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Diversity and biomass dynamics of marine algae in Biosphere II's tropical reef macrocosm

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Abstract

Macrocosms can be used to study complex ecological processes in a small physical space, but the validity of the studies depends on how well the macrocosm simulates natural ecosystem functions. We measured the standing crop of macroalgae and nutrient levels over 4 years in the Biosphere II macrocosm tropical reef biome at Oracle, Arizona. Ten years after this system was closed to outside introductions, it still contained 35 species of macroalgae, within the range found on natural reefs. The macroalgae community was recognizable as a late-successional, coralline algal turf community similar to those found in the low-energy portions of inner tropical reefs. However, biomass values for the most abundant species were in a continual state of flux over the study, and no single species was dominant. Nutrient levels were also unexpectedly dynamic, with dissolved inorganic phosphorous, nitrate, and ammonium each varying by a factor of 10 over the study. The dynamic nature of biomass and nutrient cycles would make it difficult to use this macrocosm for controlled studies. On the other hand, the community dynamics in the Biosphere II ocean may shed light on processes controlling biodiversity and succession on natural reefs. The apparently chaotic swings in biomass and nutrient levels suggested that the paradox of the plankton, which explains how seemingly uniform aquatic environments can support a wide diversity of planktonic forms, may apply to reef macroalgae as well. The Biosphere II ocean biome demonstrates that a diverse macroalgal reef community can be restored relatively easily, supporting the feasibility of actively restoring damaged natural reefs. Macrocosms such as this could be used in manipulative experiments to study the effects of nutrient enrichment and herbivory on coral–algal phase shifts.

Keywords: Biosphere II; Coral reef restoration; Seaweed; Biodiversity; Succession; Intermediate disturbance; Paradox of the plankton; Chaos; Functional form hypothesis; Niche diversification

1. Introduction

Macrocosms are models of natural systems that can be used to study the performance of complex living systems in a small physical space. Macrocosms, as well as microcosms and mesocosms, are now widely used to study linked ecological processes and their pertur-

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bation by outside agents (Todd and Josephson, 1996). Examples of disturbances that have been studied in aquatic and wetland macrocosms include: effects of trampling on macroalgal communities (Milazzo et al., 2004); effects of storm runoff on sandy beach invertebrate communities (Lercari and Defeo, 2003); effects of nutrient enrichment on nitrate removal rates in wetlands (Bachand and Horne, 2000); effects of mowing on emergent wetland vegetation (DeSzalay et al., 1996); and effect of carbon dioxide enrichment on coral reefs (Langdon et al., 2003).

The validity of these studies depends on how closely the macrocosm reproduces the processes of interest in the natural ecosystem. However, untested assumptions are often built into these studies. As examples, macrocosm studies assume that ecosystem functioning is similar across the different spatial and temporal scales represented by the real system and the model system, and that an ecosystem isolated from its surroundings will retain its original properties over time. These conditions can be difficult to meet and verify. On the other hand, by operating outside the normal boundaries of a natural ecosystem, macrocosm studies have the potential to reveal unexpected properties of ecosystem performance.

In the present study, we measured macroalgae diversity and dynamics in a tropical reef environment at Biosphere II, a large-scale macrocosm facility with several different biomes (Zabel et al., 1999). The tropical reef biome consists of a shallow (up to 7 m deep) tank filled with ocean water and containing a variety of simulated habitat types including sandy bottom, rocky reef, and shoreline communities (Atkinson et al., 1999; Langdon et al., 2003). We measured the standing crop of macroalgae and nutrient levels in this system at 1- or 2-month intervals over 4 years, starting approximately 10 years after the facility was constructed. The results are interpreted in terms of the ability of this macrocosm to maintain algal diversity and stability over time. We tested the findings against the main hypotheses that have been used to explain biodiversity and succession on natural reefs: the functional form hypothesis (Littler and Littler, 1980); the intermediate disturbance hypothesis (Connell, 1978); the niche-diversification hypothesis (Knowlton and Jackson, 1994); and the paradox of the plankton (Hutchinson, 1961).

Considering that it was not subject to major external perturbations during the experiment, the Biosphere II tropical reef biome exhibited a remarkably dynamic rate of species turnover and nutrient variability over the study period. Although this is an artificial biome, the results provide perspective on the factors controlling algal populations in both natural and human-alerted reef systems.

2. Materials and methods

2.1. Description of the experimental system

Detailed descriptions of the Biosphere II ocean biome and the experimental manipulations that have been performed in it are found in Atkinson et al. (1999) and Langdon et al. (2003). The macrocosm was designed as a large, self-sustaining community of living coral reef organisms, resembling a Caribbean fringing reef and lagoon. The macrocosm has a volume of 2650 m^3 and a water surface area of 711 m^2. It is 19.1 m wide and 45.2 m long; depth grades from 0 to 7 m with an average depth of 3.1 m. A simulated reef flat, composed of limestone rocks, covers 55% of the bottom area, whereas a sand bottom covers the remaining 45% at the deep end of the tank. A wave machine propagates 10–20 cm height waves from the deep end to the shallow end, generating currents of 2–10 cm s^{-1} above the bottom. Mixing time in the tank was about 1 h.

Over this study water, temperature was held constant at 26.5 °C (within 0.2 °C) and salinity was 34.5 ppt. Water lost to evaporation was replaced by reverse osmosis water. The tank was illuminated by natural sunlight, which was attenuated by the glass top of Biosphere II and shading from other parts of the Biosphere II structure. Photosynthetically active radiation (PAR) ranged seasonally from 8 to 25 mol photons m^{-2} day^{-1} at the water surface, about 30–50% of outdoor values. Light was also attenuated by the water in the tank, and PAR at the 2.5 m depth was approximately 25% of full sunlight, or about 50% of PAR values found at that depth on typical tropical reefs. However, due to high dissolved organic nitrogen values from the initial addition of EDTA, only 5% of blue light penetrated to 5 m; and the water appeared clear but yellow in color. The original ocean mix contained 10% natural seawater and 90% municipal well water amended with Instant Ocean salts to achieve the target salinity. The mineral composition of the Biosphere II ocean compares well with

tropical reef water for the major cations and anions, but concentrations of trace elements (<1 mM) were an order of magnitude higher than natural. As shown in Section 3, nutrient levels were low, typical of oligotropic tropical reefs.

2.2. Biological characteristics

Marine organisms were first added to the Biosphere II ocean in 1990, and a few additional species were added in 1993. Macroalgae were added as encrusting and attached organisms on Caribbean "live rocks" (Atkinson et al., 1999). Plankton were introduced by the addition of 10% southern California seawater. Fish, crabs, lobsters, urchins, and sea cucumbers were also added (most of the macrofauna has disappeared). Species list were produced in 1992 and 1996 (Atkinson et al., 1999). In 1992, 31 species of macroalgae were recorded while 28 were recorded in 1996. However, 17 species recorded in 1996 were not reported in 1992. In 1996, 11 genera of green algae, 8 genera of red algae, 2 genera of brown algae, and some cyanophytes were recorded. In contrast to macroalage, phytoplankton were low in number and diversity. There were 25 genera of corals and two genera of sponges, but they covered only 3% of the benthos. There were 16 genera of fish, but only one species, a small yellow tangs (*Zebrasoma flavescens*), was present in significant numbers. Several dozen yellow tangs were observed feeding on filamentous and fleshy macroalgae throughout the study.

In 1999, the reef community was summarized as an algal-dominated coral reef flat, with about half the community metabolism values of natural reefs (due to light attenuation by the cover) (Atkinson et al., 1999). Despite some peculiarities, it was considered to be a recognizable coral reef community resembling high-lattitude, over-fished, shallow, coral reef lagoons. In 2001 (Falter et al., 2001) and 2003 (Langdon et al., 2003), the same basic biological characteristics were reported. At time scales >1 month, photosynthesis and respiration were reported to be almost perfectly in balance (Falter et al., 2001). Water column productivity is very low, and nearly all primary production is from the macroalgae community. The stocks of carbon in the biota averaged 0.003 mol C m^{-2} in the water column compared to 8–10 mol C m^{-2} in the macroalgae (Falter et al., 2001).

During the present experiment, the chemical composition of the ocean was slightly altered from November 8 to December 18, 2000, to simulate a doubling of atmospheric carbon dioxide levels (Langdon et al., 2003). To accomplish this, sodium bicarbonate, sodium carbonate, and hydrochloric acid were added to increase dissolved inorganic carbon from 1.96 mM (pH 8.02) to 2.12 mM (pH 7.82). The alteration had no discernable effect on species composition of the macrocosm, and the carbon enrichment did not stimulate gross community productivity, as primary productivity is nutrient-limited. Other than this planned experiment, there were no systematic interventions in the macrocosm operation during the study period.

2.3. Macroalgae sampling

Macroalgae were sampled 23 times between October 1999 and October 2003. Sampling was conducted monthly for the first 6 months then approximately every other month thereafter. The ocean surface was divided into 95 equal-sized grids, each approximately 8 m^2 (2 m × 4 m), by placing 10 lines with 4 m grid marks, 2 m apart along the length of the ocean. At each sampling date, wire rings with an area of 0.073 m^2 were randomly tossed into each of the 95 sample areas. The depth of each ring was recorded, and all the macroalgae within each ring was collected by a diver and placed in a plastic bag. Care was taken not to disturb the substrate during collection. This method did not collect all the encrusting algae on the limestone rocks, as they were difficult to remove. In the laboratory, algae in each bag were sorted into species, weighed wet, then placed in an oven at 40–45 °C until they reached constant dry weight. Data were recorded as the fresh weight and dry weight of macroalgae in each grid sorted by species.

A running species list was maintained of all species encountered in the rings. Voucher specimens were preserved either as pressed specimens on herbarium paper or preserved specimens in a formaldehyde–seawater solution. Plants were tentatively identified based on photographs in Littler et al. (1989). Voucher specimens were taken to the Smithsonian Institute, Washington, DC, in July 2002, where the curator, Dr. Mark Littler, corrected the identifications by reference to archived samples in the museum collection. Final identification of some of the species was also provided by Dr. Clinton Dawes, University of South Florida, Tampa.

2.4. Other data collection

The monitoring systems for measuring physical and chemical water quality parameters in the Biosphere II ocean are described in Atkinson et al. (1999). For the present analyses, we calculated mean monthly values of radiation, dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorous (DIP), nitrate, and ammonium to correlate with standing biomass estimates. We used outdoor values of radiation corrected for light attenuation (AZMET, University of Arizona, Tucson, AZ) for the correlation analyses, because attenuation of light by the structure and water column is a near-constant (we assumed 25% light penetration at 2.5 m). Nutrient concentrations were passed through a glass-fiber filter, frozen within 1 h, then analyzed on a Technicon II Autoanalyzer with standard Technicon methods (Atkinson et al., 1999). Values for individual nitrogen species for June 19, 2000 were approximately 10 times higher than on any other month, and added to greater than the value for total nitrogen—data for this date were eliminated from the analyses. Samples of the five most abundant species were analyzed for nitrogen and phosphorous by a commercial laboratory (IAS Labs, Tempe, AZ). Four samples of each species, collected on different occasions, were analyzed.

The Shannon–Weiner Index of diversity was calculated as:

$$H' = \sum_{t=1}^{S} p_i \ln p_i \quad (1)$$

where p_i is the proportion of the population size of each individual species to the total population size, and S is the number of species (Sterling and Wilsey, 2001). We used biomass values rather than number of individuals to calculate p_i.

3. Results

3.1. Species composition and N and P contents

Thirty-five species were encountered in the sample rings, of which 14 were green algae (Ochrophyta) (Table 1), 15 were red algae (Rhodophyta) (Table 2), and 6 were brown algae (Chrysophyta) (Table 3). A few macrophytic blue-green bacteria, noted in earlier studies, were present in these samples as well. We were not able to positively identify them. While the total number of algae was about the same as in 1992 and 1996, the species lists were different. The present lists contained 19 species not found in 1992 or 1996, while 32 species noted in 1992 or 1996 were not found in the present survey (Tables 1–3). From 1992 to 2002 the number of reported green algae genera decreased from 13 to 9 whereas the number of red algae genera increased from

Table 1
Species list for green macroalgae (Chlorophyta) in the Biosphere II ocean biome in 1992, 1996, and 2000–2002

	1992	1996	2002
Acetabularia calyculus		X	
Avrainvillea sp.	X	X	
Bryopsis plumosa	X	X	
Caulerpa mexicana	X	X	
Caulerpa serrulata			X
Chaetomorpha sp.			X
Cladocephalus luteofuscus	X		
Cladophora fracatii	X		
Cladophora fuliginosa	X		
Derbesia marina	X		
Derbesia vauchriaeformis	X		
Derbesia sp.		X	
Dictyosphaeria cavernosa		X	X
Dictyosphaeria ocellata			X
Enteromorpha sp.	X		X
Ernodesmis verticillata		X	X
Halimeda incrassata	X		X
Halimeda monile	X		
Halimeda oputntia	X		
Halimeda tuna			X
Penicillus capitatus	X	X	
Penicillus dueitosus	X	X	
Polyphysa polyphysoides		X	
Rhipocephalus divericata			X
Rhipocephalus phoenix	X		X
Udeota cyanthaformis	X		
Udeota spinulosa	X		
Udeota flabellum	X		
Valonia aegagropila			X
Valonia macrophysa	X		X
Valonia utricularis	X		X
Valonia sp.		X	
Ventricaria ventricosa		X	X
Total species	20	12	14
Total genera	13	11	9

Species present in a given survey are marked with X. 1993 and 1996 data are from Atkinson et al. (1999) and 2002 data are from the present study.

Table 2
Species list for red macroalgae (Rhodophyta) in the Biosphere II ocean biome in 1992, 1996, and 2000–2002

	1992	1996	2004
Acanthophora spicifera	X	X	X
Amphiroa fragilissima		X	X
Amphiroa rigida	X	X	X
Amphiroa sp.	X	X	
Botryocladia pyriformis			X
Callithamnion sp.	X	X	
Ceramium sp.	X		
Chondria dasyphylla			X
Coelothrix irregularus		X	
Daysia haillouviana	X	X	
Daysia harveyi	X	X	
Flahaultia sp.			X
Gracilaria tikvahiae			X
Gelidiopsis intricata			X
Haliptilon cubense			X
Halymenia duchassaingii		X	X
Herposiphonia secunda	X		
Jania adhaerens		X	X
Jania rubens	X		
Mesophyllum mesomorphum			X
Peyssonnelia sp.			X
Polysiphonia haranensis	X		
Polysiphonia subtillissima	X		
Rhodogorgon carriebowensis			X
Sporolithon sp.			X
Total species	11	10	15
Total genera	8	7	14

Species present in a given survey are marked with X. 1993 and 1996 data are from Atkinson et al. (1999) and 2002 data are from the present study.

Table 3
Species list for brown macroalgae (Ochrophyta) in the Biosphere II ocean biome in 1992, 1996, and 2000–2002

	1992	1996	2004
Coilodesme rigida			X
Dictyota cervicornis		X	X
Dictyota divercata		X	X
Dictyota linearis		X	
Dictyota mertensii			X
Dictyota pulchella			X
Ectocarpus sp.	X		
Lobophora variegata		X	
Padina sp.	X		X
Total species	2	4	6
Total genera	2	2	3

Species present in a given survey are marked with X. 1993 and 1996 data are from Atkinson et al. (1999) and 2002 data are from the present study.

Table 4
Total nitrogen and total phosphorous in the five species making up most of the biomass in the Biosphere II ocean biome

Species	Biomass N ($mg\,kg^{-1}$)	Biomass P ($mg\,kg^{-1}$)
Jania adhaerens	5000 a	69 a
Amphiroa fragilissima	4100 a	66 a
Haliptilon cubense	4300 a	128 a
Chondria dasyphylla	18000 b	381 b
Gelidiopsis intricata	13700 b	385 b
S.E.M.	1100	33
F	15.8	7.6
P	0.000	0.001

Four samples of each species were analyzed, and results were analyzed and subjected to one-way ANOVA with species as the categorical variable. Values within a column followed by different letters (a and b) are different at $P < 0.05$ by the Least Significance Difference test. The first three species are coralline red algae, while the last two are fleshy red algae.

8 to 14, and brown algae genera increased from 2 to 3. A plot of log of biomass of each species (Fig. 1) shows a break after the first five species. The three most abundant species were articulated, coralline (calcified) algae (Corallina): *Haliptilon cubense*, *Amphiroa fagilissima*, and *Jania adhaerans*. The other two were fleshy/foliose species from the Ceraminales (*Chondria dasyphylla*) and Gigartinales (*Gelidiopsis intricata*). During the course of the study, these five species accounted for >95% of total biomass. Although red algae made up most of the algal biomass, nearly as many green algae as red algae species were present.

The Shannon–Weiner Index of diversity was calculated for each monthly survey (Sterling and Wilsey, 2001), and the mean value was 0.62. The total number of species encountered was high, but the biomass distribution was skewed towards a few primary species. Nitrogen and phosphorous levels were higher in the fleshy/foliose species than in the coralline species, as expected; because much of the biomass of the calcified forms consisted of calcium carbonate skeleton (Table 4).

3.2. Zonation of algal species

Unlike the phytoplankton populations of the studies by Hutchinson that led to the concept of the paradox of the plankton (Hutchinson, 1961), the Bioshpere II macrophyte populations were not uniformly

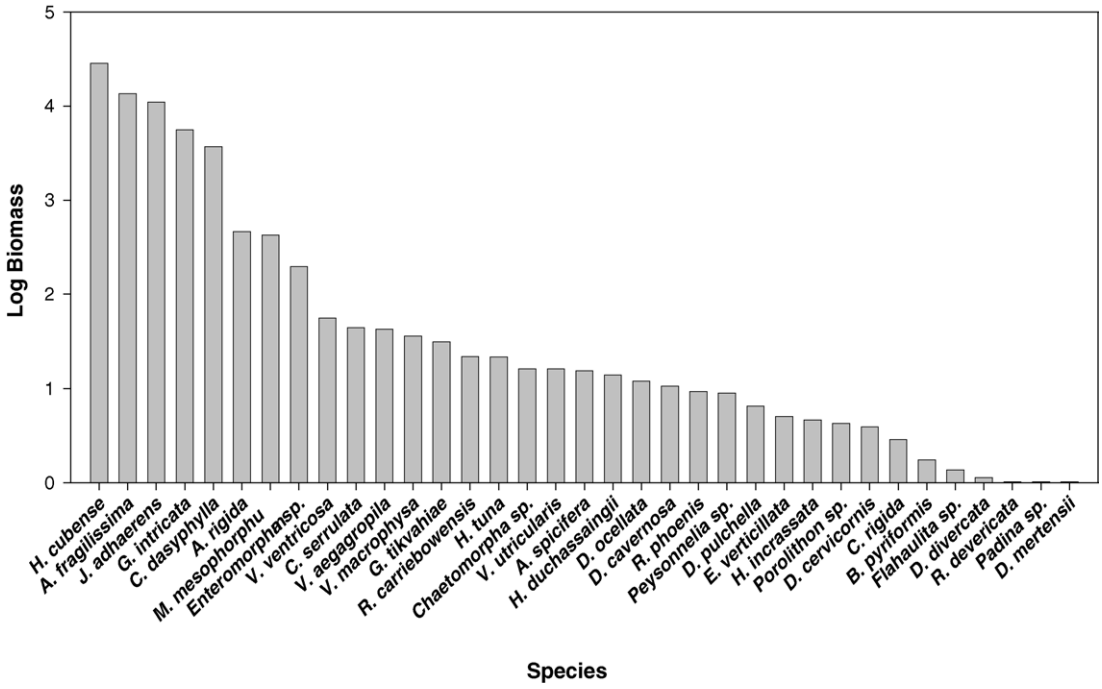

Fig. 1. Log of mean biomass for each algal species in the Biosphere II ocean biome over the study. See Tables 1–3 for species lists with genus spelled out.

distributed. The original design of the macrocosm included four distinct zones: a rocky intertidal zone, a reef slope, deep-water area with sand substratum, and a deep rocky area. It was clear during the first year of the study that there were significant differences in algal biomass among the zones (Kruskall–Wallis statistic = 205.1, $P < 0.001$). Fewer species were found in the sandy habitat, and algal populations in this area were not very dynamic. The majority of the species occurred only on hard substrate as would be expected. Some algae were clearly distributed according to depth, even though they occupied the same substrate type (limestone rock) (Fig. 2). While total algal biomass was distributed fairly evenly across depths (Fig. 2a), the green algae were most abundant in the shallow areas, especially those that were not accessible to herbivorous fishes (Fig. 2b). During the first year, the two dominant red algae were *H. cubense* and *Amphiroa fragillissima*, both of which were found at all depths. However, *A. fragillissima* clearly dominated at depths less than 4 m (Fig. 2c), while *H. cubense* dominated at depths greater than 4 m (Fig. 2d).

3.3. Algal biomass over time

Harvest weights of total algae and of the top five species are shown in Fig. 3. Total biomass (Fig. 3a) varied from 193 to 745 g m^{-2} over the study (mean = 431 g m^{-2}, S.E.M. = 31). Regression analysis showed there was no net increase or decrease in total biomass over the study ($r^2 = 0.017$, $P = 0.51$). However, differences among sample dates were significant ($F = 13$, $P < 0.001$). The biomass curve had peaks in July and August and low points in winter each year of the study. From September 2002 to June 2003, a peak biomass gain of 8 g m^{-2} day^{-1} was recorded. Peak decomposition or removal rates were nearly as rapid.

No one of the top five species was dominant over the entire study. To the contrary, each exhibited different trends (Fig. 3b–f). *H. cubense* was abundant throughout most of the study, with peaks of biomass in May or June of each year. *A. fragelissima* was also abundant throughout the study but at lower levels than *H. cubense*; it had peaks of biomass occurring March to August each year. On the other hand, *J. adhaer-*

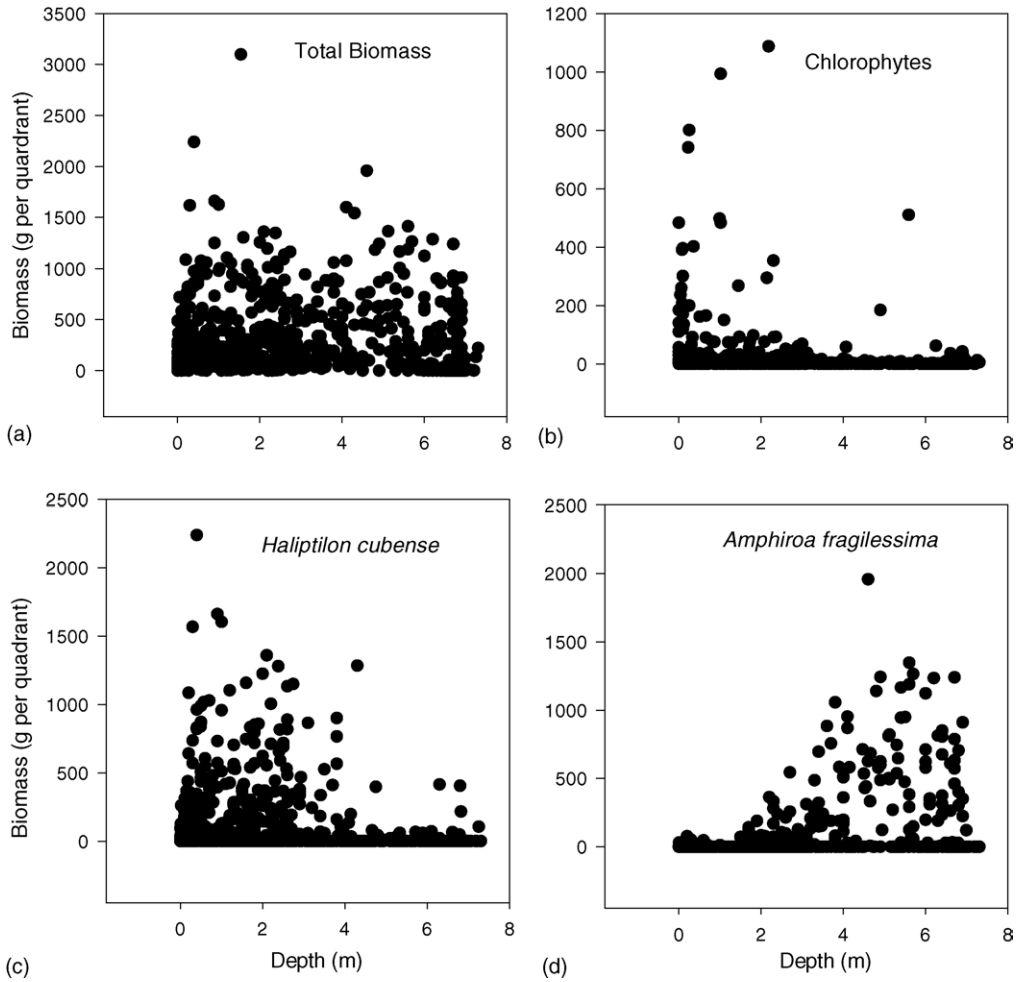

Fig. 2. Distribution of biomass by depth over 10 consecutive sampling events in 2000 in the Biosphere II ocean, showing: (a) total biomass; (b) all green algae; (c) *Haliptolon cubense*; and (d) *Amphiroa fragilissima*. *Y*-axes have different scales.

ans showed a significant net increase over the study ($r^2 = 0.66$, $P < 0.001$); it was scarcely present at the start but was the dominant species by the last harvest. *C. dasyphylla* showed an opposite trend, declining significantly over the study ($r^2 = 0.67$, $P < 0.001$). *G. intricata* decreased slightly over the study ($r^2 = 0.22$, $P < 0.05$).

3.4. Correlation of algal biomass with radiation and nutrient levels

Radiation and nutrient levels over the study are in Fig. 4. Radiation (Fig. 4a) followed a regular seasonal pattern, as expected. Nutrient levels were dynamic, with dissolved inorganic phosphorous (Fig. 4b), ammonium (Fig. 4c), and nitrate (Fig. 4d) each varying by an order of magnitude over the study. Overall, however, mean nutrient levels were low, with nitrate + ammonium at about 1 μM, and dissolved inorganic phosphorous at 0.06 μM.

A correlation matrix was calculated between radiation, nutrients, and total algal biomass (Table 5). On natural reefs, algal biomass is more closely related to the previous month's environmental factors than to the current month's (the antecedent event hypothesis) (Doty, 1971; Glenn and Doty, 1992), so we tested both concurrent environmental factors and 1-month

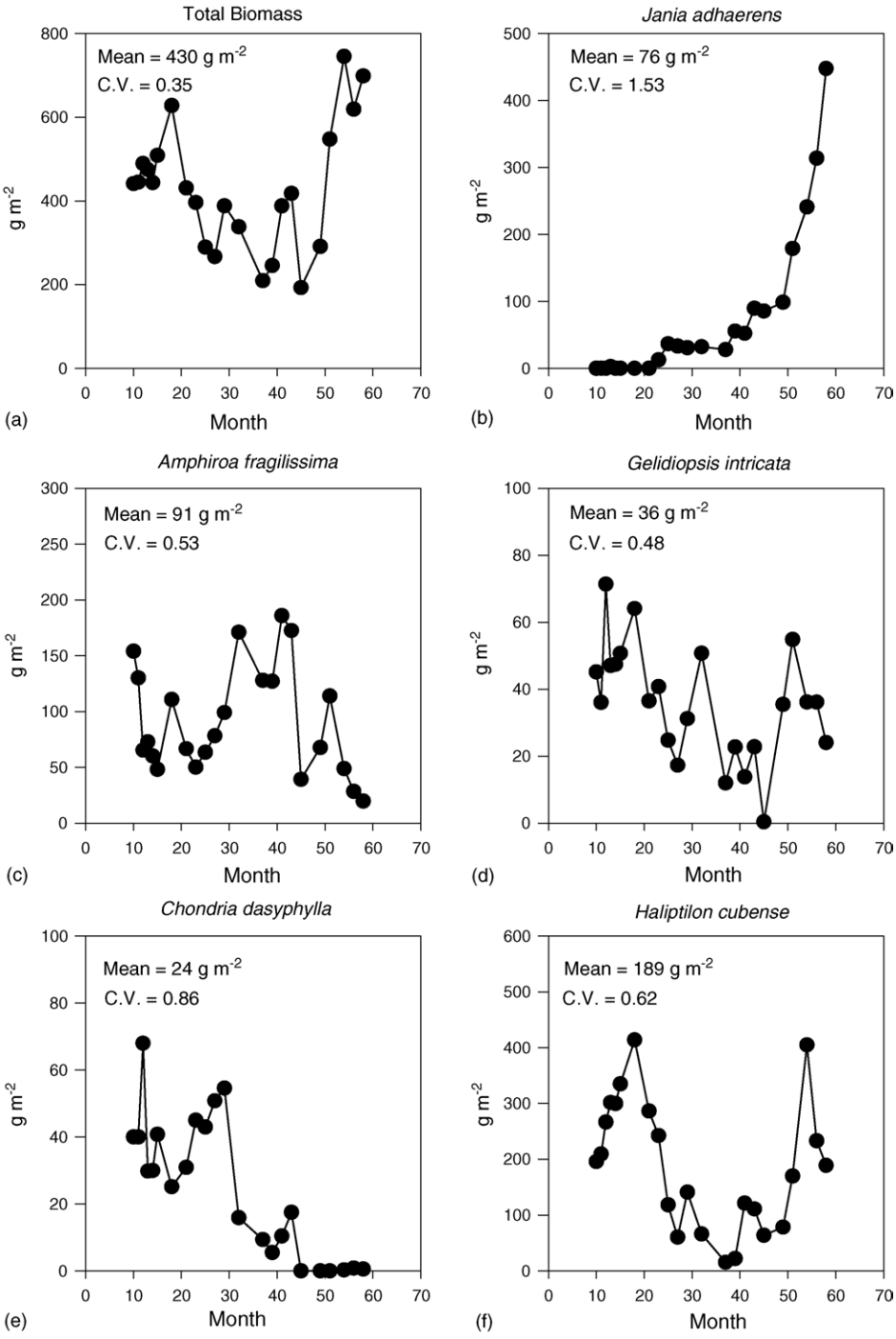

Fig. 3. Biomass of the all species combined (a) and the top five individual species (b–f) at different harvest dates in the Biosphere II ocean macrocosm. Month 1 was January 1999. Harvests were from October 1999 to October 2002. *Y*-axes have different scales. C.V., coefficient of variation.

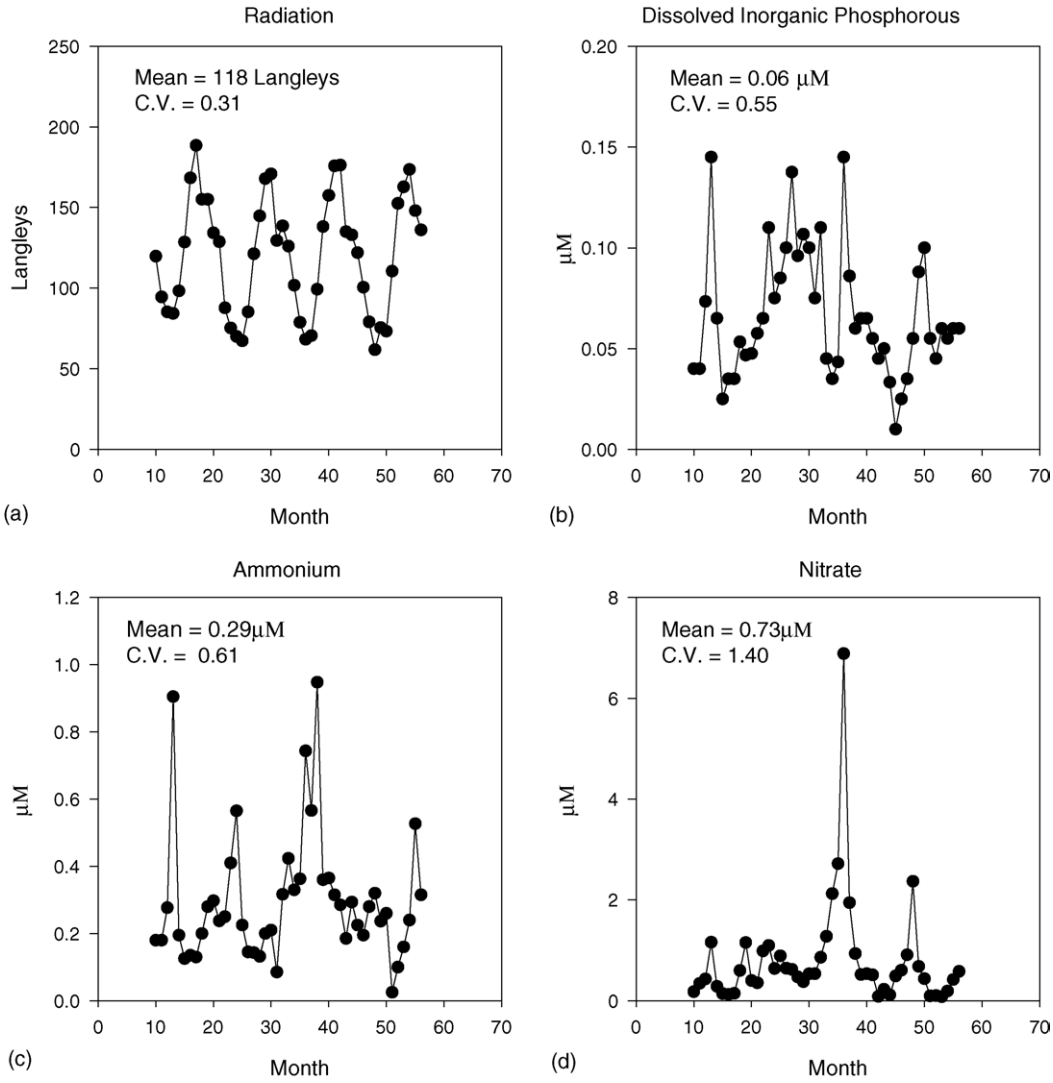

Fig. 4. Radiation (a) and nutrient levels (b–d) in the Biosphere II ocean macrocosm. Month 1 was January 1999.

Table 5
Correlation matrix between the algal standing crop in the Biosphere II ocean biome and environmental variables

	Biomass1	Biomass2	Rad	NO_3	NH_4	DIP
Biomass1	1.00	−0.27	0.31	-0.49^{*}	−0.17	0.34
Biomass2		1.00	0.44^{*}	-0.44^{*}	−0.23	−0.34
Rad			1.00	-0.47^{**}	-0.35^{*}	−0.28
NO_3				1.00	0.51^{**}	0.39^{**}
NH_4					1.00	0.34^{**}
DIP						1.00

Biomass1 is the standing crop of algae correlated with the concurrent month's environmental variables. Biomass2 is the standing crop correlated with the antecedent month's environmental variables. Rad, radiation; DIP, dissolved inorganic phosphorous. Asterisks denote significant levels at $^{*}P < 0.05$ or $^{**}P < 0.01$.

antecedent values as correlates with biomass. Biomass was significantly ($P < 0.05$) correlated with antecedent radiation. On the other hand, nitrate levels were negatively correlated with biomass. The ratio of N in the water column to N in biomass was 1:10.6, whereas the ratio for P was 1:2.2. As biomass increased, the ratio of water column to biomass N and P decreased, as these elements became depleted from the water and incorporated into biomass (Fig. 5).

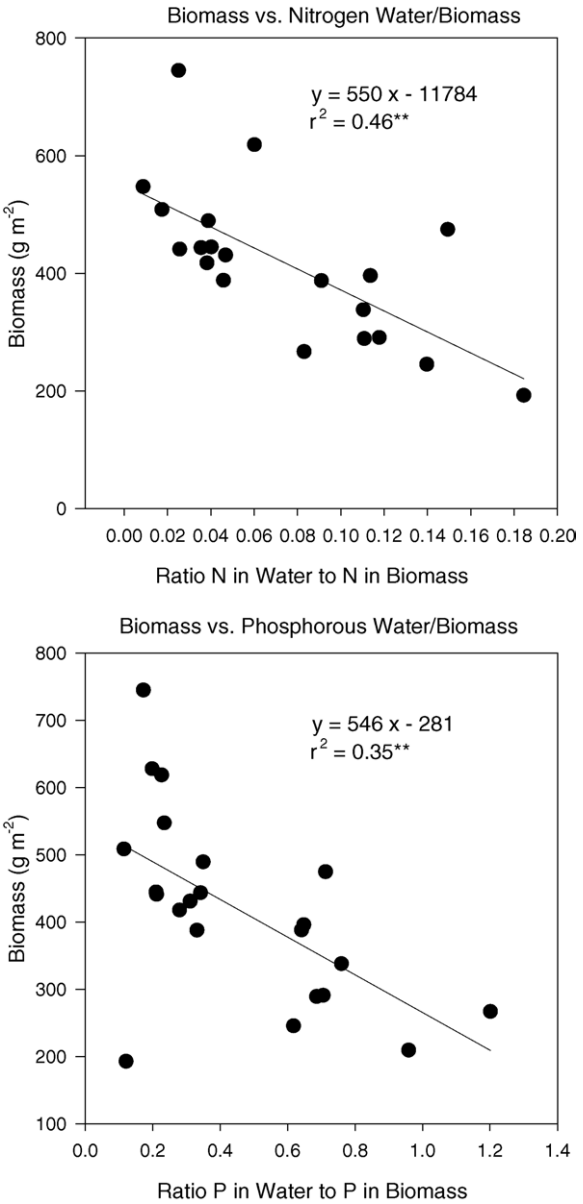

Fig. 5. Relationship between nitrogen and phosphorous in algal biomass and available nitrogen and phosphorous in the water column in the Biosphere II ocean macrocosm. Available phosphorous in the water column was total dissolved inorganic phosphorous; available nitrogen was the sum of nitrate and ammonium.

None of the five individual species tested showed significant correlations with either the current month's or the previous month's radiation or nutrient values ($P > 0.05$). However, there was a significant positive correlation between *G. intricata* and *H. cubense* biomass levels over time ($r = 0.65$, $P < 0.01$) and a significant negative correlation between *C. dasyphylla* and *J. adhaerans* ($r = -0.62$, $P < 0.01$).

4. Discussion

4.1. Relation of the Biosphere II ocean macrocosm to natural reef environments

The Biosphere II ocean macrocosm was intended to model a tropical coral reef environment (Atkinson et al., 1999), and it has been used to draw conclusions about community dynamics and carbon fluxes on natural reefs (Langdon et al., 2000, 2003; Broecker et al., 2001). However, there are many different types of natural coral reef ecosystems. The Biosphere II ocean biome has developed into a calcareous algal community dominated by small articulated coralline red and siphonous green algae (Kelaher et al., 2003; Smith and Marsh, 1973). In natural reefs, these communities are found in the inner, low-energy part of the reef. At 2–10 cm s^{-1} (Atkinson et al., 1999), water motion may be too low to support to support large, fleshy canopy seaweeds, such as *Sargassum* spp. that dominate shallow areas of many tropical reefs (Carpenter and Williams, 1993; Glenn and Doty, 1992; Larned and Atkinson, 1997). The reef has maintained a high diversity of corals (25 genera) over time (Atkinson et al., 1999); but they cover only 3% of the benthos; and their growth might also be limited by the low water motion of the Biosphere II ocean (Rex et al., 1995).

The mean standing density of algae (431 g m^{-2}) is about half the value reported for algal-dominated reef flats in other studies (e.g., Doty, 1971; Glenn et al., 1992). Similarly, Atkinson et al. (1999) and Langdon et al. (2003) reported community metabolism rates of about half the values reported for natural algal reefs.

Light levels, which are less than half of ambient values, as well as water motion, undoubtedly set an upper limit on algal productivity and the size of the standing crop in the Biosphere II ocean biome (Atkinson, 1999; Langdon et al., 2003). Mean nutrient levels were also lower than on many tropical reefs (Glenn et al., 1990; Larned and Atkinson, 1997).

Functionally, the Biosphere II ocean differs from natural reefs in two important respects. First, it is a closed system, with no possibility for recruitment of new species or replenishment of nutrients from outside the system. Second, it lacks the types of intermediate disturbances (high surf, storms, hurricanes) that are thought to drive the succession process on natural reefs (Connell, 1978). These characteristics might limit the usefulness of this macrocosm in simulating natural reef processes. However, as discussed in the following sections, they allow us to test the importance of outside recruitment, nutrient turnover, and intermediate disturbances, in controlling species diversity, succession processes, and biomass dynamics of macroalgae reefs.

4.2. *Species diversity and succession processes*

Natural reef communities are characterized by high species diversity (Littler and Littler, 1980; Phillips, 2001; Santelices, 1990). Typical reef surveys conducted by rambling sampling methods produce species checklists of 25–50 species of macroalgae per site (e.g., Doty, 1971; Smith and Marsh, 1973; Smith, 1981; Glenn et al., 1990; Neto, 2000; Milazzo et al., 2004), although the species list increases as the survey area increases. For example, 75 species were reported over four sites in an upwelling current off the coast of Brazil (DeGuimaraens and Coutinho, 1996), while along the south coast of Australia, over 700 species have been recorded (Phillips, 2001). The Biosphere II ocean biome is very small compared to a natural reef environment. Hence, low species diversity could reasonably be expected. However, species lists in 1992, 1996, and 2004 all showed 28–35 species. According to the Shannon–Weiner Index, this macrocosm is about average in species richness compared to other ecosystems (mean = 31 species for a set of 486 literature studies), but is low in terms of species evenness, since it is dominated by just a few species of coralline red algae in terms of biomass (Sterling and Wilsey, 2001).

About half the number of species recorded in 1996 and 2002 were new species, not noted in the 1992 survey. In fact, the top biomass species in the present study, *H. cubense*, was not noted in earlier surveys. Since there were presumably no new introductions after the biome was closed, the appearance of new species on the checklist indicates that not all of the species present have yet been documented. It also suggests that the abundance of individual species flucuates over time. Although the species list was dynamic, the Biosphere II ocean biome was reported to be dominated by articulated coralline red seaweeds in 1992 and 1996 (Atkinson et al., 1999), as well as in the present survey.

Seaweed spores are normally short-lived (Santelices, 1990), and the species in Tables 1–3 are not considered to have dormant or resting life stages (Graham and Wilcox, 2000). Hence, it is remarkable that this macrocosm has retained such capacity for diversity over time. This study shows that at least on a time scale of two decades, continual recruitment of new propagules (propagule pressure) (Occhipinti-Ambrogi and Savini, 2003) from outside the immediate reef area, as occurs continuously on natural reefs (Santelices, 1990), is not necessary to maintain high species diversity in a model reef system.

According to the niche-diversification hypothesis (Gage, 1996), high species diversity can be explained by the existence of numerous discrete microhabitats, allowing many individual species to co-exist in a small area, as on a coral reef (Knowlton and Jackson, 1994). This hypothesis was supported by the Biosphere II data, which showed that nearly all the species diversity was observed on the limestone rocks. These provided numerous sites for attachment and growth of algal spores and fragments, and provided many separate microhabitats with respect to light and water motion, based on the orientation of the rock on the reef. By contrast, more uniform environments, such as the tank wall and the sand bottom, supported low biodiversity. Analysis of the spatial distribution of the most abundant species showed that their habitats were differentiated by depth as well as substrate type.

According to the functional form model, macroalgae go through distinct successional stages on tropical reefs (Littler and Littler, 1980). Littler and Littler (1980) divided macroalgae into two broad classes based on survival strategies: opportunistic forms and late-successional forms. Opportunistic

forms tend to be rapid colonizers on newly cleared surfaces, with rapid growth rates but high susceptibility to grazing due to high caloric content. Late-successional forms tend to dominate more stable (less stressed) reef environments. They tend to be slow growing, often with complex life cycles, and with much structural tissue, low palatability to herbivores, and low caloric value.

This model predicts that over time reefs will tend to be dominated by late-successional forms, especially when grazed by herbivores, but in actuality, natural reefs simultaneously support both opportunistic and late-successional species. This has been explained by the intermediate disturbance hypothesis (Connell, 1978), which states that a reef ecosystem is prevented from reaching a climax state due to disturbance factors, such as tropical storms that occur at intermediate frequencies. These storms disrupt the existing reef communities, for example, by turning over reef rubble, creating new areas to be colonized by early successional species. At any given time, according to this hypothesis, a typical reef is a patchwork of habitats at different stages of succession, reflecting the past history of disturbances. Hence, all successional stages, from pioneer to climax species, can be present on the reef at the same time.

Biosphere II lacked outside disturbances, hence the intermediate disturbance hypothesis could not explain the maintenance of diversity and biomass dynamics in this macrocosm. However, greater than 90% of the algal biomass was contributed by calcified, coralline red seaweeds that typify the late-successional stage on natural reefs (Littler and Littler, 1980). Fleshy and foliose forms were reduced to minor components of the overall flora. The population structure was undoubtedly influenced by the yellow tang, which feed on fleshy and filamentous algae but not on coralline red algae (Wylie and Paul, 1988). Hence, the prediction of functional form hypothesis with respect to herbivory was supported.

4.3. Biomass and nutrient dynamics

While the Biosphere II ocean has stabilized as a coralline-red dominated system at the community level, the top five species were remarkably dynamic in terms of biomass turnover during the study. Each species, as well as total biomass, exhibited several peaks and valleys during the study; and biomass was only moderately correlated with radiation, the only environmental factor with a significant, positive relationship with biomass. Over just 44 months, and without a major external disturbance, *Jania adhaerens* went from very low levels to become the dominant species; while *Amphiroa fragilissima* made up 35% of total algal biomass at the beginning of the study but only 3% of total biomass at the end. Although not shown here, species of green algae and brown algae underwent similar fluctuations in abundance over the study.

Primary productivity was also dynamic, judging by the changes in standing biomass over time. At any given time, biomass could change at a rate as high as $8\,g\,m^{-2}\,day^{-1}$. This variability in primary production was not recognized in earlier community metabolism studies in this macrocosm, which were conducted over smaller time scales (Atkinson et al., 1999; Falter et al., 2001; Langdon et al., 2003).

Nutrient levels also showed variability over the study. Nitrate, ammonium, and inorganic phosphorous each had low base concentrations but were punctuated by spikes of high concentration that quickly decayed back to the baseline values. Atkinson et al. (1999) reported similar patterns in nutrient concentration, hence these fluctuations appear to be a characteristic feature of this macrocosm. By contrast, nutrient concentrations on natural algal reefs tend to be more uniform (e.g., Belliveau and Paul, 2002; Doty, 1971; Glenn et al., 1990; Larned and Atkinson, 1997), although they can exhibit some spatial and temporal patchiness. Mean values of N and P were two to three times lower than levels required to support high productivity of macroalgae on natural tropical reefs (Glenn et al., 1999; Larned and Atkinson, 1997). Hence, for most of the study the ocean was presumably nutrient-limited.

4.4. Paradox of the plankton applied to the Biosphere II ocean biome

The explanation for the fluctuating behavior of both algal biomass and nutrient levels may be found in the closed nature of the Biosphere II ocean. At any given time, the ratio of nitrogen in the water column to nitrogen in biomass is about 1:10 while the ratio for phosphorous is 1:2. Hence, production of new algal biomass requires the death and decomposition of existing biomass to release nutrients back to the water col-

umn. This leads to an oscillating system, with biomass inversely correlated with available nitrate in the water column. Biomass and nutrients are therefore in a constant state of flux. The decomposition of algal biomass to release inorganic nutrients presumably takes place in the sediments as well as the water column (Larned and Atkinson, 1997), but this process was not studied. Nitrogen appeared to the limiting nutrient for most of the study based on ratio of nitrogen and phosphorous in biomass and in the water column.

The paradox of the plankton (Hutchinson, 1961) drew attention to the high diversity of phytoplankton and wide population swings that occur in seemingly uniform aquatic environments, which has been interpreted as evidence that the plankton never achieve an equilibrium state because they are intrinsically chaotic systems (Huisman and Weissing, 1999). Hutchinson suggested that internal as well as external factors generated permanent non-equilibrium conditions, which keep algal populations in a continuous state of flux. As Scheffer et al. (2003) show, just five species competing for limiting resources in a uniform environment will generate chaotic fluctuations in population densities that persist over time. Chaos is an especially likely outcome if two or more oscillating components, such as predator–prey or nutrient depletion cycles, are part of the system (Scheffer et al., 2003). Hence, the paradox of the plankton appears to be a possible explanation for the fluctuating populations of the dominant species in the Biosphere II ocean.

It is not known if there is a natural analogue to this form of nutrient cycling on algal reefs. Presumably there is a more or less rapid exchange of water across a reef flat to replenish nutrients at the seaward edge of the reef, but it is conceivable that local depletions and enhancements of nutrients levels might control productivity in the inner reef. Glenn et al. (1999) found that the growth of *Gracilaria parvispora* thalli was strongly correlated ($r = 0.91$) with ammonia levels, which varied by a factor of 20 (0.2–4.0 μM at six sites on the inner portion of the fringing coral reef on the south coast of Molokai, Hawaii. Scheffer et al. (2003) suggested that the paradox of the plankton might apply to coral reef organisms, but this has gone unrecognized due to the time scale needed to document oscillations in population levels. They also pointed out that plankton communities can behave chaotically at the species level but exhibit stability at higher aggregation levels (Scheffer et al., 2003). This was true of the macroalgae in Biosphere II, which were dominated by articulated coralline red algae from 1992 to 2002 even though the dominant species varied over time. Furthermore, total biomass was correlated with radiation and nitrate levels, even though the biomass of individual species appeared to vary chaotically over time.

4.5. Applications to reef restoration efforts and creation of artificial reefs

Coral reefs are under increasing stress around the world (Bellwood et al., 2004; Jaap, 2000), but there is considerable debate about the relative importance of different stressors and how to effectively manage and restore coral reef ecosystems (Pandolfi et al., 2005). Many coral reefs are damaged by ship groundings, dredging, and other physical disturbances (Yap, 2003). These can sometimes be repaired by artificially reconstructing the reef, by providing substrates on which coral and algae can grow, and by planting “live rocks” or nursery-grown coral nubbins from other portions of the reef (Yap, 2003; Rinkevich, 2005), as was done in constructing the Biosphere II reef biome (Zabel et al., 1999). The Biosphere II experience shows that macrocosm reefs, even when closed to outside introductions, are remarkably robust in maintaining species diversity of both macroalgae and corals (Atikinson et al., 1999) over time. In this study, the macroalgae formed a self-organizing community within the reef system, that effectively recycled nutrients and maintained a diverse species composition over a period of 20 years. The results suggest that damage on natural reefs should be reversible through active restoration efforts.

Many coral reefs are also damaged by an overgrowth of macroalgae at the expense of corals, called a coral–algal phase shift (McManus and Polsenberg, 2004). A phase shift can be induced either by nutrient enrichment, which stimulates macroalgae growth (McCook, 1999; Diaz-Pulido and McCook, 2005), or reduction of herbivory by over-fishing, which allows filamentous, fleshy, and foliose macroalgae to proliferate and smother corals (McClanahan, 1997; McManus et al., 2000; Edmunds and Carpenter, 2001). The relative importance of these factors in influencing community structure, and the reversibility of coral–algal shifts under different management scenarios, are poorly understood. McManus and Polsenberg (2004) con-

cluded that there is an urgent need for studies that quantify and simulate cause and effects aspects of the phase shifts, to aid management decisions. The success of the Biosphere II ocean biome in maintaining a functioning reef community over time suggests that nutrient and herbivory levels could be deliberately manipulated in macrocosm studies to better understand and manage coral–algal phase shifts. Temperatures could also be manipulated to study the potential effects of global warming on corals and macroalage (Bellwood et al., 2004). Smaller, replicated mesocosms would be better suited to experimental manipulation than the single, large ocean macrocosm at Biosphere II.

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