

The effect of multiple stressors on the Florida Keys coral reef ecosystem: A landscape hypothesis and a physiological test

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Abstract

Changes in land use and water management practices in south Florida have altered the quality and quantity of freshwater flowing into Florida Bay. By the 1980s, reduced inflow and drought led to an extensive hypersaline phase in the bay. This phase had a drastic effect on benthic communities within the bay and possibly also on coral communities within the bay and the Florida Keys National Marine Sanctuary. Physical oceanographic measurements demonstrate the presence of warm, hypersaline, and turbid water on coral reefs offshore from the Florida Keys, especially near passes which conduct water from Florida Bay to the Atlantic Ocean.

To examine the effect of Florida Bay water intrusions on coral reefs, we tested for significant effects of two stressors, elevated temperature and salinity, on coral production, respiration, and survival. Elevated temperatures produce significant reductions in photosynthesis, respiration, and net $P:R$ ratios after 6 h of exposure, and elevated salinities produce similar results after 30 h. Exposure to both elevated temperature and salinity produces a highly significant ($P > 0.01$), but short-term, mitigative interactive effect. The combination of the two stressors was less stressful (for the response variables measured) than the sum of the stressors acting independently. After 36 h of exposure, however, the mitigating effect disappeared and corals exposed to the combined stresses did not survive. A three-dimensional response surface, which predicts $P:R$ ratios as a function of varying salinity and temperature, is used to construct a testable hypothesis to explain recent declines in coral cover on some reefs within Florida Bay and the Florida Keys. We chose salinity and temperature to test a multiple stressor model because they are relatively easy to manipulate. However, any environmentally realistic model must include other potential stressors, such as turbidity, elevated nutrients, and environmental contaminants.

Reef-building corals harbor endosymbiotic photosynthetic dinoflagellates (*Symbiodinium* spp.) in their tissues (Trench and Blank 1987; Rowan and Powers 1991). In water <10 m deep, healthy individuals of most coral species produce more oxygen than they consume (Muscatine et al. 1989). *Montastrea annularis* maintains its daily integrated net production:respiration ratio considerably above 1.0 (Achtuv and Dubinsky 1990; Patterson et al. 1991; Porter et al. in prep.). Multiple stressors can lower this $P:R$ below unity, thereby reducing the growth rate and reproductive capacity of reef-building corals. These stressors can include nutrient enrichment (both N and P), turbidity (caused by living and non-living suspended particulate matter), sedimentation, salinity, and temperature extremes.

None of the lower invertebrate groups, including the cnidaria, are capable of either osmoregulation or homoiothermy (Hoegh-Guldberg and Smith 1989). Short-term effects of either salinity or temperature stress can be exhibited as changes in basal metabolic function, including effects on animal respiration and symbiont photosynthesis. Longer term stress effects can be exhibited as increased mortality rates or reduced growth and reproductive rates (Coles and Jokiel 1992).

Experiments on the stress physiology of scleractinian corals

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als have usually been confined to single factors such as temperature (Mayer 1914; Edmondson 1928; Clausen and Roth 1975; Coles et al. 1976; Jokiel and Coles 1977, 1990; Coles and Jokiel 1992) or salinity (Muthiga and Szmant 1987). Short-term exposure of several hours to elevated temperatures causes an increase in the measured respiration rate (Coles and Jokiel 1977). In the elevated temperature experiments on *Montipora* of Coles and Jokiel (1977), photosynthesis also increased, but more slowly than respiration, leading to a lowering of the overall $P:R$ ratio and a diminishing of the autotrophic capacity of this species. Exposure of several days to elevated temperatures reduces both respiration and photosynthesis in *M. annularis* (Porter et al. 1989; Fitt and Warner 1995; Warner and Fitt 1996). Long-term exposure also leads to the induction of heat shock proteins (Hayes and King 1995) and bleaching (Cook et al. 1990; Gates 1990; Iglesias-Prieto et al. 1992) in this species. Prolonged exposure to elevated temperature reduces photosynthesis faster than respiration, and therefore the integrated $P:R$ ratio also falls precipitously (Porter et al. 1989).

Salinity stress also affects coral metabolism (Coles and Jokiel 1992). Sublethal effects of salinity stress have been recorded for the Floridian coral, *Siderastrea siderea* (Muthiga and Szmant 1987), a coral known to be highly euryhaline (Vaughan 1914). The data of Muthiga and Szmant (1987) show that an increase in salinity from 32 to 42‰ causes no change in respiration but a significant reduction in photosynthesis. Increases >10‰ cause a reduction in both photosynthesis and respiration after 6 d of exposure. Coles and Jokiel (1992) demonstrated that the instantaneous gross $P:R$ ratio for *S. siderea* falls at salinities in excess of 36‰.

A developing body of literature suggests that salinity and

temperature may have interactive effects (Coles and Jokiel 1992). Low salinity reduces a coral's ability to survive short-term exposure to elevated temperature (Jokiel and Coles 1977). The data of Jokiel and Coles (1977) show that interactions between physical factors are greatest near the limits of tolerance for a given factor and further that the thermal history of the individual coral is important in predicting the outcome of the experiment. Coles and Jokiel (1978) also suggested that a slight increase in resistance to thermal stress may be imparted by a small increase in salinity above normal salinity values. Extremes in temperature and salinity are however always lethal (Hoegh-Guldberg and Smith 1989).

Elevated salinity and temperature reduce coral growth and survival (Coles and Jokiel 1992). Wells (1932) tested the effects of elevated salinity on the survival of *M. (=Orbicella) cf. annularis*. Although none of his exposure times exceeded 12 h, Wells recorded high rates of mortality for *M. annularis* at salinity values of 43‰ and above. Elevated temperatures of only two or three degrees above the average summer maxima cause substantially increased mortality in *M. annularis* (Cook et al. 1990; Fitt et al. 1993) and a significant reduction in calcification rate among the few individuals that survive these temperature extremes (Porter et al. 1989). All zooxanthellate coral species tested so far show similar responses (Clausen and Roth 1975; Jokiel and Coles 1977, 1990). These universal responses to elevated temperature are thought to relate to the collapse of photosystem 2 (Warner and Fitt 1996). Prolonged exposure to suboptimal physical conditions causes sterility in *M. annularis* (Szmant and Gassman 1990) and significantly lower larval production for *Pocillopora damicornis* (Harriott 1983).

Materials and methods

Physical oceanographic methods—Between 1990 and 1993, standard salinity, temperature, and depth profiles were taken weekly using a YSI CTD from small boats at several localities throughout the Florida Keys (Ogden et al. 1994). Monitored locations included fore-reef environments at Tennessee Reef, Sombrero Reef, and Looe Reef as well as in passes between the Florida Keys such as Channel 5, Moser Channel, and the Long Key Viaduct (Fig. 1). In addition to these oceanographic stations, satellite imagery and surface surveys have plotted the distribution and episodic movement of "green water" masses from Florida Bay out onto offshore coral reefs (Smith 1994).

Oxygen flux experiments—Pieces of the reef-building coral *M. annularis* were collected with a coal chisel from Admiral Patch Reef off Key Largo. Specimens most closely resemble the sibling species *Montastrea annularis cf. favolata* (Knowlton et al. 1992; Szmant et al. abstr.). Following collection, specimens were left on the patch reef to acclimate for 2 weeks prior to use in the experiment. The corals were then placed on stands in scrubbed aquaria filled with newly collected seawater. Each aquarium was equipped with 500-W halogen lights providing an irradiance of $600 \mu\text{Einst m}^{-2} \text{s}^{-1}$, and the corals received 12 h of light each day. Air bubblers and water pumps provided aeration and continuous water movement. Metabolic measurements were made on each

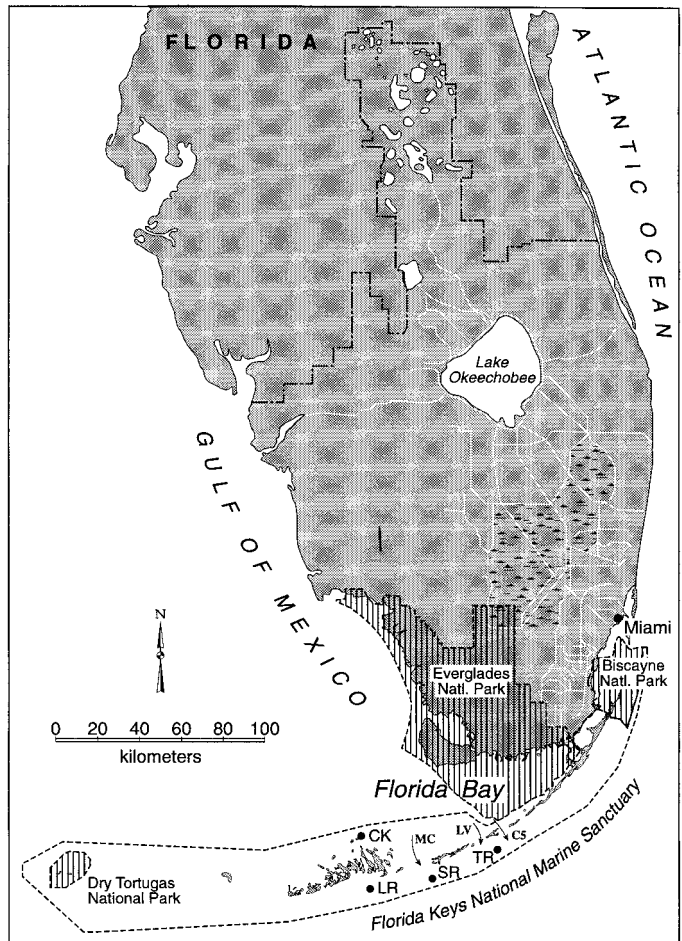


Fig. 1. The South Florida watershed stretches from the lake district of central Florida to the Everglades National Park. An extensive canal system, especially south of Lake Okeechobee, conducts surface waters southeastward to the Atlantic Ocean. Coral reefs are distributed from the Biscayne National Park to the Dry Tortugas National Park as well as in Florida Bay, for instance at Content Key (CK). Cuts between the keys allow water to flow from the bay out onto coral reefs offshore, including Looe Reef (LR), Sombrero Reef (SR), and Tennessee Reef (TR), through passages such as Moser Channel (MC), the Long Key Viaduct (LV), and Channel 5 (C5).

coral by placing it in a sealed 1.0-liter chamber and monitoring the level of dissolved oxygen with YSI oxygen electrodes and meters. Uniformity of dissolved oxygen levels throughout the chambers was achieved by rotating stir bars within the chambers. The temperature was raised by 1°C per hour to the experimental condition, and salinity was increased by 2‰ per hour to the experimental condition. Experimental incubations lasted for 36 h with oxygen flux measurements made at 6, 12, 30, and 36 h for both single stressor (elevated temperature or elevated salinity) and multiple stressor (elevated temperature and elevated salinity) conditions. No photosynthesis measurements were taken at night. Experimental chambers were periodically flushed with fresh seawater to maintain oxygen concentrations within 25% of ambient. We also conducted a series of 12-h exposures to

single stressor conditions with temperatures up to 36°C and salinities up to 60‰. Three response variables were calculated from the oxygen flux measurements: net photosynthesis, respiration, and net $P:R$ ratio. Oxygen flux measurements (in units of $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) taken under saturating light values were used to determine net photosynthetic rates using linear regression and were subsequently normalized to coral surface area. Net $P:R$ was calculated as a dimensionless ratio using the assumptions of Porter et al. (1984).

Experimental design—Two levels of salinity (35 and 40‰) and two levels of temperature (30 and 33°C) produced a 2×2 factorial experiment. Thus there were four treatments: control (35‰, 30°C), single stress temperature (35‰, 33°C), single stress salinity (40‰, 30°C), and combination stress (40‰, 33°C). Each treatment had a sample size of six. Ambient conditions at the coral collection site were 30°C and 35‰; thus these conditions were used for the control treatment. Validation of the experimental procedures is indicated by the physiological consistency of the control corals: there is no significant trend of change in any of the control response variables over time (Fig. 2).

Data for the 2×2 factorial design were analyzed using ANOVA. Tests for interactions between stressors were performed separately for each of the time periods in the experiment. Because ANOVA procedures rely heavily on the assumption of homogeneity of variances and, to a lesser extent, on the assumption of normally distributed data, tests of these assumptions were performed for all treatment combinations across all time periods. The data met the assumptions of ANOVA without transformation. The factorial ANOVA was carried out using a PC SAS package and all tests were completed using an α level of 0.05.

Results

Florida Bay water intrusions on the coral reefs—Hypersaline water was found in contact with coral reefs during both summer and winter of 1990, 1991, and 1992 (Fig. 3) and has been observed as recently as June 1997 (J. Porter pers. obs.). The salinity signal demonstrates the origin of the water mass is Florida Bay and that it flows out to the reef tract through passes between the keys. This water is quickly diluted on its way to the reef tract, as demonstrated by its slightly elevated salinity offshore (Fig. 3). During winter months, Florida Bay water can be both cold and hypersaline, with the result that this dense water mass sinks and sets up a traditional warm-over-cold thermocline (Fig. 3D). In summer, Florida Bay water can be both warm and saline. Due to its density, this warm water mass sinks and produces a stable inverted thermocline (Fig. 3A–C and E). Hypersaline bay water sinks to the bottom and comes in contact with all benthic assemblages along its path to the Atlantic Ocean (Fig. 3).

Test of alternative physiological models—The physiological response of *M. annularis* to elevated salinity or temperature is significantly influenced by both the specific stressor and the duration of exposure to that stressor. If we first examine the effect of single stressors on net photosynthesis,

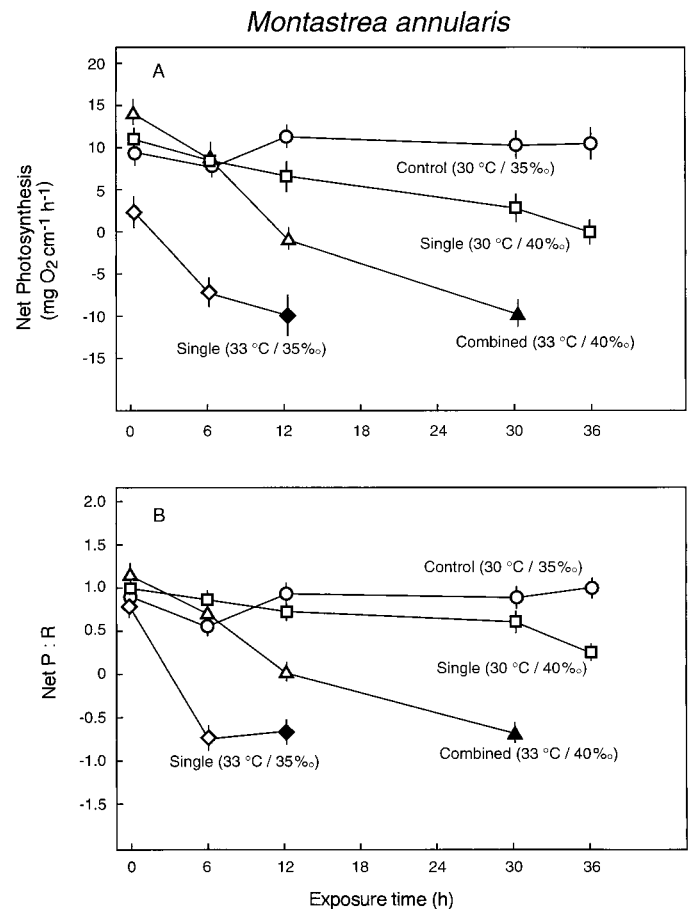


Fig. 2. Effects of multiple stressors on coral physiology in *Montastrea annularis*. A. The time-course of net photosynthetic responses to elevated temperature and salinity, as single or multiple stressors. B. The time-course of instantaneous net $P:R$ ratio responses to single and multiple stressors. Open symbols indicate survival of all specimens; closed symbols indicate mortality of all specimens during the next time interval.

Fig. 2 shows that elevated temperatures (33°C) reduce photosynthesis. Likewise, hypersalinity (40‰) reduces photosynthesis. These two stressors, however, do not produce the same magnitude of response. Even at 6 h, elevated temperature has a significantly greater effect on photosynthesis than elevated salinity. Throughout the time-course of the experiment (Fig. 2A), net photosynthesis remains positive under conditions of elevated salinity with all coral colonies surviving this single stressor treatment. Not only does net photosynthesis collapse completely under conditions of elevated temperature, all coral colonies died after 12 h of exposure (Fig. 2).

Increasing salinity alone has no discernible effect on respiration. Even after 36 h of exposure to 40‰, the experimental treatment is indistinguishable from the control. Not surprisingly, net $P:R$ values (Fig. 2B) parallel the results of net photosynthesis. The results show that although both of these physical factors reduce $P:R$ significantly, salinity alone reduces it slightly and temperature alone reduces it greatly.

Salinity / Temperature Profiles

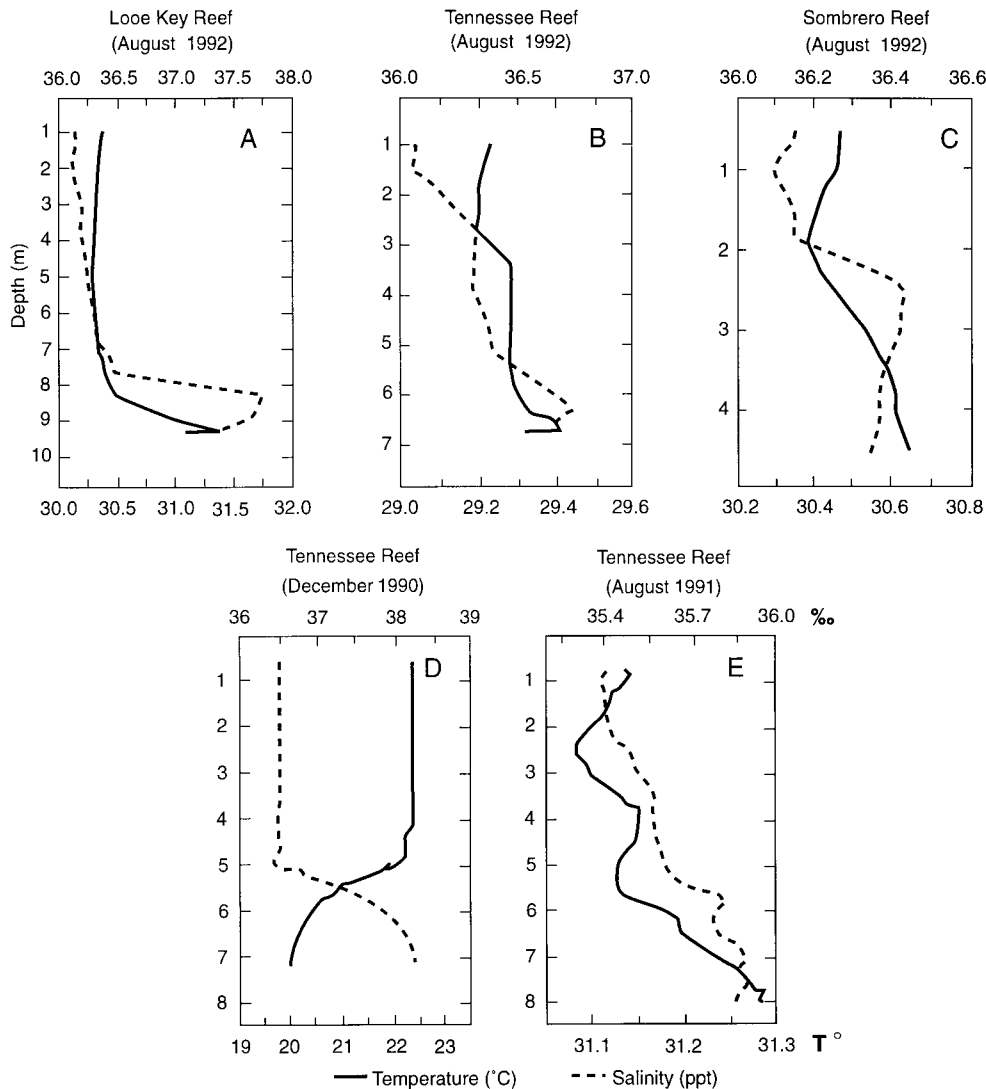


Fig. 3. Salinity-temperature-depth profiles for several Florida Keys coral reefs. In summer, warm, hypersaline Florida Bay water reaches Looe Key Reef (A), Tennessee Reef (B), and Sombrero Reef (C) producing a surprising inversion (warm water on bottom, cooler water on top). At these times, even though Florida Bay water is warm, it sinks because its high salinity makes it dense. In winter (1990/1991), cold, hypersaline water flows from Channel 2, Channel 5, and the Long Key Viaduct out onto Tennessee Reef (D), setting up a traditional thermocline. The inverted thermocline re-establishes itself on Tennessee Reef in August (E).

If multiple stressors were acting to induce an additive effect, then the expected net photosynthetic response after 6 h of exposure would be $-5.77 \mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$, i.e., 9.26 (response of the control) + 0.05 (change in response due to salinity) + -15.08 (change in response due to temperature). The observed response for the combined stress treatment, $+9.63 \mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$, (Fig. 2A) demonstrates a highly significant (ANOVA $P = 0.001$) interactive effect and invalidates the additive model as an adequate predictor of the multiple stressor effect. Further, the positive sign, and the strength of the effect, demonstrates clearly that the most ap-

propriate model is the mitigative interactive model rather than the exacerbative interactive model. This mitigative effect on net photosynthesis continues after 12 h (ANOVA $P = 0.005$) of exposure.

The time-course of mitigative effects on net $P:R$ ratio is both strong and persistent (ANOVA $P = 0.014$ and $P < 0.0001$ after 6 and 12 h, respectively) (Fig. 2). In some ways, the most dramatic mitigative effect on either photosynthesis or net $P:R$ occurs between 18 and 30 h of exposure, when all of the single stress temperature experimental cohorts have died, and yet the multiple stress specimens are all still alive

Coral Physiology *Montastrea annularis*

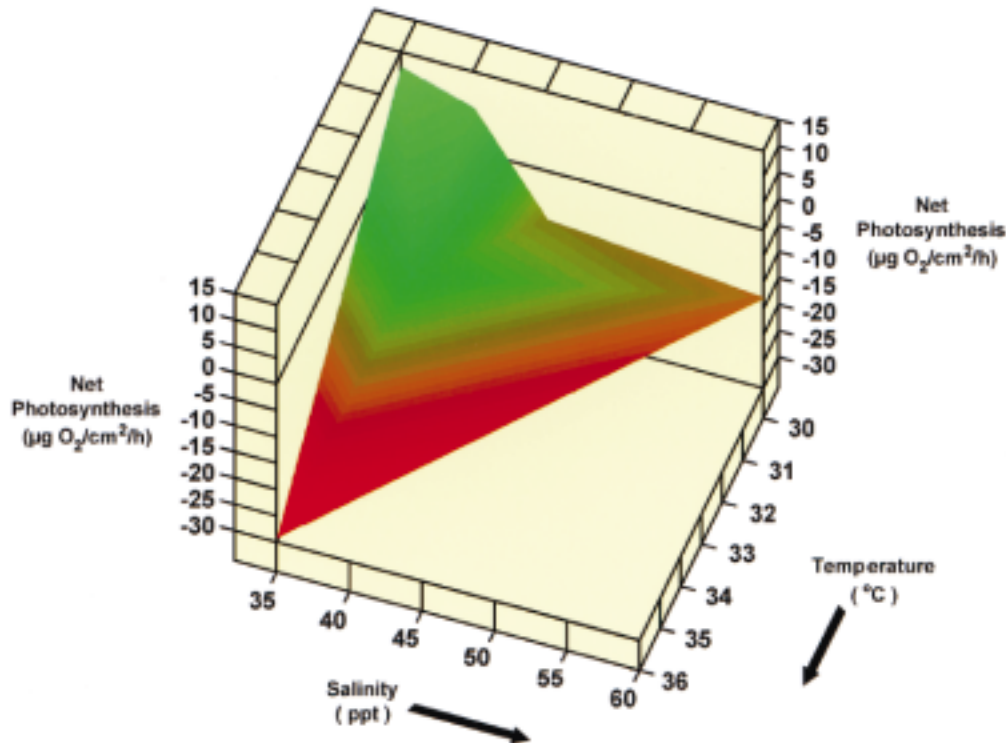


Fig. 4. Coral physiological response to two stressors. The effects of elevated salinity and temperature after 12 h of exposure on the net photosynthesis of *Montastrea annularis* are shown in this three-dimensional diagram constructed from controlled laboratory experiments. Temperature and salinity work interactively to confound any model that might attempt to predict coral photosynthesis based on single factors alone. In combination, these factors profoundly diminish the photosynthetic capacity of this coral species and reduce its net photosynthesis from positive (green) to negative (red). The initial mitigating effect of elevated salinity on elevated temperature is shown by an extension of the green area into the lower right-hand portion of the three-dimensional graph.

(Fig. 2). The mitigative effect of elevated salinity on elevated temperature, however, is short lived because after 30 h, all specimens in the combined treatment died.

Our exposure series of temperatures up to 36°C and salinities up to 60‰ allows for the construction of a physiological response surface with the combined effects of single and multiple stressors displayed in one plot (Fig. 4). Positive oxygen flux (net $P > 0$) is plotted in green, and negative oxygen flux (net $P < 0$) is plotted in red. This graph clearly shows the adverse effect on oxygen metabolism caused by elevated salinity and temperature, and further shows the interactive mitigative effect of elevated salinity on elevated temperature as a skewing of the green portion of the response surface into the lower right-hand (hypersalinity) portion of the graph (Fig. 4).

Discussion

Physiological responses to elevated salinity and temperature—Our data show that elevated salinities and temperatures have an adverse effect on coral photosynthesis and net

$P:R$ ratio. Under normal oceanographic circumstances these physical parameters do not fluctuate greatly for reef environments situated in Florida Bay or near passes between the Florida Keys, although variations that lead to physiological stress do occur. For instance, McIvor et al. (1994) reported salinities between 38 and 40‰ over coral reefs inside Florida Bay and in proximity to Content Key Reef (Fig. 1). The length of exposure is important to both the magnitude and the sign of the effect. Our experiments were of short duration to mimic periodic inundation by Florida Bay water. No data exist for the long-term tolerance of *M. annularis* to elevated salinities, but this has been determined for Floridian specimens of *Porites porites* (Marcus and Thorhaug 1981). For this species, exposure to 40‰ salinity causes release of mucus, bleaching, and 40% mortality after 20 d. Exposure to 45‰ salinity is lethal to all specimens after only 3 d.

Interactive effects occur between temperature and salinity. Up to a point, elevated salinity can mitigate the negative effects of elevated temperature (Fig. 2). In this respect, the data unequivocally support the interactive mitigative response model. Our results are consistent with the findings

of Coles and Jokiel (1977) who noted that exposure of *Montipora verrucosa* to elevated temperature in the hypersaline 40‰ treatment resulted in survival that was equivalent or superior to corals from the 35‰ treatment. They also noted that whereas the 33°C treatment was lethal at all salinities, some corals in 40‰ salinity survived slightly longer than those at lower ones. Time, however, is critical to the experimental outcome. For the first 30 h of exposure, the effect is mitigative, but after 30 h the system inevitably collapses (Fig. 2).

Florida Bay water intrusions on the coral reef—Due to the confluence of easterly currents, Florida Bay is 7 cm higher than the Atlantic Ocean; therefore on average, bay water flows between the keys and out to the Atlantic Ocean (Smith 1994). Historically, this water was primarily hyposaline, and therefore floated over offshore coral reefs in its path; however, in the recent past, this water has been hypersaline and sinks under Hawk Channel (Pitts 1994) as it moves onto coral reefs offshore (Fig. 3). Very little is known regarding the quality, frequency of occurrence, distribution, and transport of Florida Bay water masses into and within the Florida Keys National Marine Sanctuary. This information is needed to refine physiological models of the effects of multiple stressors contained in the bay water mass. Dissolved or suspended organic matter in the bay water may also cause increased oxygen demand, and living and dead suspended material may produce sedimentation on and shading of reef corals that normally experience only clear water.

The Florida Bay water hypothesis: Effects of bay water on reef corals—Studies of the flow of freshwater into Florida Bay (Tilmant 1989; Zieman et al. 1989; Fourqurean and Zieman 1992; Fourqurean et al. 1993; McIvor et al. 1994) have examined the hydrology of Florida Bay in the area north of the Florida Keys and south of the Everglades. Historical patterns of freshwater flow through the Everglades have been interrupted by the diversion of freshwater from the Everglades into canals emptying into the Atlantic Ocean to the east rather than into Florida Bay to the south. During the 1980s, lower than average rainfall may also have exacerbated this situation (McIvor et al. 1994), although the relative contribution of freshwater diversion vs. a deficit in the annual precipitation is not clear (Baratta and Fennema abstr.). The combined effect was a dramatic rise in the salinity of Florida Bay (Robblee et al. abstr.; Fourqurean and Zieman 1992). This rise was recorded as a change in the stable isotopic signal deposited in *M. annularis* skeletons throughout the decade of the 1980s (Halley et al. 1994). In addition to a reduction in the total volume of freshwater entering the bay, water management practices may also have dampened the magnitude of seasonal variations in water flow into the bay.

Coral reefs monitored in the Florida Keys between 1984 and 1992 declined in both percentage of live coral cover (average of -4% per year) and in total number of scleractinian species (average of -2% per year) (Dustan and Halas 1987; Porter and Meier 1992). Reefs near oceanographic connections to Florida Bay lost coral cover and coral species number faster than reefs distant from passes into the bay,

while reefs farthest removed from the influence of the bay, such as reefs of the Biscayne National Park (Porter and Meier 1992) and the Dry Tortugas National Park (Jaap et al. abstr.), showed little or no decline. Coral reefs within Florida Bay, such as on Content Key (Fig. 1) also show coral loss (Jaap et al. 1998). Reefs near cuts through the keys are less well developed geomorphologically, presumably due to the adverse influence of Florida Bay water over geological time scales (Shinn et al. abstr.; Ginsburg and Shinn abstr.).

In an attempt to describe this complex series of land-sea linkages, we propose the hypothetical scenario depicted in Fig. 5 (Porter et al. abstr.). The purpose of the Florida Bay water hypothesis is not to suggest that we have the final explanation, but to provide a testable one. Without a descriptive hypothesis, it will be impossible to elucidate the underlying mechanisms of change occurring on Floridian coral reefs or to propose restoration measures. While salinity elevations per se are unlikely to reduce coral reef survival offshore, the salinity signal of Florida Bay water provides both a marker as to the origin of the water moving onto the reef, as well as a predictor of its position in the water column based on its density. Multiple stressors, including, but definitely not limited to salinity and temperature, act in combination to increase coral mortality and reduce coral recruitment to inundated reefs. Temperature and salinity were chosen for an investigation of multiple stressors not because they are the most critical factors affecting coral growth and survival in the Florida Keys, but because they were the most easily manipulated in the laboratory.

Lapointe et al. (1994) demonstrated the existence of nitrogen and phosphorus gradients distributed along an on-shore to offshore transect at Looe Key in the Lower Keys and onto coral reefs in southeastern Florida (Lapointe 1997). Such plumes increase water-column turbidity in offshore environments (Smith 1994). Although the precise origin of nutrients contained within these plumes is still debated (Powell et al. 1989; Lapointe and Clark 1992; Lapointe et al. 1990; Tomasko and Lapointe abstr.; Fourqurean et al. 1993; Zieman et al. 1989), these data establish the paramount importance of understanding the fine-scale origin and movement of nutrients between the keys and offshore coral reefs.

Therefore, two impacts of Florida Bay water have occurred in the recent past. First, during the hypersaline phase, warm, turbid, nutrient-rich bay water has come in contact with reefs, lowering oxygen and light levels. Second, with an increase in rainfall and the management practice of increased freshwater flow to the bay, plumes of water, turbid with algal blooms, exit the bay through the cuts and cross over the reef. These plumes are not necessarily hypersaline, and therefore may or may not come in direct contact with the reef surface, depending on the volume of the plume and water-column mixing depth. When they do, however, sediment, temperature, nutrient, and light stresses will occur simultaneously. Only a multiple stressor model will simulate their interactive effects.

Our theory couples the effects of freshwater management practices on land with the health of coral reefs in the bay and offshore. This hypothesis explicitly includes a landscape-level perspective. If this hypothesis proves to be correct, then multiple stressor models, such as those represented

Florida Bay Hypothesis

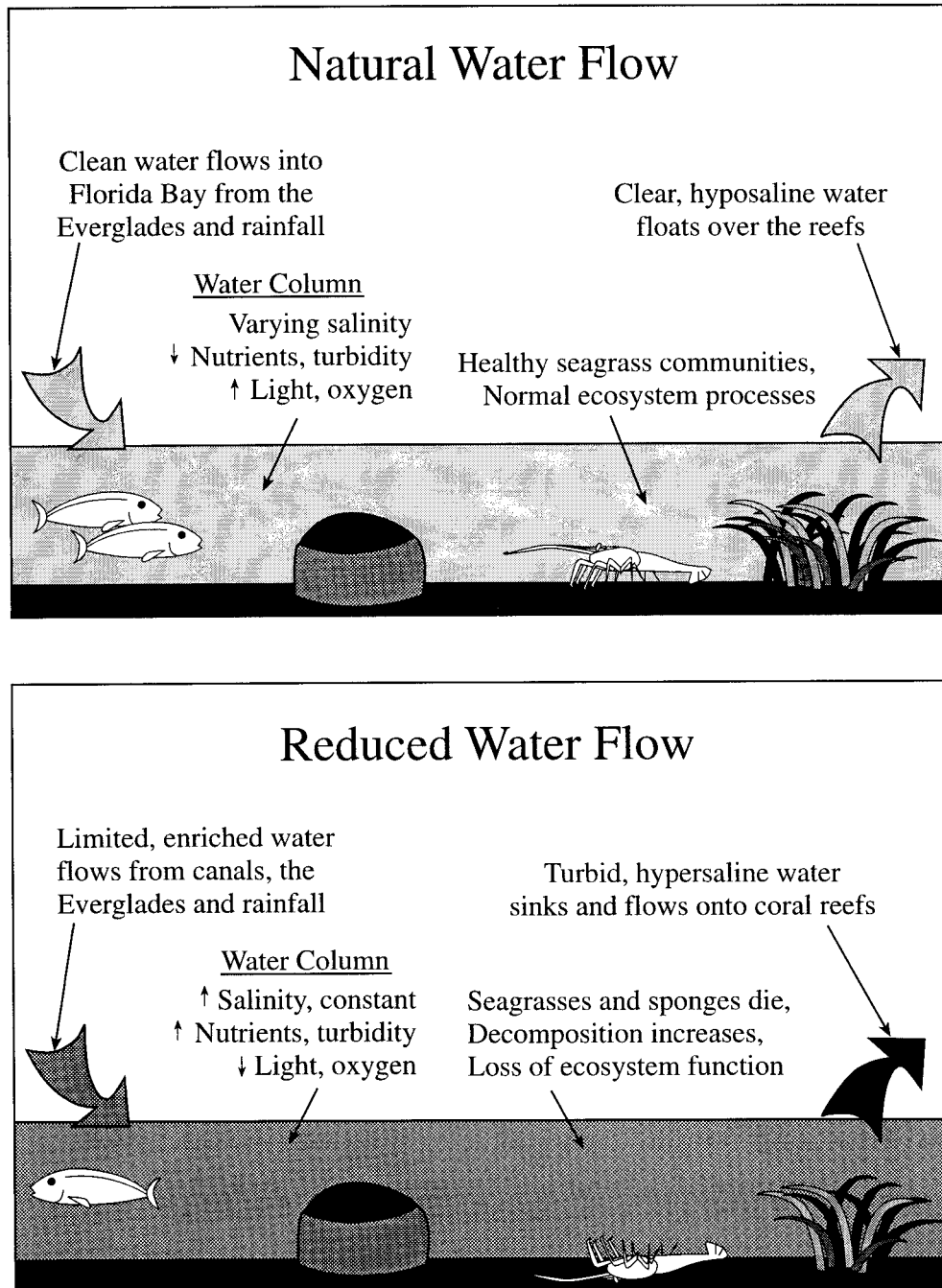


Fig. 5. The Florida Bay hypothesis provides a testable explanation for coral reef decline in Florida Bay and the Florida Keys. Under natural flow conditions (upper panel), clean, freshwater flows from the Everglades into the bay creating a water column with varying salinity, low nutrient concentrations, low turbidity, and high oxygen concentrations. Nutrient-poor hyposaline water exits the bay and floats out to sea without coming in contact with the reef surface. In contrast, under reduced flow of the hypersaline phase in the bay (lower panel), limited freshwater input creates a water column of constantly high salinity. Water entering Florida Bay may also have elevated nutrient concentrations and higher turbidity levels than is typical under the historical condition. Resuspension of sediments also has increased due to die-off of sediment-binding sea grasses. In this scenario, turbid, hypersaline water exits the bay and sinks onto coral reefs offshore. This water is too hot, too turbid, too briny, too nutrient rich, and too oxygen poor to promote optimal coral growth.

in Fig. 4, could be used to recommend water quality standards that must not be exceeded in managing coral reefs in the Florida Keys National Marine Sanctuary.

Conclusions

To test for the presence of multiple stressor interactions on coral physiology, we tested the metabolic effects of elevated temperature and salinity in a 2×2 additive vs. interactive stressor model. After exposure to elevated temperature and salinity, the interactive model was significantly better at explaining experimental results for net photosynthesis, respiration, and net $P:R$ ratio. For each of these responses, the interaction of the stressors was mitigative in nature, i.e., the combination of the two stressors was less stressful than the sum of the stressors acting independently. Furthermore, for both net photosynthesis and net $P:R$, the mitigative effect of the combination of stressors was of sufficient strength to offset the negative impact of elevated temperature. Corals exposed to elevated temperature and elevated salinity showed less stress than corals exposed to elevated temperature alone. Coral survivorship was similarly affected. Corals exposed to elevated temperature died between 18 and 30 h of exposure, whereas corals exposed to both elevated temperature and salinity died between 30 and 36 h of exposure.

The pattern of measured coral decline on some reefs in the Florida Keys and Florida Bay is consistent with an adverse influence of bay water. The decline of coral cover and species diversity cannot be attributed to a single factor, but a multiple stressor model can reasonably be invoked as a working explanatory hypothesis. Recent efforts to reduce salinity in the bay may have added additional stressors. As more nutrient-rich water is released into the bay or arrives via inputs from the Gulf of Mexico and Florida's west coast, stresses from high salinity and temperature may decline, but nutrient enrichment, shading due to algal blooms, and sedimentation may increase. Particularly these additional stressors, rather than simply temperature or salinity per se may be critical in understanding coral reef decline in the Florida Keys. Information on the duration and frequency of exposure to multiple stressors is required before a meaningful relationship between these stressors and ecosystem decline can be established. It will be especially important to conduct experiments examining the long-term effects of environmentally realistic low-level stresses on coral growth and survival. For future studies, we consider sediment loading and light penetration to be critical multiple stressors in need of investigation. As indicated by the results from this study, we expect complex and occasionally counterintuitive results from investigations of multiple stressors.

References

- ACHITUV, Y., AND Z. DUBINSKY. 1990. Carbon budgets in marine mutualistic associations between microalgae and cnidarians, p. 36–48. *In* Comparative physiology. V. 5. Animal nutrition and transport processes. 11th Conf. Eur. Soc. Comp. Physiol. Biochem.
- CLAUSEN, C. D., AND A. A. ROTH. 1975. The effects of temperature and temperature adaptation on calcification rate in the hermatypic coral *Pocillopora damicornis*. *Mar. Biol.* **33**: 93–100.
- COLES, S. L., AND P. L. JOKIEL. 1977. Effects of temperature on photosynthesis and respiration in hermatypic corals. *Mar. Biol.* **43**: 209–216.
- , AND ———. 1978. Synergistic effects of temperature, salinity, and light on the hermatypic coral *Montipora verrucosa*. *Mar. Biol.* **49**: 187–195.
- , AND ———. 1992. Effects of salinity on corals, p. 147–166. *In* D. W. Connell and D. W. Hawker [eds.], Pollution in tropical aquatic systems. CRC.
- , AND C. R. LEWIS. 1976. Thermal tolerance in tropical versus subtropical reef corals. *Pac. Sci.* **30**: 159–166.
- COOK, C. B., A. LOGAN, J. WARD, B. LUCKHURST, AND C. BERG. 1990. Elevated temperatures and bleaching on a high latitude coral reef: The 1988 Bermuda event, north Atlantic Ocean. *Coral Reefs* **9**: 45–49.
- DUSTAN, P., AND J. C. HALAS. 1987. Changes in the reef coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs* **16**: 91–106.
- EDMONDSON, C. H. 1928. The ecology of an Hawaiian coral reef. *Bull. Bernice P. Bishop Mus.* **45**: 1–54.
- FITT, W. K., H. J. SPERO, J. HALAS, M. W. WHITE, AND J. W. PORTER. 1993. Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 “bleaching event.” *Coral Reefs* **12**: 57–64.
- , AND M. E. WARNER. 1995. Bleaching patterns of four species of Caribbean reef corals. *Biol. Bull.* **189**: 298–307.
- FOURQUREAN, J. W., R. D. JONES, AND J. C. ZIEMAN. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: Inferences from spatial distributions. *Estuarine Coastal Shelf Sci.* **36**: 295–314.
- , AND J. C. ZIEMAN. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol. Oceanogr.* **37**: 162–171.
- GATES, R. D. 1990. Seawater temperature and sublethal coral bleaching in Jamaica West Indies. *Coral Reefs* **8**: 193–198.
- HALLEY, R. B., P. K. SWART, R. E. DODGE, AND J. H. HUDSON. 1994. Decade-scale trend in sea water salinity revealed through $\delta^{18}\text{O}$ analysis of *Montastrea annularis* annual growth bands. *Bull. Mar. Sci.* **54**: 670–678.
- HARRIOTT, V. J. 1983. Reproductive seasonality, settlement, and post-settlement mortality of *Pocillopora damicornis* (Linnaeus), at Lizard Island, Great Barrier Reef. *Coral Reefs* **2**: 151–157.
- HAYES, R. L., AND C. M. KING. 1995. Induction of 70-kD heat shock protein in scleractinian corals by elevated temperature: Significance for coral bleaching. *Mol. Mar. Biol. Biotechnol.* **4**: 36–42.
- HOEGH-GULDBERG, O., AND G. J. SMITH. 1989. The effect of sudden changes in temperature, light, and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J. Exp. Mar. Biol. Ecol.* **129**: 279–303.
- IGLESIAS-PRIETO, R., J. L. MATTA, W. A. ROBINS, AND R. K. TRENCH. 1992. Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. *Proc. Natl. Acad. Sci.* **89**: 10302–10305.
- JAAP, W. C., P. DUSTAN, J. W. PORTER, AND J. L. WHEATON. 1998. EPA water quality protection program: Coral reef and hard-bottom monitoring project. U.S. EPA, 1998 annual report, region 4.
- JOKIEL, P. L., AND S. L. COLES. 1977. Effects of temperature on the

- mortality and growth of Hawaiian reef corals. *Mar. Biol.* **43**: 201–208.
- , AND ———. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* **8**: 155–162.
- KNOWLTON, N., E. WEIL, L. A. WEIGHT, AND H. M. GUZMAN. 1992. Sibling species in the *Montastrea-annularis* coral bleaching and the coral climate record. *Science* **255**: 330–333.
- LAPOINTE, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnol. Oceanogr.* **42**: 1119–1131.
- , AND M. W. CLARK. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. *Estuaries* **15**: 465–476.
- , W. R. MATZIE, AND M. W. CLARK. 1994. Phosphorus inputs and eutrophication on the Florida reef tract, p. 106–112. *In* Global aspects of coral reefs: Health, hazards, and history. Proc. Colleg. Univ. Miami RSMS.
- , J. D. O'CONNELL, AND G. S. GARRETT. 1990. Nutrient couplings between on-site sewage disposal systems, groundwaters, and nearshore waters of the Florida Keys. *Biogeochemistry* **10**: 289–307.
- MGIVOR, C. C., J. A. LEY, AND R. D. BJORK. 1994. Changes in freshwater inflow from the Everglades to Florida Bay including effects on biota and biotic processes: A review, p. 117–146. *In* S. Davis and J. C. Ogden [eds.], Everglades: The ecosystem and its restoration. St. Lucie.
- MARCUS, J., AND A. THORHAUG. 1981. Pacific versus Atlantic responses of the subtropical hermatypic coral *Porites* spp. to temperature and salinity effects, p. 15–20. *In* Proc. 4th Int. Coral Reef Symp. V. 2.
- MAYER, A. G. 1914. The effects of temperature on tropical marine animals. Publ. Carnegie Inst. Wash. **183**: 1–24.
- MUSCATINE, L., J. W. PORTER, AND I. R. KAPLAN. 1989. Resource partitioning by reef corals as determined from stable isotope composition: 1. $\delta^{13}\text{C}$ of zooxanthellae and animal tissue versus depth. *Mar. Biol.* **100**: 185–193.
- MUTHIGA, N. A., AND A. M. SZMANT. 1987. The effects of salinity stress on the rate of aerobic respiration and photosynthesis in the hermatypic coral *Siderastrea siderea*. *Biol. Bull.* **173**: 539–550.
- OGDEN, J. C., AND OTHERS. 1994. A long-term interdisciplinary study of the Florida Keys seascape. *Bull. Mar. Sci.* **54**: 1059–1071.
- PATTERSON, M. R., K. P. SEBENS, AND R. R. OLSON. 1991. In situ measurements of flow effects on primary production and dark respiration in reef corals. *Limnol. Oceanogr.* **36**: 936–948.
- PITTS, P. A. 1994. An investigation of near-bottom flow patterns along and across Hawk Channel, Florida Keys. *Bull. Mar. Sci.* **54**: 610–620.
- PORTER, J. W., W. K. FITT, H. J. SPERO, C. S. ROGERS, AND M. W. WHITE. 1989. Bleaching in reef corals: Physiological and stable isotopic responses. *Proc. Natl. Acad. Sci.* **86**: 9342–9346.
- , AND O. W. MEIER. 1992. Quantification of loss and change in Floridian reef coral populations. *Am. Zool.* **32**: 625–640.
- , L. MUSCATINE, Z. DUBINSKY, AND P. FALKOWSKI. 1984. Primary production and photosynthesis in light- and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. *Proc. R. Soc. Lond. Ser. B* **222**: 161–180.
- POWELL, G. V. N., W. J. KENWORTHY, AND J. W. FOURQUREAN. 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull. Mar. Sci.* **44**: 324–340.
- ROWAN, R., AND D. A. POWERS. 1991. A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbiosis. *Science* **251**: 1348–1351.
- SMITH, N. P. 1994. Long-term Gulf to Atlantic transport through tidal channels in the Florida Keys. *Bull. Mar. Sci.* **54**: 602–609.
- SZMANT, A. M., AND N. J. GASSMAN. 1990. The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* **8**: 217–224.
- TILMANT, J. T. [ORGANIZER]. 1989. Symposium on Florida Bay, a subtropical lagoon. *Bull. Mar. Sci.* **44**(1).
- TRENCH, R. K., AND R. J. BLANK. 1987. *Symbiodinium microadriaticum* (Freudenthal), *Symbiodinium goreauii* (new species), *Symbiodinium kawagutii* (new species), and *Symbiodinium pilosum* (new species) gymnodinioid dinoflagellate symbionts of marine invertebrates. *J. Phycol.* **23**: 469–481.
- VAUGHAN, T. W. 1914. The corals of the Bahamas and South Florida. Carnegie Inst. Wash. Year Book **13**: 222–233.
- WARNER, M. E., AND W. K. FITT. 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef corals. *Plant Cell Environ.* **19**: 291–299.
- WELLS, J. W. 1932. Study of the reef corals of the Tortugas. Carnegie Inst. Wash. Year Book **31**: 290.
- ZIEMAN, J. C., J. W. FORQUREAN, AND R. L. IVERSON. 1989. Distribution, abundance, and productivity of seagrasses in Florida Bay. *Bull. Mar. Sci.* **44**: 292–311.