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The Biosphere 2 coral reef biome

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Abstract

The Biosphere 2 coral reef biome is a large tank of living coral reef organisms (water volume of 2650 m^3, water surface area of 711 m^2 and 590 m^2 of reef benthos). The water of the biome is characteristically very low in dissolved nutrients and phytoplankton. The present community of organisms is largely comprised of macroalgae, including 11 genera of green algae, eight genera of red algae, two genera of brown algae, and some blue-green algae. There are 25 genera of coral and two genera of sponges, but they do not dominate the benthos. Fish comprise 16 genera, with seven genera of echinoids and three genera of crustaceans. The coral reef biome water is presently monitored continuously for temperature, salinity, light, O$_2$, and pCO$_2$, and monitored daily to weekly for alkalinity, ΣCO$_2$, pH, nutrients and δ^{13}C$_{DIC}$ and δ^{18}O$_{water}$ values. There are a number of filtration devices, pumps and aerators which have been used in the past to manipulate water movement and composition, but at present the community has come to steady-state without this machinery. Diel changes in O$_2$ and CO$_2$ allow measurements of community metabolism under different experimental conditions of water chemistry, water motion, seasonal light changes, and temperature. Typical values for community metabolic parameters under steady state condi-

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tions are: gross production (P), ~ 290 mmol C m^{-2} d^{-1}, respiration (R), ~ 270 mmol C m^{-2} d^{-1}, P/R, ~ 1.1 and community calcification, ~ 23 mmol $CaCO_3$ m^{-2} d^{-1}, or only 8% of gross production. Calcification rate has been altered, 0–140 mmol $CaCO_3$ m^{-2} d^{-1}, and is positively correlated to saturation state or CO_3^{-2} concentration. The community metabolism values are about half of a natural tropical algal/coral reef flat, but typical of high latitude, shallow, coral reef lagoonal environments. Even though there are some peculiar characteristics of the Biosphere coral reef, the coral reef biome functions as a recognizable coral reef community. The Biosphere 2 coral reef system offers an excellent opportunity to test questions of how environmental factors influence processes at community and organismal scales. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Biosphere 2; Coral reef biome; Mesocosm research

1. Introduction

Biosphere 2, located 50 km north of Tucson, Arizona, at the northern base of the Catalina mountains (32°34’N; 110°51’W; elevation 1200 m), is an enclosed group of synthetic ecosystems, featuring five major biomes, a tropical rain forest (Leigh et al., 1999), a savannah, a desert, a mangrove (Finn, 1996), and a coral reef (for a review see Peterson et al., 1992). Biosphere 2 was originally operated as a single enclosed system (Nelson and Allen, 1999). When the complex became an institute of Columbia University in 1996, the facility was subdivided into different biomes to facilitate specialized research in each biome (Marino and Odum, 1999). The coral reef biome is a completely enclosed marine system, offering a unique opportunity for marine scientists to test a variety of questions both at the organism-scale and the community-scale. The purpose of this paper is to describe the coral reef biome as a research facility, covering both the details of the physical structure of the facility and the composition and functioning of the coral reef.

2. Coral reef biome system

2.1. The tank and reef design

The tank containing the coral reef was constructed of 6XN high-grade stainless steel, coated with an epoxy resin to reduce corrosion (Zabel et al., 1999). The tank is 45.2 m long, 19.1 m wide and has two depths, 6.8 and 4.3 m (Fig. 1 and Table 1). The deep end of the tank is 16.9 m long and the shallow end of the tank is 28.3 m long.

The Biosphere 2 coral reef biome is designed as a fore-reef and lagoon of fringing coral reefs such as those typically found in the Caribbean Sea. These coral reefs are usually zoned with a fore-reef community that breaks incoming waves, a reef flat, 50–300 m wide and 0–2 m deep, and a back-reef or lagoon. The community of organisms on such a typical fore-reef produces excess particulate and dissolved carbon (i.e. gross production exceeds respiration, $P/R > 1.0$) while back-reef communities consume carbon (i.e. respiration exceeds gross production, $P/R < 1.0$ Kinsey 1985). The Biosphere 2 reef attempts to mimic these physical features (Fig. 1) with a fore-reef separating the 'ocean' part of the tank from a 'lagoon' area, however, there is no extended reef flat and no autotrophic to heterotrophic zonation of biota. Consequently, the characteristic spatial pattern of gross production and respiration are not observed in this system.

Limestone boulders and rocks from Arizona and Florida form the foundation of the fore-reef, the lagoon patch reefs and the beach in the tank (2700 metric tons) (Scarborough, R. 1994, technical report on file, Biosphere 2). Calcium carbonate rich clays from Arizona fill the interstices between the rocks on the beach. The foundation layer is covered with smaller rocks and crushed Arizona limestone. Local limestone carbonate consists of low-Mg calcite, while most carbonate on coral reefs consists of aragonite and high-Mg calcite. The reef mounds are faced with Caribbean limestone, live rock, and coral. Crushed oyster shells fill the cracks and crevices of the outer layer and are readily visible. The bottom of the deep ocean and lagoon are covered with 30–45 cm of aragonitic beach sand from the Caribbean.

Surface water covers 711 m^2, with the deep part of the tank and the reef flat and lagoon covering 45% (320 m^2) and 55% of the total area, respectively. The beach area covers 152 m^2 or about 21% of the water surface. The fore-reef covers 208 m^2 or 29% of the water surface. The sides of the walls that are covered with benthic organisms covers 260 m^2 and are included in the total area of the benthic cover or 850 m^2 (Table 1). The volume of water in the tank is 2650 m^3, determined by dilution of tank water with 3 kg of LiCl. Thus, the volume to surface area ratio (V/A) of the coral reef mesocosm is 2650 m^3/850 m^2 or 3.1 m. The overall design and depth is more typical of shallow lagoonal environments of coral reefs than a true fore-reef, reef-flat complex.

There are several limitations imposed by the design. Most of the tank is in deep water, which reduces light to the bottom. The reef flat zone is much too small to simulate reef dynamics of carbon production and utilization with a reef ecosystem. Waves will break on the fore-reef but waves larger than 0.3 m will re-suspend the clay from the foundation of the beach causing serious erosion to the beach itself. Thus, the reef morphology appears to have the form of a fore-reef but it cannot function structurally in a high-energy mode typical of fore-reef environments; it is merely a display feature.

2.2. Water circulation

Water can be re-circulated within the tank in three ways (Fig. 1). (1) Six airlift pumps are mounted vertically at the southwest end of the tank under the walkway and provide horizontal mixing of water in the deep end. Compressed air is pumped to a diffuser at the bottom of the 2.4 m high, 0.3 m diameter PVC pipe, forming tiny air bubbles that rise and entrain water to the surface (4.2 $m^3\ min^{-1}$). A 90° elbow at the surface directs water horizontally across the ocean. (2) Five Ingersol Rand centrifugal pumps are located along the wall behind the walkway. These pumps move water (0.6 m^3 min^{-1}) from either the lagoon or from under the dive platform to a variety of filters and a heat exchanger. One pump controls flow to the plate and rotary filters, a pair of pumps operates the algal turf scrubber and the heat exchanger, and the other pair of pumps controls oxygen injection and the shallow to deep circulation. (3) A vacuum wave generator along the south wall of the ocean creates sufficient waves to move water around the tank. The entire length

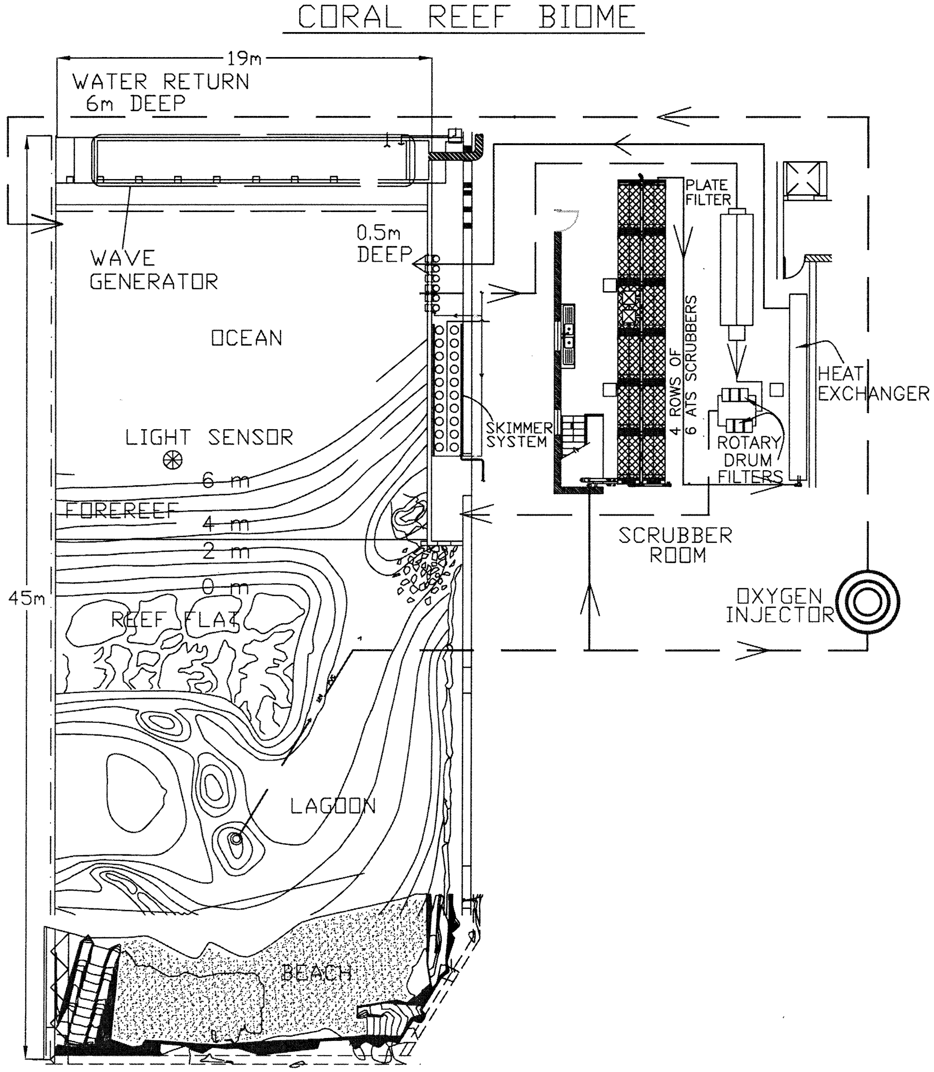

Fig. 1. The coral reef biome at Biosphere 2 is designed as a fore-reef, lagoon coral reef complex, 45 m long, 19 m wide, with depth of the bottom varying from 0.5 to 7 m. The system has a variety of filtration devices, including protein skimmers, plate filters, and rotary drum filters; a temperature control and a wave machine.

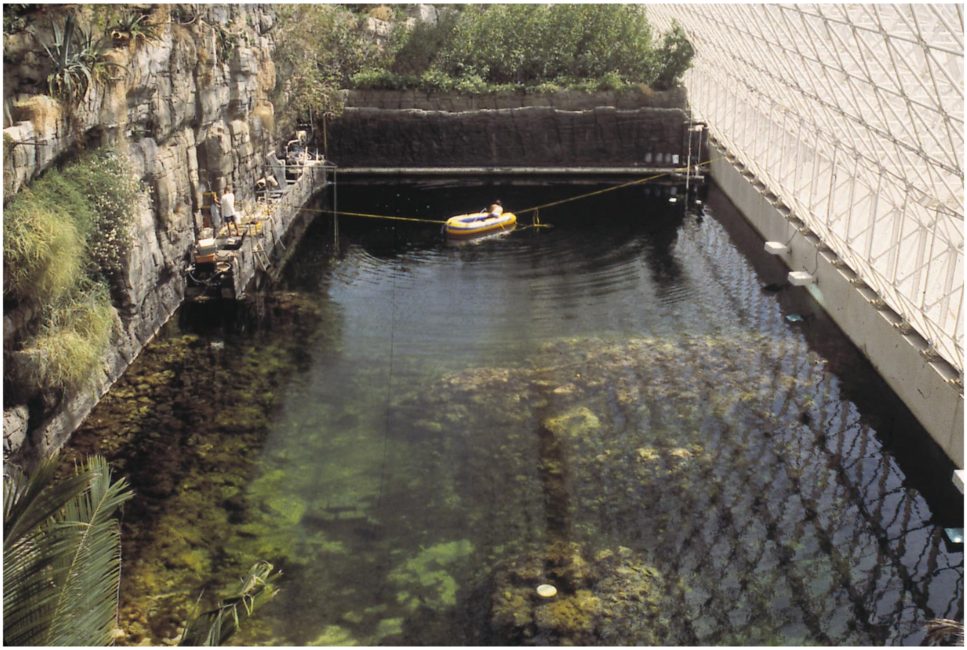

Fig. 1. (*Continued*)

of the wave wall is partitioned into five sections (1 m wide by 4 m long) of enclosed air space above the water surface. Vacuum in these chambers is created by pulling air out of the chambers. The water level rises and falls, as a computer controls the opening and closing of air valves in the head space. The wave machine simulates oceanic waves propagating to the fore-reef and breaking on the reef crest, generating a current through the lagoon. The most effective method to create this natural circulation system is to generate a wave on the eastern half of the north wall so there is no wave propagating through the channel to the beach. At present, the

Table 1
Dimensions of Biosphere 2 coral reef biome

Ocean area	Length (m)	Width (m)	Area (m^2)	Volume (m^3)	Volume/Area
Ocean	16.9	19.1	323		
Lagoon	28.3	19.1	540		
Overall	45.2	19.1	863	2650	3.06
Water surface			711		
Beach			152		
Reef flat			382		
Forereef			208		
Walls with benthos			260		
Total benthic			850		

Table 2
Species list for coral reef biome in Biosphere 2[a]

	1992	1996
ALGAE		
Chlorophyta		
Acetabularia calyculus		X
Avrainvillea sp.	X	X
Bryopsis plumosa	X	X
Caulerpa mexicana∼		X
Cladocephalus luteofuseus	X	
Clodophora fracatii	X	
Clodophora fuliginosa	X	
Derbesia marina	X	
Derbesia vaucheriaeformis	X	
Derbesia sp.		X
Dictyospaeria cavernosa		X
Enteromorpha sp.	X	
Ernodesmis verticillata		X
Halimeda incrassata	X	
Halimeda monile	X	
Halimeda opuntia	X	
Penicillus capitatus	X	X
Penicillus dumetosus	X	X
Polyphysa polyphysoides		X
Rhipocephalus phoenix	X	
Udotea cyanthiformis	X	
Udotea spinulosa	X	
Udotea flabellum	X	
Valonia macrophysa	X	
Valonia utricularis	X	
Valonia sp.		X
Ventricaria ventricosa		X
Rhodophyta		
Acanthophora spicifera	X	X
Amphiroa fragilissima		X
Amphiroa rigida	X	X
Amphiroa sp.	X	X
Callithamnion sp.	X	X
Ceramium sp.	X	
Coelothrix irregularis		X
Daysia baillouviana	X	X
Daysia harveyi	X	X
Jania adherens		X
Jania rubens		X
Halymenia duchassaignii		X
Herposiphonia secunda	X	
Polysiphonia haranensis	X	
Polysiphonia subtilissima	X	
Phaeophyta		
Dictyota bartayresii		X

Table 2 (Continued)

	1992	1996
Dictyota cervicornis		X
Dictyota divaricata		X
Dictyota linearis		X
Ectocarpus sp.	X	
Lobophora sp. (∼*variegata)*		X
Padina sp.	X	
Note: No attempt was made to identify encrusting coralline algae		
INVERTEBRATES		
Porifera (Sponges)		
Callyspongia plicifera	X	NS
Cliona delitrix	X	NS
Cliona spp.	X	NS
Iricinia spp.	X	NS
Siphonidictyom coralliphagum	X	NS
Spinosella plicifera	X	NS
Anemones		
Actinoporus elegans		X
Bartolomea annulata	X	X
Condalactis gigantia	X	X
Lebrunia coralligens	X	
Lebrunia danae	X	
Stochactis helianthus	X	
Stoichactis sp.	X	
Ricordea florida	X	Last seen July 1995
Palythoa caribbeorum	X	
Parazoanthus parasiticus	X	
Zoanthus sociatus	X	
Coelenterata		
Hydrocorals		
Cnidoscyphus marginatus	X	
Millepora alcicornis	X	X
Millepora complata	X	
Soft Corals		
Briarium asbestinum	X	X
Erythropodium caribaeorum		X
Eunicea sp.	X	X
Muricea		
Plexaura homomalla	X	X
Plexaurella sp.	X	X
Psuedopterogorgia sp.	X	X
Hard Corals		
Acropora cervicornis	X	X
Agaricia agarcites	X	X

Table 2 (Continued)

	1992	1996
Agaricia sp.	X	X
Colpophyllia natats	X	X
Colpophyllia breviserialis	X	
Dichocoenia stokesi	X	X
Diploria clivosa	X	X
Diploria labyrinthiformis	X	X
Diploria strigosa	X	X
Eusimilia fastigiata	X	X
Favia Fragum	X	X
Isophyllastrea rigida	X	
Isophyllastrea sinuosa	X	
Madracis decactis	X	
Madracis mirabilis	X	
Madracis sp.		X
Manicina areolata	X	
Meandrina meandrites	X	
Montastrea annularis	X	X
Montastrea cavernosa	X	X
Mussa angulosa	X	X
Mycetophyllia aliciae	X	
Mycetophyllia lamarkiana	X	
Mycetophyllia sp.	X	X
Porites asteroides	X	X
Porites divaricata	X	X
Porites furcata	X	X
Porites porites	X	X
Scolymia sp.	X	X
Siderastrea siderea	X	X
Siderastrea radians	X	X
Stephanocoenia mechelinii	X	X
Hard Corals (Pacific) introduced in 1996		
Acropora austera		X
Acropora elseyi		X
Acropora formosa		X
Acropora microphthalma		X
Caulastrea furcata		X
Montipora digitata		X
Montipora remucosa		X
Pocillopora damicornis		X
Porites compressa		X
Mollusca		
Snails and limpets		
Acmaea spp.	X	NS
Cerithium litteratum	X	NS
Cittarium pica	X	NS
Columbella mercatoria	X	NS
Cyphoma gibbosum	X	NS
Diodora dysoni	X	NS

Table 2 (Continued)

	1992	1996
Fasciolaria tulipa	X	NS
Haminoea spp.	X	NS
Littorina ziczac	X	NS
Melongena melongena	X	NS
Nerita peloronta	X	NS
Nerita tessellata	X	NS
Nerita versicolor	X	NS
Puperita pupa	X	NS
Strombus gigas	X	NS
Tectarius muricatus	X	NS
Trivia quadripunctata	X	NS
Turbo fluctuosus	X	NS
Chitons		
Acanthochitona pygmaea	X	Chitons are still abundant in the Bio2 ocean, but species have not been verified
Chiton spp.	X	
Bivalves		
Anomia simplex	X	
Barbitia domingensis	X	
Botula fusca	X	
Chione cancellata	X	
Hormomya exusta	X	
Isognomon radiatus	X	
Lima lima	X	
Lopha frons	X	
Pteria colymbus	X	
Spondylus americanus	X	
Tridacns gigas	X	
Crustacea (decapoda)		
Calcinus tibicen	X	
Callinectes ornatus	X	
Clibanarius tricolor	X	
Dardanus fucosus	X	
Dromidia antillensis	X	
Macrocoeloma trispinosum	X	
Microphrys bicormatus	X	
Mithrax pleuracanthus	X	
Mithrax sculptus	X	
Mithrax spinossissimus	X	
Pagurus operculatus	X	
Panulirus argus	X	X (seen July 1996)
Panulirus guttatus	X	X (seen June 1996)
Periclimenes pedersoni	X	
Petrochirus diogenes	X	
Pilmnus dasypodus	X	
Portunus sebae	X	
Scyllarides aequinoctialis	X	X (seen August 1996)
Stenopus hispidus	X	X (seen December 1995)

Table 2 (Continued)

	1992	1996
Stenorhynchus seticornis	X	
Sea urchins (echinoidea)		
Diadema antillarum	X	X
Echinometra lucunter	X	X
Echinometra viridis	X	X
Eucidaris tribuloides	X	X
Meoma ventricosa	X	X
Tripneustes esculentus	X	X
Sea cucumbers (holothuroidea)		
Eutapa lappa	X	
Holothuria mexicana	X	X
Holothuria parula	X	X
Parathyone surinamensis	X	
Brittle stars (ophiuoidea)		
Ophicoma echinata	X	X
Ophiothrix oerstedii	X	X
Sea stars (asteroidea)		
Oreaster reticulatus	X	
Polychetes		
Eupolymnia nebulosa	X	NS
Filograna implexa	X	NS
Hermodice carunculata	X	NS
Pomatostegus stellatus	X	NS
Potamilla fonticula	X	NS
Sabella melanostigma	X	NS
Sabellastarte magnifica	X	NS
Spirobranchus giganteus	X	NS
Sipuncula		
Golfingia sp.	X	NS
Tunicates		
Clavelina spp.	X	NS
Distaplia bermudensis	X	NS
Distaplia stylifer	X	NS
Fish		
Abudefduf saxatilis	X	X
Acanthurus bahianus	X	X
Acanthurus chirugus	X	X
Acanthurus coeruleus	X	X
Aluterus sp.	X	X
Amphiprion clarkii	X	
Anisotrmus virginicus	X	X
Apogen maculatus	X	
Apogen sp.	X	
Balistes vetula	X	

Table 2 (Continued)

	1992	1996
Bodianus rufus	X	
Canthigaster rostrata	X	
Chaetodon capistratus	X	X
Chaetodon striatus	X	
Chromis cyaneus	X	X
Chromis enchrysurus	X	X
Clepticusparrai	X	
Equetus acuminatus	X	
Equetus punctatus	X	
Gramma loreto	X	X
Gramma melacara	X	
Haemulon aurolineatum	X	
Haemulon flavolineatum	X	X
Halichoeres bivattatus	X	X
Halichoeres garnoti	X	
Halichoeres pictus	X	X
Halichoeres radiatus	X	
Hippocampus hippocampus	X	
Holocanthus bermudensis	X	
Holocanthus ciliaris	X	X
Holocanthus tricolor	X	X
Holocentrus rufus	X	X
Hypleurochilus bermudensis	X	X
Lactophrys bicaudalis	X	
Microspathodon chrysurus	X	X
Myripristis jacobus	X	
Oxycirrhtus typus	X	
Scarus croicensis	X	X
Scarus taeniopterus	X	X
Scarus vetula	X	X
Sparisoma viride	X	X
Stegastes fuscus	X	X
Stegastes leucostictus	X	X
Stegastes planifrons	X	X
Stegastes partitus	X	X
Stegastes variabilis	X	X
Thalassoma bifasciatum	X	

[a] NS, not surveyed.

ocean is operated by re-circulating water through the heat exchanger and creating sufficient waves to mix the water.

2.3. Filtration systems

At present the water in the coral reef biome is not filtered to encourage the development of a full planktonic community that supports the reproduction of the benthos. The filtration systems are described here in detail however, to aid in the

Table 3
Elemental composition of surface sea-water (SW), Instant Ocean (IO) and Biosphere 2 coral reef biome (B2) for 1991 through 1994 and from 1995 through 1997[a]

	SW	IO	B2: 1991–1994	B2: 1995–1997	MW[b]
Major cations (mmol kg^{-1})					
Na^{+}	470	462	490 (64)	492 (3.2)	23
K^{+}	10.2	9.4	9.4 (1.0)	9.1 (0.15)	39.1
Mg^{+2}	53	52	58 (67)	49.6 (0.53)	24.3
Ca^{+2}	10.3	9.4	10.2 (1.9)	9.3 (0.11)	40.1
Sr^{+1}	0.09	0.19		0.082 (0.001)	87.6
Major anions (mmol kg^{-1})					
Cl^{-}	550	521	645 (74)		35.5
SO_4^{-2}:S	28	23	26 (3.6)		32.1
Nutrients (μmol kg^{-1})					
PO_4:P	0.20	0.05		0.2–0.00	31
NO_3:N	0.20	1.00	5–0.2	3–0.01	14
NH_4:N	0.20	10.2		2–0.1	14
SiO_3:Si	5	4.2		3–25	28.1
DOP:P	0.2	0.1		0.6–0.02	31
DON:N	10	2.9		65–38	14
TOC:C	50	29		230 (18)	12.0
pH	8.25	8.35	7.3–8.1	8.1–8.2	
TA	2.3	2.3	2.3–4.3	1.7–4.0	
Trace (μmol kg^{-1})					
Li	20	54			69
Si	5	16			28.1
Mo	0.1	1.8			95.9
Ba	0.04	0.85			137
V	0.04	2.95			50.9
Ni	0.004	1.7			58.7
Cr	0.003	7.5		0.078 (0.016)	52.0
Al	0.002	240			30.0
Cu	0.001	1.8			63.5
Zn	0.001	0.50			65.4
Mn	0.0004	1.2			54.9
Fe	0.0001	0.24			55.8
Cd	0.0001	0.24		0.003 (0.002)	112
Pb	0.00006	2.1		0.013 (0.004)	207
Co	0.00005	1.3			58.9
Ag	0.00001	2.3			108
Ti	0.00001	0.67			47.9

[a] Numbers in parentheses are standard deviations, $n = 30$ for 1991–1994 and $n = 6$ for 1995–1997. The high variability of the 1991–1995 samples are due largely to analytical error. [b]MW is the molecular weight of the element.

development of potential specific research programs. However, it is likely that the existing mechanical systems destroy some forms of plankton. The coral reef biome has four filtration systems; algal turf scrubbers, protein skimmers, plate filters, and rotary drum filters (Fig. 1).

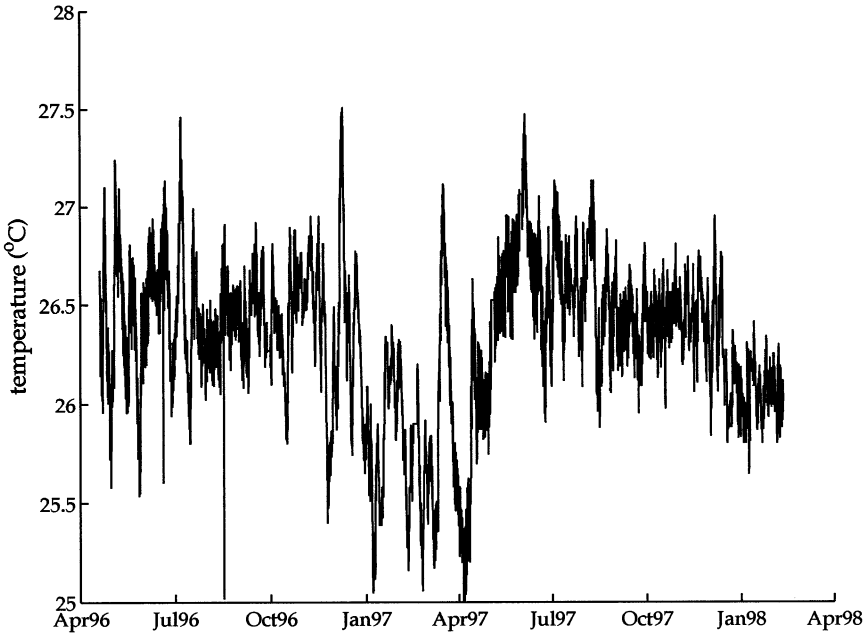

Fig. 2. Ocean temperature (C°) for the period April 1996 to April 1998. Water temperature has been maintained between 25 and 27 C° since 1996.

A total of 24 algal turf scrubbers (Adey and Loveland, 1991) are located in the scrubber room adjacent to the ocean. Each scrubber consists of a sloping tray fitted with an algal covered mat. Water from the ocean drains into a bucket at the upper end of the tray. When the bucket is full of water, it tips the water into the tray, creating a surge of water across the algal mat. Water draining from the scrubbers

Table 4a
Composition of trace metal preparation[a]

Salt	Name	(g)
KI	Potassium iodide	4000
$MnSO_4.H_2O$	Manganous sulphate monohydrate	261
$NH_4Mo.4H_2O$	Ammonium molybdate tetrahydrate	28.4
$ZnSO_4.7H_2O$	Zinc sulphate heptahydrate	35.5
$CoCl.6H_2O$	Cobalt sulphate hexahydrate	21.6
$Vn.2H_2O$	Vanadyl sulfate dihydrate	14.2
$NaFe\ C_{10}N_2O_8H_{12}$	Sodium, iron EDTA	7000
$Na2\ C_{10}N_2O_8H_{12}$	Di-sodium EDTA	1700
Na citrate	Sodium citrate	4540
Total		17 600

[a] 17.6 kg mixture, recommended dose 0.733 kg each month for 2 years.

Table 4b
Chemical additions to coral reef biome water[a]

Date	Na_2CO_3	$NaHCO_3$	$CaCl_2$	Other
17 December 1994	0.86	11.36	8.27	–
22 December 1994	0.86	11.36	8.27	–
22 December 1994	0.86	11.36	8.27	–
24 December 1994	0.86	11.36	8.27	–
26 December 1994	0.86	11.36	8.27	–
27 December 1994	0.86	11.36	8.27	–
27 December 1994	0.86	11.36	8.27	–
4 January 1995	0.86	11.36	8.27	–
16 January 1995	45.45	3.45	–	–
27 March 1995				Ten packets of trace metals
24 July 1995	19.5	–	–	–
25 July 1995	19.58	–	–	–
18 August 1995	4.6	–	–	–
22 August 1995	–	–	11.52	–
24 August 1995	–	–	15.04	–
26 August 1995	–	–	9.97	–
22 September 1995	–	–	27.81	–
23 September 1995	–	–	24.85	–
26 September 1995	–	–	28.20	–
27 September 1995	–	–	23.54	–
28 September 1995	–	–	20.53	–
29 September 1995	–	–	35.91	–
30 September 1995	–	–	17.27	–
12 October 1995	–	–	13.81	–
13 October 1995	–	–	29.46	–
27 December 1995	–	–	–	2821 kg Instant Ocean since 26 October 1995
2 March 1995	86.68	20.23	–	–
8 July 1996	100	50	–	–
10 July 1996			77.27	–
15 August 1996	–	–	–	1 kg NH_4Cl, 0.334 kg KH_2PO_4, 3 kg LiCl
29 October 1996	–	–	87.73	–
30 October 1996	45.45	18.18	–	0.73 kg packet of trace metals
31 October 1996	45.45	–	–	–
6 March 1997	–	–	–	1 kg NH_4Cl, 0.334 kg KH_2PO_4
6 June 1997	–	108.18	94.55	–
7 June 1997	24.41	–	–	–
30 June 1997	–	7.73	90.91	–
1 July 1997	–	90.91	–	–
2 July 1997	50.91	90.91	–	–
9 September 1997	45.45	–	–	–
10 September 1997	–	90.91	–	–
11 September 1997	5.45	27.27	–	–
15 September 1997	7.27	17.27	–	–
8 October 1997	71.36	85.00	–	–
19 November 1997	38.18	45.45	–	–
21 November 1997	38.18	45.45	–	–

[a] Weights are in kg, note water of hydration should be estimated for compounds.

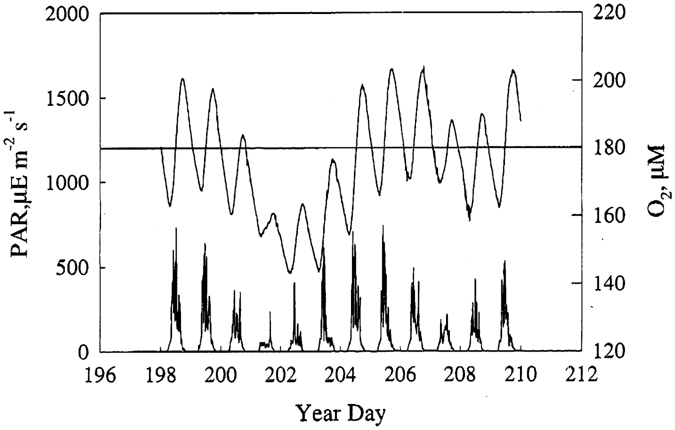

Fig. 3. Oxygen and light time series for the period July 17 to July 29 1997. The light sensor is located at a depth of 2.5 m in the ocean (location shown in Fig. 1). The solid reference line denotes the saturation concentration of oxygen at the temperature, salinity and barometric pressure of the Biosphere 2 sea-water.

passes through the heating–cooling system before discharging into the southwest corner of the ocean. Light to the scrubbers for algal growth is provided by 1000 W multi-vapor lamps.

A total of 20 protein skimmers (reverse-flow, Keeton Fisheries of Fort Collins, Colorado.) are installed on the dive platform (Fig. 1). Each skimmer has two airlift pumps, an outer PVC pipe with a sealed lid, an inner PVC pipe, an export line for removal of foam, and a water feed line for back-flushing the system. The skimmers share a compressed air line, a foam export pipe and a back flush water line.

Four plate filters located in the scrubber room remove particles from the reef water through settling and bio-filtration. Each plate filter consists of a rectangular tub, 3 m long, 0.8 m wide and deep. A centrifugal pump delivers water to all four plate filters. Water enters at the bottom of one end of the tubs, and exits through an overflow orifice near the top of the opposite end of the filter. The outflow from the plate filters can be directed to flow directly into the rotary drum filters or the water can be sent directly back to the reef. The tubs also have plastic coils in them that act as heat exchangers.

Water feeds into two rotary drum filters from the out-flow of the plate filters. These filters screen out particles larger than 80 µm using a rotating mesh screen. The trapped material is back-washed with fresh condensate water collected from other biomes (see Zabel et al., 1999). Backwash pressure is generated by the condensate pump and manually controlled valves located on the rotary drum filters.

Three AirSep (AirSep, Buffalo, NY) O_2 generators strip N_2 and CO_2 from the air, thereby concentrating O_2. Oxygen is mixed into water in the injector, a 3 m long vertical pipe with plastic honeycomb matrix, and returned to the southeast corner of the ocean at a depth of 1 m. Ozonated air can be used in the protein skimmers and the air lift pumps to aid in the oxidation of collected proteinaceous material.

2.4. Temperature control

Ocean water flows into a tub similar to the plate filters, filled with plastic coils. Hot or cold water from the energy center (8–10 l s^{-1}) is pumped through the plastic coils (Zabel et al., 1999), which heat or cool the ocean water in the tub. Manual adjustments to the flows of hot or cold water maintain daily water temperatures to within 0.5°C.

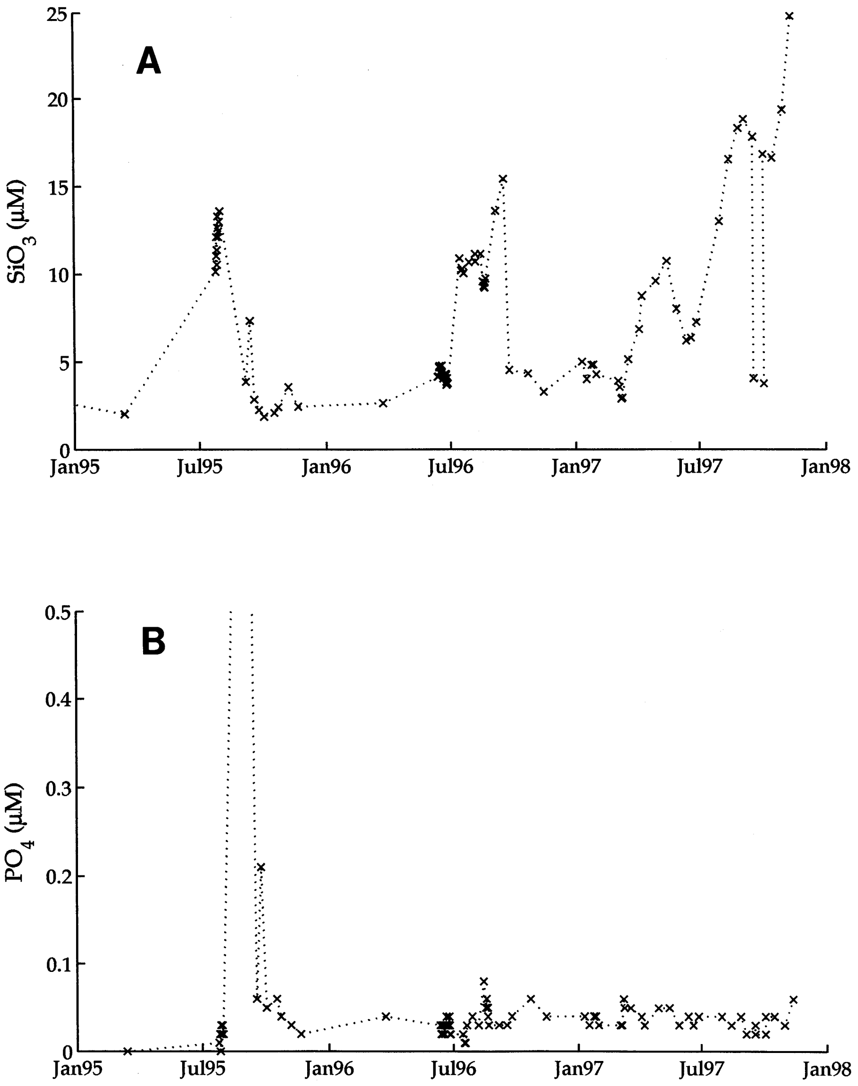

Fig. 4. Concentration of inorganic nutrients, (A) SiO_3, (B) PO_4, (C)NO_3^-, and (D) NH_4, given in μM, for the coral reef biome water in Biosphere 2 for the period January 1995 to January 1998.

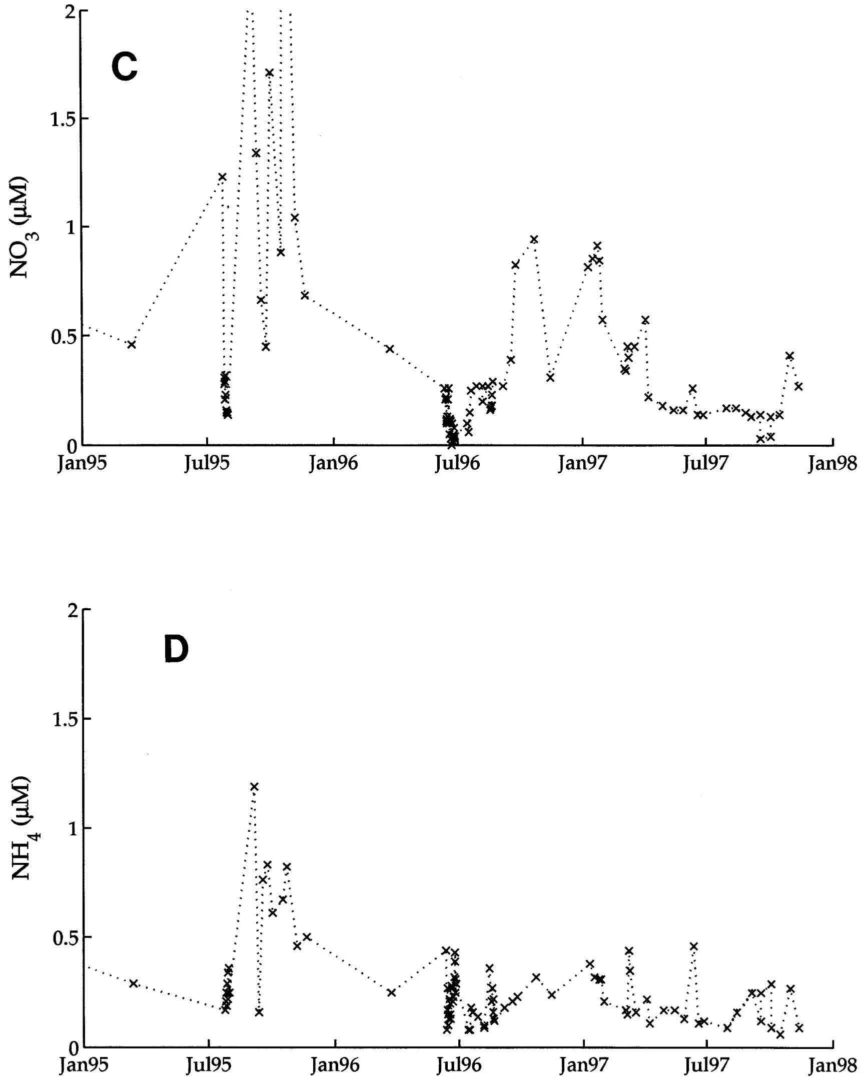

Fig. 4. (*Continued*)

2.5. Biota

In the spring of 1990, marine organisms were added to the reef biome in planned succession, designed to provide the basis of a food web. Plankton were introduced from an addition of southern California sea-water (10% of total volume). Rocks with encrusting invertebrates and plants, or 'Caribbean live rock' were added next. After the organisms on the rocks began to colonize and propagate within the system, fish, crabs, lobsters, urchins and sea cucumbers were introduced. The biota was comprised of 24 known phyla before the closure of the system in 1991 (Adey and Loveland, 1991; Alling and Alvarez-Romo, 1991; Finn, 1992). In 1993, 27 species were re-inoculated in an effort to re-establish failed populations or to try new organisms. These additions were not well documented.

Species lists for the ocean biomes were produced in July 1992 and August 1996 (Table 2). Apparently all bivalves and crustaceans died between 1992 and 1996. Some species of algae that were not listed in 1992, were abundant in 1996, especially the brown alga, *Dictyota* sp., and the green alga, *Ernodesmis* sp. Existing coral colonies suffered. Dustan (1993) indicates coral colony mortality of 12% and

Table 5
Monthly quantities of water added to coral reef biome[a]

Month	RO (l)	WC (l)
December 1994	9984	7562
January 1995	54117	114
February 1995	134 717	59 506
March 1995	95 356	78 756
April 1995	88 833	69 746
May 1995	127 812	45 821
June 1995	146 225	18 706
July 1995	117 246	0
August 1995	143 617	15 660
September 1995	137 937	0
October 1995	173 791	543
November 1995	216 991	0
December 1995	183 435	0
January 1996	205 058	0
February 1996	140 432	0
March 1996	193 237	0
April 1996	138 163	0
May 1996	46 050	0
June 1996	26 971	0
July 1996	34 928	0
August 1996	26 899	0
September 1996	12 514	0
October 1996	31 757	0
November 1996	15 502	0
December 1996	57 513	0
January 1997	54 735	0
February 1997	53 206	0
March 1997	42 987	0
April 1997	55 403	0
May 1997	74 294	0
June 1997	83 436	0
July 1997	23 804	0

[a] RO, reverse osmosis water; WC, wilderness condensate. RO water is relatively low in nutrients compared to WC water (RO: $PO_4 = 0.0$, $NO_3 = 1.0$; $NH_4 = 5.0$, $Si = 0.0$, $DOP = 0.5$ $DON = 4.2$; WC: $PO_4 = 0.0$, $NO_3 = 211$; $NH_4 = 54$, $Si = 10$, $DOP = 0.7$ $DON = 52$).

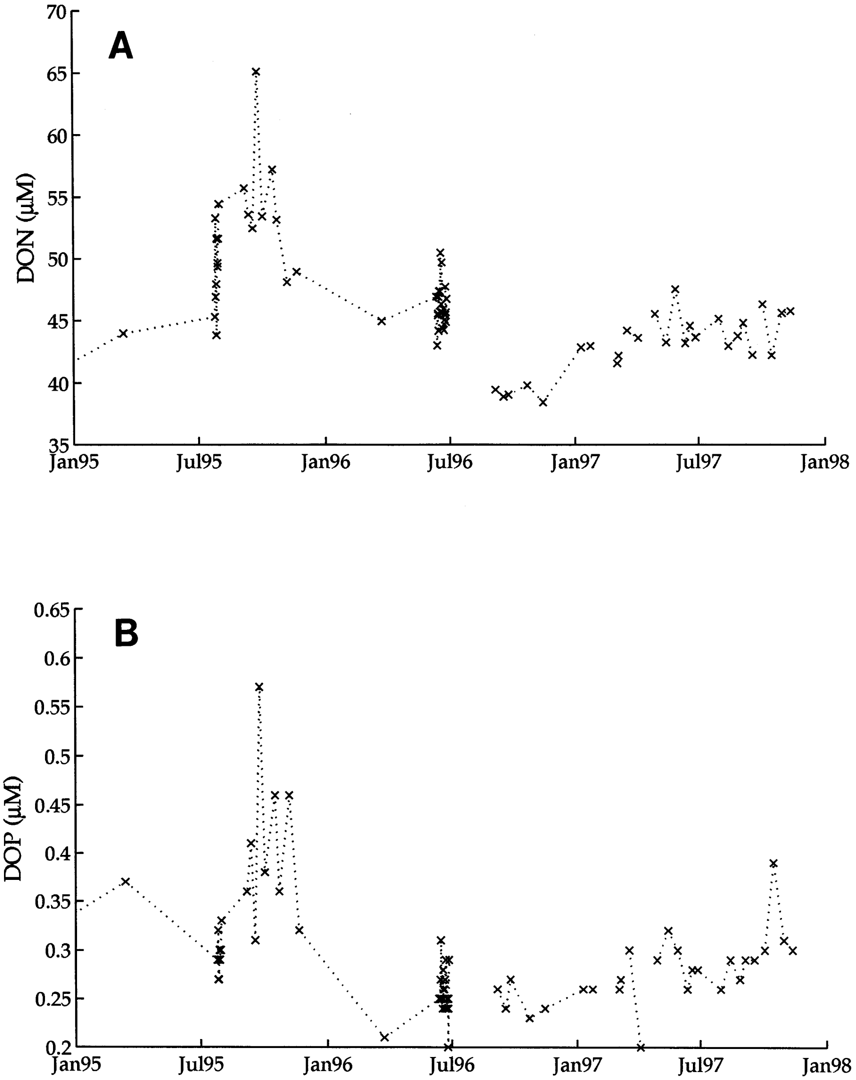

Fig. 5. Concentrations of organic nutrients, (A) DON, and (B) DOP, given in µM, for the coral reef biome water.

tissue recession of 24% between 1992 and 1993, despite successful recruits of *Porites astreoides*, *Favia fragum* and *Agaricia* sp.; additional successful colonies of *Scolymia* sp., *Siderastrea* sp., and *Acropora cervicornis* were identified in 1994 and 1995. Fragments of corals from Hawaii and Fiji were also added in 1996 for experiments on coral physiology and growth. These corals are showing excellent increases in weight and branching extension. *Pocillopora damicornis*, which was introduced in 1996 has reproduced.

3. Water chemistry

The water of the coral reef biome was initially comprised of 10% natural sea-water from the southern California coast and 90% local well-water mixed with Instant Ocean®. Concentrations of major ions, Na^+, K^+, Mg^{2+}, Ca^{2+}, Sr^{2+}, Cl^-, $SO_4^=$, and nutrients (N and P compounds) in water prepared from Instant Ocean® compare favorably with sea-water, but concentrations of trace elements (< 0.1 mM) are orders of magnitude higher than sea-water (Table 3; Atkinson and Bingman, 1997). Analyses of major ions from 1991 to 1995 and most recently in 1996 show that the water composition is near that of sea-water (1991–1995 analyses were of dubious quality; (Table 3)). Additions of Instant Ocean® and CaCl were sporadic and could have affected the measurements. Significant decreases in Ca^{2+}, and to a lesser extent, Sr^{2+} and Mg^{2+} concentrations are anticipated due to calcification by corals (aragonite) and calcareous algae (Mg-calcite and aragonite, e.g. Carpenter and Lohmann, 1992). The few trace elements that were measured during 1991–1995, Cr, Cd, and Pb, are about 100-fold lower than Instant Ocean®, indicating a net removal of those metals to the benthos and sediments. Large and unknown quantities of a trace element mixtures (Tables 4a and 4b) were occasionally added to the ocean and merely noted in a journal. Our estimates indicate that there was sufficient organic C and N from ethylenediamine tetra-acetate (EDTA) to equal

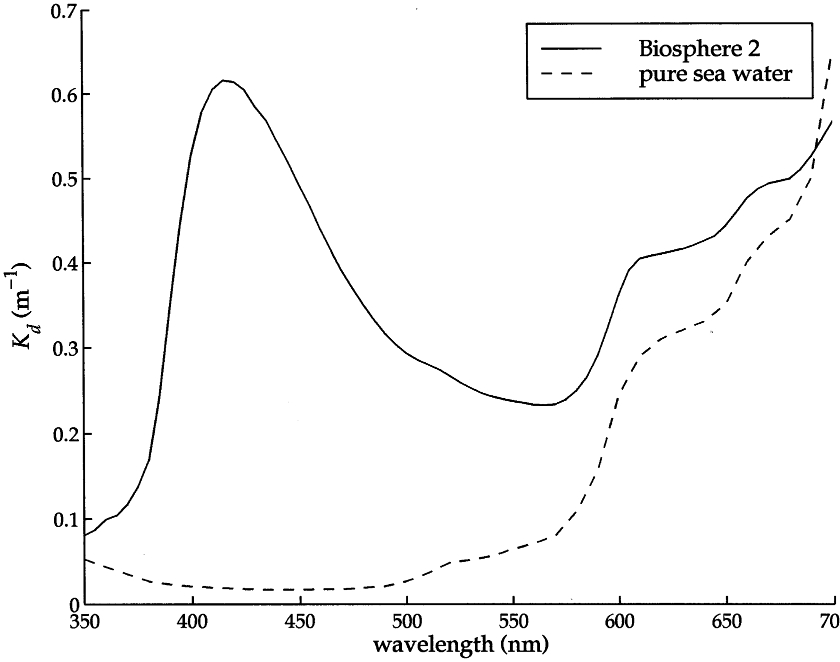

Fig. 6. Diffuse attenuation coefficients as a function of wavelength in coral reef biome water. The high absorption in the blue by DON creates yellow-colored water. There is little plankton in the water.

about half of the present dissolved organic C and N pool. We do not have a thorough analysis of the DON to determine its exact nature.

The coral biome water is presently monitored continuously for temperature, salinity, light, O_2, and pCO_2, and monitored daily to weekly for alkalinity, ΣCO_2, pH, nutrients and $\delta^{13}C_{DIC}$ and $\delta^{18}O_{water}$ values. Based on results of a mixing experiment with LiCl, the water in the coral reef biome is mixed within 1 h. Monitoring of the bulk water takes place at one location adjacent to the dive platform and above the skimmer system (Fig. 1). An instrument package hangs from a boom that is mounted on the side of the dive platform to a depth of 2 m. The instrument package includes a Sea Bird Electronics, Bellevue WA, (SBE) 3 thermister, an SBE 4 conductivity sensor, an SBE 22y oxygen sensor (YSI O_2 polarographic oxygen probe) and an ENDECO pulsed oxygen sensor (designed by C. Langdon, Lamont-Doherty). The instrument package is cleaned weekly to keep bio-fouling to a minimum. Oxygen sensors are calibrated with data from Winkler titrations of water samples every 3 days for the YSI polarographic sensor and 3–4 weeks for the ENDECO pulsed sensor. The ocean temperature has been maintained between 25 and 27°C for the last year (Fig. 2). Oxygen concentrations increase during day and decrease at night (Fig. 3). The oxygen varies about 30 to 40 μM O_2 throughout a daily period. On cloudy days, the amplitude of the diel O_2 signal dampens and the mean decreases; and during periods of clear weather, O_2 increases 20 μM above oxygen saturation (Fig. 3). The air lift pumps and protein skimmers strongly affect the rate of atmospheric gas exchange and therefore O_2 fluctuations. The rate constant for gas diffusion, determined from artificially increasing O_2 above saturation and measuring the decay, and from radon flux experiments, is 2.1 m s^{-1} (Sweeney, 1999).

The pCO_2 of the water in the coral reef biome and overlying atmosphere are continuously monitored by a pCO_2 equilibrator system (Takahashi, T. 1994, technical report on file, Biosphere 2). Sea-water is sprayed through a common shower head within the CO_2 equilibrator. The sea-water rapidly exchanges gas with air contained within a plastic cylinder. The enclosed air is then circulated through a condensation trap, 1/4 inch Nylaflow tubing to the savannah plenum, and back to the equilibrator. A subsample of air is dehydrated by passage through a Permapure gas dryer tube and then analysed for CO_2 concentration by a LI-COR 6251 infrared gas analyzer. The LI-COR 6251 alternately analyzes samples from the equilibrator and from the atmosphere overlying the ocean. It is calibrated using four tank standards, and data are corrected for sample pressure and temperature (Rosenthal et al., 1999).

Diurnal changes in pCO_2 are also apparent, and opposite those of O_2. Sea-water pCO_2 fluctuations are smaller than those in the overlying atmosphere, which are influenced by terrestrial plant photosynthesis and air management within Biosphere 2. In general, both atmosphere and ocean pCO_2 vary from 350 to 1400 μatm, while levels in excess of 3500 μatm were previously observed during winter when Biosphere 2 was operated as a closed system (Marino et al., 1999). pH has varied from 7.7 to 8.1 from 1991 to 1997, generally low for warm surface water. Alkalinity has also varied from 2.0 to 4.0 mequiv. l^{-1}. Only recently, beginning in 1997, have the pH and alkalinity been experimentally controlled to alter the carbonate ion concentration (CO_3^{-2}) and maintain constant pH.

Water samples for laboratory analysis are collected by pumping water through a plastic hose into a bucket on the dive platform. Water samples are taken directly from the bucket, filtered through an in-line glass-fiber filter (Whatman GF/C) to remove particles and stored in Nalgene bottles. Water samples for nutrients are frozen within 1 h of collection and those for elemental analysis are refrigerated. Nutrient data reported here are from Technicon standard methods on a Technicon Autoanalyzer II (Walsh, 1989). At present, silica (Si) varies seasonally from 2 to 25 μM (Fig. 4a), phosphate (PO_4) is extremely low even for tropical surface water at < 0.03 μM (Fig. 4b), and nitrate (NO_3) and ammonia (NH_4) are between 0.01 and 0.3 μM (Fig. 4c, d). The low PO_4 and NH_4 indicate that excretion rates are relatively low. The relatively high NO_3 indicates that nitrogen fixation and nitrification have produced sufficient NO_3 to support metabolic demand, rather typical of a number of shallow water communities (Smith, 1984; Smith and Atkinson, 1984, 1994). From 1991 to 1995, NO_3 decreased from 5 to 0.2 μM, consistent with a slow net removal of the nutrients by the benthos and reductions in the amount of condensate water for ocean replacement; condensate water from the wilderness biomes is typically high in NO_3 (Table 5, Marino et al., 1999). At present, the low inorganic nutrients support an extremely low biomass of phytoplankton, < 0.05 μg chlorophyll a l^{-1}. It is likely that uptake of nutrients into the benthos of this system is mass transfer limited (Baird and Atkinson, 1997), and if confirmed, indicates that the actual flux of N and P into the benthos is proportional to the concentration of those compounds, roughly an N:P ratio of 30:1.

Dissolved organic nitrogen (DON) (Fig. 5a) and phosphorus (DOP) (Fig. 5b) are more abundant than the inorganic nutrients, at around 45 μM N (on the high side), and 0.25 μM P (typical of many tropical sea-waters), respectively. The peaks in nutrients during 1995 could be related to the additions of the trace metal preparations and additions of some recycled Biosphere water (called wilderness condensate water (Table 5)). The wilderness condensate water (measured in July 96) is two orders of magnitude higher in DOP and DON than the reverse osmosis water presently used to offset evaporation (Table 5). The lack of UV irradiation due to absorption by the glass roof, and slow filtration of the water probably contribute to these high levels of DON.

3.1. Light

Two light sensors are used to monitor light, a LiCor spherical sensor mounted on the cliff above the north wall of the coral reef biome, and an underwater LiCor sensor, mounted at a depth of 2.2 m on the southeast side of the reef (Fig. 1). Ambient light is reduced by as much as 50–30% by the glass roof of Biosphere 2 (Zabel et al., 1999), giving a maximum PAR of about 700 μE m^{-2} s^{-1} (Fig. 3). The sea-water in Biosphere 2 is extremely clear, but yellow from the high DON and DOC. The diffuse attenuation coefficients, the exponential decay constant that describes the depth dependence of down-welling solar radiation, as a function of wavelengths were determined using an Ocean Optics SD-1000 fiber optic underwater spectrometer (Fig. 6). These data indicate that at 5 m depth the blue light (400–450 nm) is reduced to 5% of the surface intensity, while the green light (500–550 nm) was reduced to 30% of the surface intensity. Thus, light in the coral reef biome is relatively low, some 50% of the PAR normally found on reefs, and is much lower for the blue wavelengths.

4. Coral reef metabolism

Does this indoor reef function similarly to a natural reef, and thus serve as a meaningful experimental system? There are some notable features of this reef that are not typical of most natural reef systems, but for which a natural analog is recognizable. The water is clear because of extremely low chlorophyll concentrations and the lack of suspended particles (one can easily see to the bottom and across the width of the tank) but has a characteristic yellow color often seen at low tide on reef flats (‘gelbstoff’). There are uncharacteristically few zooplankton, even at night. Even though there are 30 species of coral, their biomass is low relative to the biomass of the dominant red algae, *Amphiora f.* There are few fish (~ 100), fewer echinoderms and almost no benthic crustaceans. Consequently, there appears to be little bioerosion occurring in the tank; carbonate fine sediments are not observed accumulating in the system. Thus, one’s immediate realization is that this is an algal-dominated, ‘over-fished’ and plankton-starved algal-coral reef. Many fringing reefs in populated areas of the world fit this scenario. An exception is that the Biosphere 2 reef has a few large, fat fish, which seem to be selective feeders, whereas truly over-fished reefs have guilds of small undersized fish, a condition that could be easily changed by introduction of small fish to the tank.

What is the metabolism of this reef in terms of gross productivity, net productivity, respiration and nutrient budget? Diel changes in O_2 from July 1995 to December 1997 have been about 30 mmol m^{-3}, with a 10 mmol O_2 m^{-3} oversaturation (Fig. 3, Langdon and Sweeney, 1995). Gross production is therefore the net photosynthetic rate plus the respiration rate over the daylight period, or 60 mmol $m^{-3}d^{-1}$. The production is mostly confined to the shallow reef flat areas and the fore-reef, giving a benthic area of 590 m^2 and a V/A of 4.5 m (2650 m^3/590 m^2) or a gross production of about 270 mmol O_2 m^{-2} d^{-1}. This number is only an approximation because the area is not well-defined and the net production will change with light intensity and quality. The net production can also be estimated from the net efflux rates of O_2 based on 10 mmol O_2 m^{-3} oversaturation. The measured gas transfer rate constant of 2.1 m d^{-1} gives a net production of oxygen of 20 mmol O_2 m^{-2} d^{-1}. During periods of low light the net production can be negative (Table 6). Thus P/R ratios probably vary from 0.9 to 1.1, depending on light levels. The seasonal P/R ratios will be discussed in another paper.

Changes in TCO_2 (as measured by pCO_2 and Total CO_2) less calcification over the period July 1995, give values of 25 mmol C m^{-2} d^{-1} for net, comparable to that determined by O_2. This result gives confidence to the gas transfer rates. Calcification, as determined by changes in calculated total alkalinity (0.20 mequiv m^{-3}), indicate a calcification rate of 10 mequiv m^{-3} $d^{-1} \times 4.5$ or 45 mequiv m^{-3}

Table 6
Net community production of the Biosphere 2 coral reef biome estimated from the oxygen saturation anomaly and the gas exchange coefficient ($G = 2.2$ m d^{-1})

Date	Average O_2	(O_2-Ceq)	NCP, mmol O_2 m^{-2} d^{-1}
18 May 1997	187.3	7.6	21.3
19 May 1997	186.5	6.8	19.0
20 May 1997	178.4	−1.3	−3.6
21 May 1997	181.2	1.5	4.2
22 May 1997	193.2	13.5	37.8
23 May 1997	193.9	14.2	39.8
		Mean	19.7
Date	Avg. O_2	(O_2-Ceq)	NCP, mmol O_2 m^{-2} d^{-1}
17 July 97	182.0	2.3	5.1
18 July 97	182.2	2.5	5.5
19 July 97	172.7	−7.0	−15.4
20 July 97	158.6	−21.1	−46.4
21 July 97	152.9	−26.8	−59.0
22 July 97	160.3	−19.4	−42.7
23 July 97	176.0	−3.7	−8.1
24 July 97	185.3	5.6	12.3
25 July 97	187.0	7.3	16.1
26 July 97	179.0	−0.7	−1.5
27 July 97	175.4	−4.3	−9.5
28 July 97	183.0	3.3	7.3
		Mean	−11.4

d^{-1}. Thus, $P = 290$ mmol C m^{-2} d^{-1}, $R = 270$ mmol C m^{-2} d^{-1}, $P/R = 1.1$ and $G = 23$ mmol $CaCO_3$ m^{-2} d^{-1}, or only 8% of P. These community metabolism rates are roughly half of the rates reported by Kinsey (1985) for algal-dominated reef flats, but are well within the range observed for coral reef environments. These rates are most typical for some of the shallow water lagoonal environments of higher latitude reefs, such as One Tree Island, Great Barrier Reef and French Frigate Shoals, Hawaii (reviewed by Kinsey, 1985). Recent experimental results have shown that the Biosphere lagoon community calcifies from 0–140 mmol $CaCO_3$ m^{-2} d^{-1}, depending on the concentration of CO_3^{-2}.

Light levels in the coral reef biome range from 5 to 20 E m^{-2} d^{-1} between summer and winter; thus the efficiency of conversion of solar energy to organic C is about 4%. This value is high relative to the algal-reef flats at French Frigate Shoals (1.9%, Atkinson and Grigg, 1984), but similar to an algal-coral reef at the Houtman Abrolhos Islands, Western Australia (4.0%, Smith, 1981). French Frigate Shoals showed a strong seasonal variation in gross production (50%), community respiration (53%), net production (47%) and calcification (28%), but not P/R (22%) (Atkinson and Grigg, 1984). We expect to measure the seasonal changes in the coral reef biome as monitoring continues. Thus, even though there are some peculiar features and history of the coral reef biome at Biosphere 2, it has similar metabolic performance as natural reef areas with a similar morphology.

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