of benthic algae on coral reefs (Adey et al. 1977; Hay 1981; Hatcher and Larkum 1983; Hatcher 1983; Carpenter 1986). For example, several studies found no significant correlation between grazing intensity and algal biomass (e.g., Hatcher 1981; Schmitt 1997; Lirman and Biber 2000). A dramatic increase in algal biomass due to eutrophication was reported (Fishelson 1973) without any concomitant reduction in herbivore populations. The importance of the very low nutrient levels involved in eutrophication (either natural or anthropogenic) has only recently come to light (Bell 1992; Lapointe et al. 1997; Small and Adey 2001). Such low levels can sometimes correlate with the phase shifts from corals toward macroalgal dominance without changing herbivory. These kinds of biotic phase shifts also have been attributed to overfishing (e.g., see Hughes 1994), in concert with cultural eutrophication (Goreau et al. 1997; Lapointe et al. 1997).

Smith et al. (2001) rigorously conducted the first appropriate experimental test of the RDM in a natural oligotrophic coral-reef setting, in conjunction with natural successional and competitive bouts, to determine dominance among the major benthic producer groups over an adequate time scale. The results precisely fitted all tenets of the RDM, confirming its efficacy as an important management tool. In contrast, a sophisticated nutrient-enrichment experiment (Larkum and Koop 1997; Encore Group 2001) did not produce results relevant to the RDM because ambient nutrient levels were well above threshold concentrations and the experimental organisms were isolated on raised grids, precluding natural encroachment, overgrowth, or other key competitive interactions critical to testing the RDM. Another short-term study produced equivocal findings that showed herbivory effects, but

not nutrient effects (Miller et al. 1999); however, the choice of enrichment (chlorinated tree stakes) was unfortunate. Highly diverse living model systems of coral-reef communities (i.e., microcosms), operated for decades (Small and Adey 2001), have profoundly demonstrated that minute increases in nitrogen and phosphorus reduce coral growth. In addition, such systems require an abundance of grazers to maintain a high coral and algal diversity (see section 12.3). Therefore, both the processes of productivity (bottom-up) and those of disturbance (top-down) must be appreciated to manage the mechanisms that mediate the competitive interactions that determine reef health.

INTERPRETATION OF FUNCTIONAL INDICATOR GROUPS

The fast growth and turnover rates of algae compared to other reef organisms suggest their use as early-warning indicators of reef degradation. The three algal representatives of ubiquitous form and function groups are increasingly encountered as dominants on coral reefs, particularly those subjected to human activities (e.g., Lapointe 1989). From a management perspective (fig. 12.1), (1) a predominance of corals and calcareous coralline algae relative to frondose macroalgae and algal turfs would indicate a desirable healthy state reflecting low nutrients and high herbivory; (2) an abundance of frondose macroalgae indicates the least desirable condition of elevated nutrient levels and reduced herbivory, possibly reflecting pollution in concert with destructive fishing practices; (3) high coverage of coralline algae could indicate problems with elevated nutrients, but healthy high-herbivory levels; and (4) domination by turf algae suggests desirably low nutrient levels, but an inadequate herbivory component. As with any environmental indicator group, however, knowledge of distribution, variability and natural history is needed to justify its application. To provide such information, the four functional indicator groups have been characterized in detail.

Macroalgae

With an increase in nutrients, the growth of undesirable fleshy algae is favored over the slower-growing but highly desirable corals (Genin et al. 1995; Miller and Hay 1996; Lapointe et al. 1997), and the latter become inhibited by competition for space and light. On some healthy oligotrophic coral reefs, even very low nutrient increases may exceed critical levels that can shift relative dominances by stimulating macroalgal production. Birkeland (1977) noted that filamentous and frondose algae can outcompete corals (but see also McCook et al. 2001), some of which are inhibited under elevated nutrient levels (reviewed in Marubini and Davies 1996). Fast-growing algae are not just opportunists that depend on disturbances to release space resources from established longer-lived populations, but become the superior competitors when provided with abundant nutrients (Birkeland 1977). As a result, frondose macroalgae as a group are now generally recognized as harmful to the longevity of coral reefs because of the linkage between excessive blooms and coastal eutrophication (ECOHAB 1995). Potential competitive dominance of macroalgae

is inferred from their overshadowing canopy heights, as well as from inverse correlations in abundances between algae and the other producer groups (Lewis 1986), particularly at higher nutrient concentrations (e.g., Littler et al. 1993; Lapointe et al. 1997). Turbulent water motion driven by wind and wave action can be sufficient to reduce boundary-layer diffusion gradients and can increase delivery rates to support considerable macroalgal growth (e.g., Atkinson and Bilger 1992), but the abundant herbivores may mask these effects. The fleshy-macroalgal form group has proven to be particularly vulnerable to herbivory (see Hay 1981; Littler et al. 1983a; Littler et al. 1983b) and becomes abundant only where grazing is low or herbivores become swamped by excessive algal growth. Such overcompensation by herbivory may explain some of the reported cases (e.g., Crossland et al. 1984; Szmant 1997) of specific corals surviving high-nutrient reef environments.

Crustose Coralline Algae

Members of the crustose coralline algae tend to be slow-growing, competitively inferior (relative to corals, turfs, and frondose macroalgae) understory taxa abundant in most reef systems (Littler 1972). Crustose corallines generally are conspicuous, but not dominant, under low concentrations of nutrients and high levels of herbivory (Littler et al. 1991). Accordingly, they do well under both low and elevated nutrients. Therefore, crustose coralline algae do not require elevated nutrients, as might be interpreted from the RDM (fig. 12.1); instead, their rise to dominance is largely controlled indirectly by the factors influencing the abundances of the other groups, primarily corals and fleshy macroalgae. The key point is that crustose corallines predominate mainly by default (i.e., under conditions of minimal competition), where either elevated nutrients inhibit corals or intense herbivory removes fleshy algae.

Turf Algae

Turf algae tend to become dominant under minimal inhibitory top-down and minimal bottom-up controls. Their relatively small size and rapid perennation result in moderate losses to herbivory at low grazing pressures. They have opportunistic life-history characteristics, including the ability to maintain substantial nutrient uptake and growth rates under low-nutrient conditions (Rosenberg and Ramus 1984), and contain an abundance of nitrogen-fixing cyanobacteria (Adey and Goertemiller 1987; Adey 1998) that can enrich other low-growing members of the turf community. Microcosm studies have consistently shown that nutrient increases can thicken algal turfs and increase the cyanobacteria component, while lessening the overall productivity (Adey and Goertemiller 1987; Adey 1998). Algal turfs have been shown to be favored under reduced nutrient-loading rates (Fong et al. 1987) or episodic nutrient pulses (Fujita et al. 1988) and can form massive horizontal mats. Numerous studies have shown the expansion of algal turfs, not macroalgae, resulting from the removal of grazers in a wide variety of sites worldwide (e.g., Vine 1974; Hatcher and Larkum 1983; Sammarco 1983; Lewis 1986; Klumpp et al. 1987; Carpenter 1988; Littler and Littler 1997).

Reef-Building Corals (Cnidaria)

Because of their three-dimensional heterogeneity, which provides habitat for other reef organisms, their roles in producing the carbonate structure of reefs, and their aesthetic qualities, corals are the most desirable components of biotic reefs. The vertical structure and horizontal canopies of branching forms allow abundant populations of shade-dwelling crustose coralline algae to co-occur. Reef-building corals, while preyed upon by a few omnivorous fishes and specialist invertebrates (e.g., the crown of thorns sea star), generally achieve dominance under the top-down control of intense herbivory (Lewis 1986; Lirman 2001) and extremely low nutrient concentrations (Bell 1992; Lapointe et al. 1993). Massive corals are resistant to grazing at the highest levels of herbivory. Hard mound-shaped forms show little colony mortality under high grazing pressure, even though occasionally rasped by parrot fish. In contrast, some delicately branched corals such as *Porites porites* are quite palatable and readily eaten by parrot fish (Littler et al. 1989; Miller and Hay 1998). However, some corals are inhibited by increases in nitrate, ammonium or orthophosphate (see Townsley cited in Doty 1969; Stambler et al. 1991; Muller-Parker et al. 1994; Marubini and Davies 1996; Hoegh-Guldberg et al. 1997). Nutrient inhibition of coral larval settlement has been shown for *Acropora longicyathis* (Ward and Harrison 1997).

CONCLUSIONS

The recent increased awareness of coral-reef degradation worldwide (see Ginsberg 1993; chapters in Birkeland 1997), particularly from coastal pollution (e.g., Windom 1992; Bell 1992) and destructive fishing (e.g., Hughes 1994), makes the RDM timely and important. To effectively manage the mechanisms that mediate the competitive interactions within ecosystems, the processes of productivity (bottom-up) and disturbance (top-down) must be considered. The RDM addresses the roles of top-down and bottom-up controls in the benthic community structure of coral reefs. The model provides a management perspective for the mechanisms that initiate and sustain harmful blooms of algae that degrade tropical coral-reef communities. For example, if managers see a transition from coral to coralline algae, then they should attempt to limit nutrients; if a transition to turf algae occurs, grazer populations should be augmented; and a shift to macroalgal domination indicates that both excessive nutrification and destructive fishing should be curtailed. Because of global-scale degradation of coral-reef ecosystems (e.g., Ginsberg 1994; Wilkinson 1999), we emphasize the need to obtain relevant information on nutrient and herbivory thresholds for bottom-up and top-down controls, respectively. This section has evaluated the essential literature and addressed this need by providing new management insights for ascertaining and monitoring the nutrient and herbivore status of coral reefs.

LITERATURE CITED

- Adey, W. H. 1998. Coral reefs: algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *Journal of Phycology* 34:393-406.
- Adey, W. H., Adey, P., Burke, R., and Kaufman, L. 1977. The Holocene reef systems of eastern Martinique. *Atoll Research Bulletin* 281:1-40.
- Adey, W. H., and Goertemiller, T. 1987. Coral reef algal turfs: master producers in nutrient poor seas. *Phycologia* 26:374-386.
- Atkinson, M. J., and Bilger, R. W. 1992. Effects of water velocity on phosphate uptake in coral reef-flat communities. *Limnology and Oceanography* 37:273-279.
- Atkinson, M. J., Falter, J. L., and Hearn, C. J. 2001. Nutrient dynamics in the Biosphere 2

- coral reef mesocosm: water velocity controls NH_4 and PO_4 uptake. *Coral Reefs* 20:341–346.
- Atkinson, M. J., and Grigg, R. W. 1984. Model of a coral reef ecosystem. Part 2, Gross and net benthic primary production at French Frigate Shoals, Hawaii. *Coral Reefs* 3:13–22.
- Banner, A. H. 1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. *Proceedings of the Second International Coral Reef Symposium* 2:685–702.
- Bell, P. R. F. 1991. Status of eutrophication in the Great Barrier Reef Lagoon. *Marine Pollution Bulletin* 23:89–93.
- . 1992. Eutrophication and coral reefs: some examples in the Great Barrier Reef Lagoon. *Water Resources* 26:555–568.
- Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proceedings of the Third International Coral Reef Symposium* 1:15–21.
- . 1997. *Life and death of coral reefs*. Chapman and Hall, New York.
- Brawley, S. H. 1992. Mesoherbivores. Pp. 235–264 in John, D. M., Hawkins, S. S., and Price, J. H., eds., *Plant-Animal Interactions in the Marine Benthos*. Systematic Association Special Volume. Clarendon Press, Oxford.
- Bruno, J. F., Petes, L. E., Harvell, C. D., and Hettinger, A. 2003. Nutrient enrichment can increase the severity of coral diseases. *Ecology Letters* 6:1056–1061.
- Cambridge, M. L., and McComb, A. J. 1984. The loss of seagrass in Cockburn Sound, Western Australia. Part 1, The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany* 20:229–243.
- Cameron, A. M. 1977. *Acanthaster* and coral reefs: population outbreaks of a rare and specialized carnivore in a complex high-diversity system. *Proceedings of the Third International Coral Reef Symposium* 1:193–200.
- Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56:345–363.
- . 1988. Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. *Proceedings of the National Academy of Science USA* 85:511–514.
- Carpenter, S. R., Kitchell, J. F., and Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Convention on Biological Diversity. Secretariat of the Convention on Biological Diversity. <http://www.biodiv.org>.
- Crossland, C. J., Hatcher, B. G., Atkinson, M. J., and Smith, S. V. 1984. Dissolved nutrients of a high-latitude coral reef, Houtman Abrolhos Island, Western Australia. *Marine Ecology Progress Series* 14:159–163.
- Cuet, P., Naim, O., Faure, G., and Conan, J. Y. 1988. Nutrient-rich groundwater impact on benthic communities of La Saline fringing reef (Reunion Island, Indian Ocean): preliminary results. *Proceedings of the Sixth International Coral Reef Symposium* 2:207–212.
- Darcy, G. H. 1985. Synopsis of biological data on the pinfish, *Lagodon rhomboides* (Pisces: Sparidae). NOAA Technical Report NMFS23. FAO Fisheries, Synopsis. Seattle.
- Done, T. J. 1992a. Effects of tropical cyclone waves on ecological and geomorphological structures on the Great Barrier Reef. *Continental Shelf Research* 12:859–872.

- . 1992b. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132.
- Doty, M. S. 1969. The ecology of Honaunau Bay, Hawaii. Hawaii Botanical Science Paper no. 14. University of Hawaii, Manoa.
- . 1971. Physical factors in the production of tropical benthic marine algae. Pp. 99–121 in Costlow, J. D. Jr., ed., *Fertility of the Sea*, vol. 1. Gordon and Breach, New York.
- ECOHAB (Ecology and Oceanography of Harmful Algal Blooms). 1995. The ecology and oceanography of harmful algal blooms: a national research agenda. Proceedings of the National Workshop. Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.
- Encore Group. 2001. The effect of nutrient enrichment on coral reefs: synthesis of results and conclusions. *Marine Pollution Bulletin* 42:91–120.
- Fishelson, L. 1973. Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. *Oecologia* 12:55–67.
- Fong, P., Rudnicki, R., and Zedler, J. B. 1987. Algal community response to nitrogen and phosphorus loading in experimental mesocosms: management recommendations for southern California lagoons. Report of the California State Water Control Board, San Diego.
- Frankovich, T. A., and Zieman, J. C. 1994. Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science* 54:679–695.
- Fujita, R. M., Wheeler, P. A., and Edwards, R. L. 1988. Metabolic regulation of ammonium uptake by *Ulva rigida* (Chlorophyta): a compartmental analysis of the rate-limiting step for uptake. *Journal of Phycology* 24:560–566.
- Gacia, E., Littler, M. M., and Littler, D. S. 1999. An experimental test of the capacity of food web interactions (fish-epiphytes-seagrass) to alleviate the consequences of eutrophication on seagrass communities. *Estuarine, Coastal, and Shelf Science* 48:757–766.
- Gardner, T. A., Côte, I. M., Gill, J. A., Grant, A., and Watkinson, A. R. 2003. Long-term region wide declines in Caribbean coral reefs. *Science* 301:958–960.
- Genin, A., Lazar, G., and Brenner, S. 1995. Vertical mixing and coral death in the Red Sea following the eruption of Mt. Pinatubo. *Nature* 377:507–510.
- Gilmore, R. G. 1988. Subtropical seagrass fish communities: population dynamics, species guilds, and microhabitat associations in the Indian River Lagoon, Florida. Ph.D. diss., Florida Institute of Technology, Melbourne.
- Ginsberg, R. N., comp. 1993. *Global Aspects of Coral Reefs: Health, Hazards, and History*. University of Miami, Florida.
- . 1994. *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*. University of Miami, Florida.
- Goreau, T. J., Dalay, L., Ciappara, S., Brown, J., Dourke, S., and Thacker, K. 1997. Community-based whole-watershed and coastal zone management in Jamaica. *Proceedings of the Eighth International Coral Reef Symposium* 2:2093–2096.
- Grime, J. P. 1979. *Plant Strategies and Vegetation Processes*. John Wiley and Sons, New York.
- Hallock, P., Müller-Karger, F. E., and Hallas, J. C. 1993. Coral reef decline. *National Geographic Research and Exploration* 9:358–378.
- Hatcher, A. I., and Hatcher, B. G. 1981. Seasonal and spatial variation in dissolved nitrogen

- in One Tree Reef Lagoon. Proceedings of the Fourth International Coral Reef Symposium 2:419–424.
- Hatcher, B. G. 1981. The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. Proceedings of the Fourth International Coral Reef Symposium 2:515–524.
- . 1983. Grazing in coral reef ecosystems. Pp. 164–179 in Barnes, D. J., ed., Perspectives on Coral Reefs. Australian Institution of Marine Science, Townsville, Australia.
- Hatcher, B. G., and Larkum, A. W. D. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. Journal of Experimental Marine Biology and Ecology 69:61–84.
- Hay, M. E. 1981. Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquatic Botany 11:97–109.
- Heijs, F. M. L. 1987. Qualitative and quantitative aspects of the epiphytic component in a mixed seagrass meadow from Papua New Guinea. Aquatic Botany 27:363–383.
- Hoegh-Guldberg, O., Takabayashi, M., and Moreno, G. 1997. The impact of long-term nutrient enrichment on coral calcification and growth. Proceedings of the Eighth International Coral Reef Symposium 1:861–866.
- Howard, R. K., and Short, F. T. 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. Aquatic Botany 24:287–302.
- Huang, H., Han, X., Kang, L., Raven, P., Wyse Jackson, P., and Chen, Y. 2002. Conserving native plants in China. Science 297:935–936.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551.
- Jackson, L. E., Kurtz, J. C., and Fisher, W. S., eds. 2000. Evaluation Guidelines for Ecological Indicators. EPA/620/R-99/005. U.S. Environmental Protection Agency, Office of Research and Development, Research Triangle Park, North Carolina.
- Kemp, W. M., Twilley, R. R., Stevenson, J. C., Boynton, W. R., and Means, J. C. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. Marine Technology Society Journal 17:78–89.
- Kiorboe, T. 1980. Production of *Ruppia cirrhosa* in mixed beds in Rinkobing Fjord (Denmark). Aquatic Botany 9:135–143.
- Klumpp, D. W., McKinnon, D., and Daniel, P. 1987. Damsel fish territories: zones of high productivity on coral reefs. Marine Ecology Progress Series 40:41–51.
- Klumpp, D. W., Salita-Espinosa, J. T., and Fortes, M. D. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. Aquatic Botany 43:327–349.
- Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32:674–679.
- Lapointe, B. E. 1987. Phosphorus- and nitrogen-limited photosynthesis and growth of *Gracilaria tikvahiae* (Rhodophyceae) in the Florida Keys: an experimental field study. Marine Biology 93:561–568.
- . 1989. Caribbean coral reefs: are they becoming algal reefs? Sea Frontiers 35:82–91.
- Lapointe, B. E., Barile, P. J., Yentsch, C. S., Littler, M. M., Littler, D. S., and Kakuk, B. 2004. The relative importance of nutrient enrichment and herbivory on macroalgal communi-

- ties near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment. *Journal of Experimental Biology and Ecology* 298:275-301.
- Lapointe, B. E., Littler, M. M., and Littler, D. S. 1993. Modification of benthic community structure by natural eutrophication: the Belize barrier reef. *Proceedings of the Seventh International Coral Reef Symposium* 1:323-334.
- . 1997. Macroalgal overgrowth of fringing coral reefs at Discovery Bay, Jamaica: bottom-up versus top-down control. *Proceedings of the Eighth International Coral Reef Symposium* 1:927-932.
- Lapointe, B. E., Matzie, W. R., and Clark, M. W. 1994. Phosphorus inputs and eutrophication on the Florida Reef Tract. Pp. 106-112 in Ginsberg, R. N., comp., *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*. University of Miami, Miami, Florida.
- Lapointe, B. E., and O'Connell, J. D. 1989. Nutrient-enhanced productivity of *Cladophora prolifera* in Harrington Sound, Bermuda: eutrophication of a confined phosphorus-limited marine ecosystem. *Estuarine, Coastal, and Shelf Science* 28:347-360.
- Larkum, A. W. D., and Koop, K. 1997. ENCORE, algal productivity, and possible paradigm shifts. *Proceedings of the Eighth International Coral Reef Symposium* 1:881-884.
- Levitan, C. 1987. Formal stability analysis of a plankton fresh-water community. Pp. 71-100 in Kerfoot, W. C., and Sih, A., eds., *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, New Hampshire.
- Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56:183-200.
- Lirman, D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19:392-399.
- Lirman, D., and Biber, P. 2000. Seasonal dynamics of macroalgal communities of the northern Florida Reef Tract. *Botanica Marina* 43:305-314.
- Littler, M. M. 1971. Standing stock measurements of crustose coralline algae (Rhodophyta) and other saxicolous organisms. *Journal of Experimental Marine Biology and Ecology* 6: 91-99.
- . 1972. The crustose Corallinaceae. *Oceanography and Marine Biology, Annual Review* 10:311-347.
- . 1973. The population and community structure of Hawaiian fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). *Journal of Experimental Marine Biology and Ecology* 11:103-120.
- . 1980. Morphological form and photosynthetic performances of marine macroalgae: tests of a functional/form hypothesis. *Botanica Marina* 22:161-165.
- Littler, M. M., and Arnold, K. E. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. *Journal of Phycology* 18:307-311.
- Littler, M. M., and Littler, D. S. 1984a. Models of tropical reef biogenesis: the contribution of algae. Pp. 323-364 in Round, F. E., and Chapman, D. J., eds., *Progress in Phycological Research*, vol. 3. Biopress, Bristol, United Kingdom.
- . 1984b. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *Journal of Experimental Marine Biology and Ecology* 74:13-34.

- . 1990. Productivity and nutrient relationships in psammophytic versus epilithic forms of Bryopsidales (Chlorophyta): comparisons based on a short-term physiological assay. *Hydrobiologia* 204/205:49–55.
- . 1997. Disease-induced mass mortality of crustose coralline algae on coral reefs provides rationale for the conservation of herbivorous fish stocks. *Proceedings of the Eighth International Coral Reef Symposium* 1:719–724.
- Littler, M. M., Littler, D. S., and Lapointe, B. E. 1993. Modification of tropical reef community structure due to cultural eutrophication: the southwest coast of Martinique. *Proceedings of the Seventh International Coral Reef Symposium* 1:335–343.
- Littler, M. M., Littler, D. S., and Taylor, P. R. 1983a. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *Journal of Phycology* 19:229–237.
- . 1995. Selective herbivore increases biomass of its prey: a chiton-coralline reef-building association. *Ecology* 76:1661–1681.
- Littler, M. M., Littler, D. S., and Titlyanov, E. A. 1991. Comparisons of N- and P-limited productivity between high granitic islands vs. low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. *Coral Reefs* 10:199–209.
- Littler, M. M., Taylor, P. R., and Littler, D. S. 1983b. Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2:111–118.
- . 1986. Plant defense associations in the marine environment. *Coral Reefs* 5:63–71.
- . 1989. Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80:331–340.
- Lough, J. M. 1994. Climate variation and El Niño–Southern Oscillation events on the Great Barrier Reef, 1958–1987. *Coral Reefs* 13:181–195.
- Macintyre, I. G. and Glynn, P. W. 1990. Upper limit of El Niño killoff. *Coral Reefs* 9:92.
- Marszalek, D. S. 1981. Effects of sewage effluents on reef corals. *Proceedings of the Fourth International Coral Reef Symposium* 1:213. Abstract.
- Marubini, F., and Davies, P. S. 1996. Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Marine Biology* 127:319–328.
- McClanahan, T. R., and Shafir, S. H. 1990. Causes and consequences of sea-urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83:362–370.
- McCook, L. J. 2001. Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. *Coral Reefs* 19:419–425.
- McCook, L. J., Jompa, J., and Diaz-Pulido, G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417.
- McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series* 122:239–252.
- McQueen, D. J., Johannes, M. R. S., Post, J. R., Stewart, T. J., and Lean, D. R. S. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecological Monographs* 59:289–309.
- Mergener, H. 1981. Man-made influences on and natural changes in the settlement of the Aqaba reefs (Red Sea). *Proceedings of the Fourth International Coral Reef Symposium* 1:193–207.

- Miller, M. W., and Hay, M. E. 1996. Coral-seaweed-grazer-nutrient interactions on temperate reefs. *Ecological Monographs* 66:323-344.
- . 1998. Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia* 113:231-238.
- Miller, M. W., Hay, M. E., Miller, S. L., Malone, D., Sotka, E. E., and Szmant, A. 1999. Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. *Limnology and Oceanography* 44:1847-1861.
- Morrisson, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* 69:1367-1382.
- Muller-Parker, G., McCloskey, L. R., Høegh-Guldberg, O., and McAuley, P. J. 1994. Effects of ammonium enrichment on animal and algal biomass of the coral *Pocillopora damicornis*. *Pacific Science* 48:273-283.
- National Research Council. 1994. *Priorities for Coastal Ecosystem Science*. National Academy Press, Washington, DC.
- Nixon, S. W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41:199-219.
- Odum, W. E. 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. Pp. 222-240 in Steel, J. H., *Marine Food Chains*. University of California Press, Berkeley.
- Ogden, J. C., Brown, R. A., and Salesky, N. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182:715-717.
- Ogden, J. C., and Lobel, P. S. 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fishes* 3:49-63.
- Orth, R. J., and Montfrans, J. van. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquatic Botany* 18:43-69.
- Pollock, J. B. 1928. Fringing and fossil coral reefs of Oahu. *Bulletin of the Bernice P. Bishop Museum* 55:1-56.
- Rosenberg, G., and Ramus, J. 1984. Uptake of inorganic nitrogen and seaweed surface area:volume ratios. *Aquatic Botany* 19:65-72.
- Russ, G. R. 1987. Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes? *Journal of Experimental Marine Biology and Ecology* 110:1-17.
- Sammarco, P. W. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *Journal of Experimental Marine Biology and Ecology* 45:245-272.
- . 1983. Effects of fish grazing and damselfish territoriality on coral reef algae. Part 1, Algal community structure. *Marine Ecology Progress Series* 13:1-14.
- Sammarco, P. W., Levinton, J. S., and Ogden, J. C. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. *Journal of Marine Research* 32:47-53.
- Sand-Jensen, K. 1977. Effects of epiphytes on eelgrass photosynthesis. *Aquatic Botany* 3:55-63.
- Sand-Jensen, K., and Borum, J. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* 41:137-175.

- Santavy, D. L., and Peters, E. C. 1997. Microbial pests: coral disease in the western Atlantic. *Proceedings of the Eighth International Coral Reef Symposium* 1:607–612.
- Schmitt, E. F. 1997. The influence of herbivorous fishes on coral reef communities with low sea urchin abundance: a study among reef community types and seasons in the Florida Keys. Ph.D. diss., University of Miami, Florida.
- Short, F. T., and Short, C. A. 1984. The seagrass filter: purification of coastal water. Pp. 395–413 in Kennedy, V. S., ed., *The Estuary as a Filter*. Academic Press, New York.
- Silberstein, K., Chiffings, A. W., and McComb, A. J. 1986. The loss of seagrass in Cockburn Sound, Western Australia. Part 3, The effect of epiphytes on productivity of *Posidonia australis* Hook. *Aquatic Botany* 24:355–371.
- Small, A., and Adey, W. H. 2001. Reef corals, zooxanthellae, and free-living algae: a microcosm that demonstrates synergy between calcification and primary production. *Ecological Engineering* 16:443–457.
- Smith, J. E., Smith, C. M., and Hunter, C. L. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332–342.
- Stambler, N., Popper, N., Dubinsky, Z., and Stimson, J. 1991. Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. *Pacific Science* 45:299–307.
- Steneck, R. S. 1989. Herbivory on coral reefs: a synthesis. *Proceedings of the Sixth International Coral Reef Symposium* 1:37–49.
- Steneck, R. S., and Dethier, M. N. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–498.
- Stephenson, W., and Searles, R. B. 1960. Experimental studies on the ecology of intertidal environments at Heron Island. Part 1, Exclusion of fish from beach rock. *Australian Journal of Marine and Freshwater Research* 2:241–267.
- Stoner, A. W., and Waite, J. M. 1991. Trophic biology of *Strombus gigas* in nursery habitats: diets and food sources in seagrass meadows. *Journal of Molluscan Studies* 57:451–460.
- Szmant, A. M. 1997. Nutrient effects on coral reefs: a hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. *Proceedings of the Eighth International Coral Reef Symposium* 2:1527–1532.
- Szmant, A. S. 2001. Introduction to special issue, Coral Reef Algal Community Dynamics. *Coral Reefs* 19:299–302.
- Threlkeld, S. T. 1988. Planktivory and planktivore biomass effects on zooplankton, phytoplankton, and the trophic cascade. *Limnology and Oceanography* 33:1362–1375.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D., and Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281–284.
- Tomascik, T., and Sander, F. 1985. Effects of eutrophication on reef-building corals. Part 1, Growth rate of the reef-building coral *Montastrea annularis*. *Marine Biology* 87:143–155.
- . 1987. Effects of eutrophication on reef-building corals: reproduction of the reef-building coral *Porites porites*. *Marine Biology* 94:77–94.
- Tomasko, D. A., and Lapointe, B. E. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. *Marine Ecology Progress Series* 75:9–17.

- Twilley, R. R., Kemp, W. M., Staver, K. W., Stevenson, J. C., and Boynton, W. R. 1985. Nutrient enrichment of estuarine submerged vascular plant communities. Part I, Algal growth and effects on production of plants and associated communities. *Marine Ecology Progress Series* 23:179–141.
- Verheij, E. 1993. *Marine Plants of the Spermonde Archipelago, SW Sulawesi Indonesia: Aspects of Taxonomy, Floristics, and Ecology*. Rijksherbarium, Leiden.
- Vine, P. J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral reef ecology. *Marine Biology* 4:131–136.
- Vitousek, P. M., Aber, J., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H., and Tilman, D. G. 1997a. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Adaptation* 7:737–750.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. 1997b. Human domination of earth's ecosystems. *Science* 277:494–499.
- Ward, S., and Harrison, P. L. 1997. The effects of elevated nutrient levels on settlement of coral larvae during the Encore experiment, Great Barrier Reef, Australia. *Proceedings of the Eighth International Coral Reef Symposium* 1:891–896.
- Weiss, M. P., and Goddard, D. A. 1977. Man's impact on coastal reefs: an example from Venezuela. *American Association of Petroleum Geologists, Studies in Geology* 4:111–124.
- Wilkinson, C. 1999. Global and local threats to coral reef functioning and existence: review and predictions. *Marine and Freshwater Research* 50:867–878.
- Williams, S. L., and Carpenter, R. C. 1988. Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. *Marine Ecology Progress Series* 47:145–152.
- Windom, H. 1992. Contamination of the marine environment from land-based sources. *Marine Pollution Bulletin* 25:1–4.
- Wittenberg, M., and Hunte, W. 1992. Effects of eutrophication and sedimentation on juvenile corals. Part 1, Abundance, mortality, and community structure. *Marine Biology* 112:131–138.
- Wyse Jackson, P. S. 2002. *International Review of the Ex Situ Collections of the Botanic Gardens of the World*. Botanic Gardens Conservation International, Kew, Richmond, Surrey, United Kingdom.
- Wyse Jackson, P. S., and Sutherland, L. A. 2000. *International Agenda for Botanic Gardens in Conservation*. Botanic Gardens Conservation International, Kew, Richmond, Surrey, United Kingdom.

Edited by Gary A. Krupnick and W. John Kress

PLANT CONSERVATION

Chicago



PLANT CONSERVATION

A NATURAL HISTORY APPROACH



Edited by Gary A. Krupnick and W. John Kress

With a foreword by Daniel H. Janzen



ISOLE
I 5057
Watsonia distans L. Bolus
Annals Bolus Herb. 4: (45) 51. 1926.
lectotypified by T. G. Tutin, Annals Kirstenb. Bot. Gen.
et who cites # 7305



UNITED STATES NATIONAL MUSEUM

Plantae Schlechterianae Austro-Africanae.
Iter secundum.

925. *Katsomia humilis* Miller
French Herb 360w
Terra Capensis
Regio occidentalis
S. G. F.

1896.