

Organism Responses to Rapid Change: What Aquaria Tell Us About Nature¹

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SYNOPSIS. Living corals are routinely collected and shipped to destinations thousands of miles from their point of origin. The fact that corals can survive the rigors of collecting, transport, and acclimation to totally artificial environments was considered impossible not long ago, but hobbyists and some researchers have persevered and have developed aquarium systems and techniques capable of maintaining corals in apparently healthy condition for many years. In particular, new lighting equipment, advances in the control of water chemistry, and new technology for simulating water movement have all contributed to the ability to keep corals alive indefinitely in captivity. Despite the completely artificial conditions of most aquariums, coral extension rates and calcification rates in some aquarium systems are close to those reported for natural reefs, although anomalies have been observed such as decreased skeletal density and unusual changes in colony morphology. Nonetheless, aquariums present real opportunities to culture corals for a variety of bioassay, medicinal, and conservation purposes. As model reef communities (“microcosms”), these systems allow us to test hypotheses concerning the effects of rapidly changing environmental conditions.

INTRODUCTION

Colonies of alcyonarian and scleractinian corals have survived more than a decade in some closed-system aquariums, contrary to the notion that corals are too delicate to survive in captivity. Even the most difficult corals, such as *Acropora* spp. are now cultured in home aquariums and public aquariums in Europe, the United States, Australia, Japan and elsewhere. Despite these successes, the general opinion remains that corals are too delicate to survive the rigors of collecting, shipping, and acclimation to artificial conditions. This opinion has persisted because little information on this subject has been published in the primary literature. This view is clearly in need of revision. At best, skeptics have stated that corals might survive in aquariums, but they would not reproduce (Porter, in Derr, 1992). But even this goal has been achieved. Asexual planulation and the formation of new colonies by *Pocillopora damicornis* and

Tubastrea spp. are common occurrences in aquariums. And recently, spawning among captive acroporids and other coral species has been observed, although colony formation following these spawnings has not been reported (Atkinson *et al.*, 1995; Alf Nilsen, personal communication).

Corals do not survive equally well in all aquarium systems and the reasons why may be instructive in understanding how coral reefs function in nature. But this problem is not likely to be resolved soon because few rigorous analyses have been conducted and some systems involve proprietary or patented devices. Furthermore, much of the information is anecdotal and reported in hobby magazines and popular books. Nevertheless, the review presented here may be useful to provide a different perspective on the ability of corals to acclimate to a unique set of rapidly changing environmental conditions that are very different from any natural habitat.

The development of reef-aquarium systems

Reef fishes have been maintained in aquariums for decades, both in large public aquariums and in home aquariums, but corals never survived more than a few months

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in these simple saltwater aquarium systems. Carlson (1987) and Delbeek and Sprung (1994) have reviewed the development of systems designed specifically to maintain living corals. A brief historical account is presented here both to familiarize readers with some of the terms used by aquarists, and also because it is instructive to understand how simple aquarium systems were transformed into the complex systems now used to maintain living corals.

The first long-term success maintaining living corals (apart from marine laboratories with running seawater) was reported by the Noumea Aquarium in New Caledonia in 1956 (Catala, 1964). The Noumea Aquarium collected corals on local reefs and utilized natural, unfiltered seawater, and natural sunlight to illuminate their aquariums. The Waikiki Aquarium, the Monaco Aquarium, and a few other public aquariums developed exhibits of living corals beginning in the mid- to late-1970s. These aquarium systems were dependent on a continuous supply of seawater ("open system") and thus the aquarium seawater conditions were not much different than those on the reef.

Straughan (1959) published one of the first comprehensive accounts describing the methods to set up a "closed-system" marine aquarium for fishes. This system has been called the "sterile system" because everything in the aquarium was either thoroughly cleaned or quarantined before going into the aquarium. The substratum was sterile silica sand placed over a sub-gravel filter plate. The saltwater was made from commercially prepared seasalt and mixed with dechlorinated tap water or distilled water. Sterile system aquariums are still in wide use today with few modifications from those originally described by Straughan. However, while fish survive reasonably well in these aquariums, corals do not. In the early years, the lack of plankton was cited as the primary reason for failure with corals. The corals did not die immediately, but gradually regressed over weeks or months, even when significant amounts of plankton were added. Clearly, one or more environmental components were lacking. We now know that inadequate management

of water chemistry, insufficient lighting, and poor water circulation were responsible for these early failures.

An Indonesian aquarist, Lee Chin Eng, described a completely different aquarium system (Eng, 1961). He called his system "nature's system," but it has since become known as the "natural system." He used unfiltered natural seawater, reef rocks with all their associated plants and invertebrates, living corals, and provided natural sunlight supplemented with fluorescent lighting. He argued against the use of any filtration but did recommend vigorous aeration with the use of an airstone. Risely (1971) published a book describing Eng's system and its success in keeping a wide variety of corals alive. Hobbyists in the United States and elsewhere were unable to duplicate this system and as a result, it was virtually ignored for many years and the conclusion persisted that living corals were too delicate to survive in aquariums.

A few hobbyists and researchers in Europe and the United States persisted during the 1970s and early 1980s to develop aquarium systems that would duplicate conditions prevailing on coral reefs with the goal of keeping corals, and entire reef systems, alive indefinitely. Two divergent systems emerged from these efforts by the early 1980s, and have since become known as the "algal turf scrubber system," and the "Berlin system." A third system, known as the "Jaubert system" was under development during the same period but has only recently become popular among aquarists.

All three systems share similarities in the use of aragonite sand; live rocks; moderate to strong water circulation; and intense lighting using metal halide, very-high-output (VHO) fluorescent lamps and blue actinic lamps. They differ in the methods used to eliminate nitrate and maintain calcium and alkalinity levels. The understanding of the importance of these environmental components finally led to the successful maintenance of corals in closed-system aquariums.

Algal turf scrubber system

Walter Adey developed a reef mesocosm as a tool for researchers to maintain and

monitor reef systems in the confines of an aquarium; this system has since been patented (Adey, 1983; Adey and Loveland, 1991; Goodlett, 1983). Adey's mesocosm is based on the concept that coral reefs tightly recycle nutrients, and that algal turfs play a significant role in moderating inorganic nutrients on reefs. To simulate this, Adey directs water from the aquarium to shallow trays where turf algae are cultured. Nitrate generated by the aquarium organisms is removed by these "algal turf scrubbers," and the treated water is returned to the exhibit. Excess algae from the scrubbers may be dried and returned to the system, although it is often weighed and discarded.

Calcium and alkalinity are presumably maintained through dissolution of aragonitic rock and sand in the aquarium, although opinions vary on whether dissolution alone is sufficient to maintain calcium levels. Maintaining constant light on the algal turf scrubbers minimizes day-night pH shifts because algae remove CO₂ that would otherwise accumulate overnight and reduce the pH.

Some changes to the original concept have evolved over time (W. Hoffman, personal communication). Freshwater additions are now pre-treated through a deionizer and reverse-osmosis purifier, then passed over activated carbon. The pH of this freshwater is around 6.0. To raise the pH, the freshwater is poured through a column of *Halimeda* sand—a process that both raises the pH and increases the calcium concentration and alkalinity. The resulting water has a pH of 9.0 when it is added to the aquarium. In addition, the 6,800 liter Smithsonian tank receives about 4–8 liters of ocean water daily. Originally, this water was taken directly from the ocean and processed to remove excess nitrate, but more recently a commercial seasalt (Instant Ocean[®]) is used for water replacements.

The Great Barrier Reef Aquarium in Townsville is the largest algal turf scrubber system (2.5×10^6 liters), but it too has been modified from the original concept. The water is now dosed with ozone (0.3 ppm) to clear the water of yellowing, organic compounds (Paul Hough, personal communication). These organic compounds are

the result of waste products produced by the corals, plants, and other organisms in the aquarium, and they may also include degradation products from chlorophyll originating in the algal scrubbers (T. Goertemiller, personal communication). Many of the corals in the Great Barrier Reef Aquarium have survived very well, but acroporids have proven difficult to maintain for long periods in this system (P. Hough, personal communication).

Adey was concerned not only with the maintenance of macro-algae, invertebrates and fishes, but also with plankton. He stressed the importance of using screw or diaphragm pumps that he felt were less damaging to plankton than centrifugal pumps used on most aquarium systems. He also provided refugia tanks as sanctuaries for small invertebrates and plants to grow and reproduce in isolation from the herbivores and predators in the main aquarium.

The Berlin system

While Adey's goal was to simulate the physical, chemical, and biological conditions of a coral reef, hobbyists, particularly those in Germany, took a different approach. These aquarists were not focused on creating coral reef microcosms. Rather they concluded that mini-reef aquariums are not self-maintaining systems, and therefore they developed equipment, additives, and techniques to maintain the physical conditions in their aquariums.

Wilkens (1975, 1976) and others in Europe, developed what they called the "mini-reef" aquarium system which has become known in the United States as the "Berlin System." Delbeek and Sprung (1994), and Nilsen (1996) have published thorough descriptions of this system. Rather than relying on biological processes to regulate water quality in the aquarium, they instead developed mechanical devices to achieve the desired results. The Berlin system is not an intentional simulation of nature, but rather a practical method for achieving water quality parameters approximating those that occur on reefs. These aquarists recognized that organic nutrients are not rapidly recycled in aquaria, and also that calcium and alkalinity levels decline even in the pres-

ence of significant volumes of aragonitic sand and rocks.

The Berlin system requires the manual maintenance of calcium and alkalinity levels. Calcium-water ("*kalkwasser*") additions are made daily, or continuously, to replace water loss due to evaporation, and to restore calcium loss due to calcification. The controlled addition of a saturated solution of CaOH_2 (or sometimes CaCl_2 or CaOH) is sufficient to maintain both calcium and alkalinity at levels within the range of those recorded on coral reefs.

Organic nutrients tend to accumulate in aquarium systems. To minimize this, a simple but effective device was developed that takes advantage of the adsorptive properties of small air bubbles to remove carbohydrates, proteins, phenolic compounds and other dissolved organic molecules. This device is known as a protein skimmer or foam fractionator. By forcing water down a column against a counter-current of fine bubbles, the water is stripped of organic compounds by adsorption to the bubbles. A thick, brown froth collects in a cup at the top of the column and clean water exits at the bottom where it returns to the aquarium. The protein skimmer thus serves as an export mechanism to remove organic nutrients before they can be broken down and mineralized to ammonia and ultimately oxidized to nitrate. Marlin Atkinson (personal communication) has suggested that these devices may also facilitate the rapid exchange of CO_2 with the atmosphere, and thereby constrain CO_3^{2-} especially if used in conjunction with *kalkwasser*, and if the pH is maintained at or above 8.2.

There is a persistent belief among hobbyists that corals grow best when additions of SrCl_2 , KI, and various trace elements are periodically added to their tanks (Delbeek and Sprung, 1994; Sprung and Delbeek, 1997; Nilsen, 1996). A discussion on the validity of adding SrCl_2 appeared in the winter 1995 issue of *Aquarium Frontiers* (Shimek, 1995; Buddemeier, 1995; Bingham, 1995; Sprung, 1995). However, few rigorous studies have been undertaken to determine what, if any, beneficial effects these additions provide.

The Jaubert system

Jean Jaubert introduced a different concept for the removal of excess nitrate from reef aquarium systems using the sand bed for denitrification (Frakes, 1993; Jaubert, 1989). Nitrate in the water is reduced by anaerobic bacteria in deep layers of the sand bed and ultimately released as nitrogen gas. To improve the diffusion efficiency through the sand bed, the bed is elevated off the bottom of the tank using a grating covered with fine screen. This false-bottom creates a water space, or plenum, below the sand which aids in the uniform mixture of dissolved gases and nutrients throughout the overlying sand. The depth and fineness of the sand is critical; sand that is too deep or too fine may impede diffusion and create anoxic zones where hydrogen sulfide may form, which can be highly detrimental to the corals and fishes.

A calcium ion concentration of 480–520 mg liter^{-1} is maintained in this system apparently by the dissolution of the aragonitic sand due to acids produced by the denitrifying bacteria and other biological activity in the sand. Low pH during the night may result in some additional calcium being released from the sand. The design of the sand bed is reportedly sufficient to maintain calcium and alkalinity without the need for additions of *kalkwasser*, as in the Berlin system and the algal turf scrubber system.

Of the three systems briefly described here, all three are capable of maintaining living corals, but aquarists have not been rigorous in tracking and reporting the long-term survival of individual corals and entire collections. One home aquarist using the Berlin Method in New York has maintained various acroporids for more than 7 years, and *Turbinaria* sp. and *Plerogyra sinuosa* both for more than 10 years (T. Siegel, personal communication), and judging from comments received from other aquarists, this longevity in captivity is not unusual. However, the number of corals lost while learning the techniques to keep them alive is unclear. For algal turf scrubber systems, the Great Barrier Reef Aquarium reports coral survival at 85% per year for all genera, which increases to 98.6% if the genus

Acropora is excluded (Paul Hough, personal communication).

Collection conditions

The methods used by us (Waikiki Aquarium) are described here as an example of the conditions corals experience from the time they are collected to the time they are received at the Waikiki Aquarium. These methods are not used by all collectors, and may in fact be far less stressful than the conditions experienced by corals in the commercial trade. These techniques have not been completely described in hobby publications, nor in the primary literature, and therefore they are presented here in some detail both as an indication of the conditions that corals may experience, and also as a guide to researchers who may be unfamiliar with techniques for collecting and handling living corals.

We collect small fragments of *Acropora* spp. and other branching corals rather than whole colonies, whenever possible. These fragments are often found lying around the base of parent colonies. In our experience, fragments between 5–10 cm in length are the easiest to handle and survive better than larger or smaller fragments. We place each fragment inside a small plastic bag underwater and then place it inside a 3-liter plastic container with a tight-fitting lid. A dozen or more bags with fragments can be stuffed inside one plastic container. The plastic bags provide cushioning to protect the corals from damage during the dive, and also from touching other corals. On the boat, each bag containing a coral is transferred to an insulated cooler filled with seawater. The corals remain in the bags submerged in the cooler during the trip back to shore, which can take several hours.

Once in the shore-based holding tanks, we feel it is important to stabilize the corals as soon as possible so they cannot roll around. We glue a square plastic plug to the base of each coral (“faucet adapters” obtained from hardware stores) using an underwater epoxy (Z-Spar Splash Zone Compound[®]). The plastic plugs are inserted into plastic eggcrate trays allowing dozens of fragments to be maintained in small shallow holding tanks each equipped with an

airstone. Water changes are made once or twice daily. Corals can be maintained this way for at least one week under standard fluorescent lighting.

In 1995, while in the Solomon Islands, we maintained four, 5 cm fragments of *Acropora grandis*, and *A. latistella* for 18 days in a 4-liter, clear plastic container. The corals were mounted on plastic plugs on an eggcrate tray inside the container. Aeration was provided by a battery-powered air pump, and they were exposed to direct sunlight for 30 min each day. As of August, 1998, these fragments are now large colonies 24 cm in height at the Waikiki Aquarium.

We have observed that newly collected fragments often deteriorate in holding tanks within a few days after collection, despite frequent water changes. Preliminary trials using chloramphenicol at a dosage of 8 mg liter⁻¹ over 48 hr on *Acropora* spp., *Seriatorpora hystrix*, *Porites cylindrica*, *Echinopora* sp., *Tubipora musica*, and *Sarcophyton elegans* have shown positive results and no mortality. But further controlled studies are needed to verify the validity of this application.

One major coral importer in the United States, who also cultures corals in large tanks in a greenhouse in Michigan, has described how corals are commercially collected in the south Pacific (R. Perrin, personal communication). Collectors using a hammer and chisel collect entire colonies that are placed loosely in buckets, usually touching each other. These buckets are filled with seawater and kept shaded. The shore-based holding facilities are shaded concrete troughs filled with seawater and aerated. The corals are collected 1–3 days prior to shipping, and then packed for the 12-hour flight to Los Angeles where they are trans-shipped to Michigan.

Shipping conditions

Corals we collect are shipped to Hawaii inside the same plastic containers used underwater on the reef and on the boat. The shipping procedure has been described as the “dry method” (Bronikowski, 1982; Carlson, 1987). Each fragment is wrapped with one or more plastic strips (about 60

cm × 1.5 cm) much as a spider would wrap an insect. Additional strips are placed on the bottom of the container for cushioning, and a layer of wrapped fragments is then placed inside, followed by another layer of strips and then more fragments until the container is full. The container is then filled with seawater. Usually 10–20 fragments can be packed in one container.

When all of the fragments are packed, each container is drained leaving the corals damp but not submerged, hence the designation “dry method.” Oxygen is injected into each container, with care taken not to chill the corals. Immediately thereafter the lid is snapped on the container and taped shut. All of the containers are packed together inside an insulated box. This method is successful provided the corals reach their destination within 20 hr, and provided the box is not exposed to extreme temperature fluctuations. Since there is virtually no water surrounding the corals, the corals are more vulnerable to temperature extremes when shipped “dry.” We have successfully shipped over a thousand fragments of corals, mostly *Acropora* spp. using the dry method with excellent results and little mortality.

Commercial collectors may use the dry method, but more often they ship their corals in bags of seawater. They usually collect whole colonies rather than fragments, but these are generally small colonies under 15 cm in diameter or branch length. One successful shipping method involves tying the coral to a piece of styrofoam with a rubber band, then floating the coral upside down in a plastic bag partially filled with seawater. Oxygen is usually injected into the bag, which is then sealed and shipped in an insulated box to its destination. Corals from Tonga are flown directly to Michigan, and arrive after 40 hr (R. Perrin, personal communication). These corals are each wrapped in a 35-cm² plastic sheet and then placed in bags with seawater. Survival of these corals after arrival is reported to be excellent, but no quantitative data are available on the survival of commercial coral shipments between collecting and arrival.

Aquarium conditions

Living corals are more difficult to maintain in aquariums than are most marine fishes. Aquarists have to be more cognizant of the physical, chemical and biological requirements of corals if they expect to achieve success. Lighting, water chemistry, water motion, and temperature are the primary factors of concern to aquarists maintaining living corals. Biological factors, e.g., coral aggression, corallivory, disease and competition from algae, are also important but will not be discussed here (see Delbeek and Sprung, 1994).

Lighting

Corals, or more correctly their zooxanthellae, require light of the right intensity, spectrum and duration. Aquarists have a variety of lamps to choose from to illuminate their aquariums. Metal halide lamps and very-high-output (VHO) fluorescent lamps are popular either as the sole source of light or in combination, and are often used in conjunction with blue actinic fluorescent lamps. As a rule-of-thumb, aquarists use 2–5 watts of light per gallon for standard aquariums up to about 600 liters. The lamps most used by aquarists have a color temperature of 5,500–20,000°K, although some higher temperature bulbs are also in use.

Several aquarists using LiCor quantum meters have measured light levels in aquariums. Most home aquariums are less than 60 cm deep and measurements from five aquariums ranged from 327–900 $\mu\text{E m}^{-2}$ (D. Riddle, personal communication). Another aquarist using the same instrument measured light levels of 200–400 $\mu\text{E sec}^{-1}$ just below the surface of the water (R. Harker, personal communication; Harker, 1997). Adey and Loveland (1991) reported light levels of 500–900 $\mu\text{E m}^{-2} \text{sec}^{-1}$ in the Smithsonian coral reef microcosm, illuminated with 1,000-watt metal halide lamps. This is less than the 1,100 $\mu\text{E m}^{-2} \text{sec}^{-1}$ measured by Adey at a depth of 1 m on a Caribbean coral reef.

Ultraviolet light is nearly absent in home aquariums, and most aquarists are not concerned about this situation. Metal halide lamps may generate some ultraviolet light

but glass or plastic shields usually eliminate this. UV A + B measured just below the surface on an indoor aquarium at the Waikiki Aquarium ranged from 3–27 $\mu\text{E m}^{-2} \text{sec}^{-1}$. This aquarium is illuminated by two 400-watt metal halide lamps (20,000°K) plus direct sunlight passing through a 0.6-cm plexiglass skylight. Outdoor aquariums measured at the same time received between 137–192 $\mu\text{E m}^{-2} \text{sec}^{-1}$ (using an Apogee Instruments Ultra Violet Meter [model UVM] with underwater sensor, 250–400 nm range).

Water chemistry

Hobbyists have to make, and adjust, the chemistry of artificial seawater using commercially available seasalts, plus various reagents and natural additives. There are many brands of seasalt on the market and most are very good at creating saltwater which is a close approximation of seawater. Fresh water to mix with the seasalt is first processed through reverse osmosis/deionizing units that are also readily available to hobbyists.

Perhaps the most significant advance in the care of living corals in aquariums came about when aquarists understood the importance of maintaining alkalinity, pH and calcium levels approximating those on coral reefs. These three parameters determine calcium carbonate saturation state, which has been shown to be a control on calcification (Gattuso *et al.*, 1999; Kleypas *et al.*, 1999; Langdon *et al.*, 1999). Prior to this time, hobbyists (and researchers) too often focused on nutrients in the water as the most important quantities to measure and minimize, while often nearly ignoring alkalinity and calcium. A variety of test kits is available today to hobbyists to measure alkalinity, pH and calcium in their aquariums. While these kits are not always dependable and techniques may vary, the results do give an indication that hobbyists are maintaining values close to those in nature. These test kits invariably give calcium readings in mg liter^{-1} , and either degrees of hardness (dKH) or millequivalents (meq) for alkalinity.

The controlled addition of a saturated solution of CaOH_2 (*kalkwasser*), is capable of

maintaining a calcium ion concentration of 350–500 mg liter^{-1} and an alkalinity of 2.5–3.0 meq in home aquariums. But these levels may fluctuate dramatically in a small closed-system aquarium. According to Delbeek and Sprung (1994) corals will survive and grow in aquariums with calcium levels less than 400 mg liter^{-1} , but only when the alkalinity (carbonate hardness) is normal or high. They state that difficulty maintaining living coral occurs more often as a result of low carbonate hardness than low calcium levels. Without the addition of calcium to a reef aquarium, calcium levels will fall to about 250–350 mg liter^{-1} .

Accidental overdosing with CaOH_2 will cause a sudden increase in pH. One aquarist has reported that many of his corals died when the pH reached 9.5–10.0 for about 6 hr (A. Nilsen, personal communication). He lowered the pH back to normal by injecting CO_2 into the water. While many of his corals died, small pieces survived and later grew back. Another aquarist reported a pH of 9.0 for over 12 hr with no effect on corals including *Montipora* sp., *Trachyphyllia geoffroyi*, and the soft corals *Cladiella* sp., and *Sarcophyton* sp. (Larry Jackson, personal communication).

The waters around coral reefs are generally oligotrophic and therefore aquarists strive to maintain low levels of inorganic nutrients such as ammonia, nitrate and phosphate. Most hobby test kits are inadequate to detect very low levels of these nutrients (lower limit of detection for nitrate-N is about 10 mg liter^{-1} , and phosphate at about 0.2 mg liter^{-1}) and hobbyists often report, probably erroneously, zero readings for ammonia, nitrate and phosphate in their aquariums. Atkinson *et al.* (1995) reported that corals can thrive in water with relatively high levels of inorganic nutrients but these are rapidly removed by the corals and algae.

Water motion

Atkinson *et al.* (1994) have demonstrated the importance of water motion for corals through the disruption of the so-called “diffusion boundary layer.” A variety of submersible pumps, dump buckets, automatic siphons, and other surge generating devices

are in use on both large and small aquariums with living corals (Adey and Loveland, 1991; Carlson, 1996). Aquarist Dana Riddle using a Marsh-McBinney FloMate 200 electronic water velocity meter has recorded water velocity measurements in home aquariums. The most popular water motion devices are submersible power heads that produce flow rates at the nozzle of 26–157 cm sec⁻¹, but this rate rapidly diminishes with distance to 3 cm sec⁻¹ or less. The maximum flow rates recorded by Riddle were obtained from an automatic siphon device (see Carlson, 1996) producing flow rates up to 2.0 m sec⁻¹.

Temperature

Aquarists maintain their aquariums at temperatures similar to those on coral reefs, around 21°–27°C. Higher temperatures often occur during summer months and when refrigeration systems malfunction. Temperatures of 32°–35°C over a one-day period caused all corals in one aquarium to bleach (C. Bingman, personal communication). However, most of the corals in this system quickly recovered, including several acroporid corals.

Calcification rates

Only a few measurements of calcification rates in aquariums are available, and all are from public aquariums. The Great Barrier Reef Aquarium in Townsville, Australia uses an algal turf scrubber system. They report seasonal calcification rates ranging from 0.8–2.3 gm CaCO₃ m⁻², with an annual mean of 5.7 kg CaCO₃ m⁻² yr⁻¹ over a ten-year period, based on pH, alkalinity and temperature data used in Kinsey's (1985) calcification formula (P. Hough, personal communication). The Ocean biome at the Biosphere 2 Center, which also has an algal turf scrubber system, has reported calcification rates of 0.7–5.0 kg CaCO₃ m⁻² yr⁻¹ (Langdon *et al.*, submitted). At the Waikiki Aquarium, the community calcification rate in an outdoor tank was estimated at 4.7 kg CaCO₃ m⁻² yr⁻¹ (Atkinson *et al.*, 1995). Community calcification in the indoor "surge corals" exhibit was determined from the increase in wet weight of the corals over a 37-month period (Table 1). Fol-

lowing Atkinson *et al.* (1995), we attributed 80% of the weight to the calcium carbonate skeleton, and measured the area of the tank at 1.4 m⁻². The calcification rate was estimated to be 6.5 kg CaCO₃ m⁻² yr⁻¹. Kinsey (1985) has reported calcification rates in the field ranging from 0.5–6.5 kg CaCO₃ m⁻² yr⁻¹ for a reef flat to 4.0–12.0 kg CaCO₃ m⁻² yr⁻¹ for "high activity areas of near total cover by hard substratum."

While aquarists often report rapid growth of their corals, actual extension rates have rarely been measured. Stanley Brown (personal communication) has reported extension rates ranging from 2 cm yr⁻¹ in *Pavona cactus* to 15.2 cm yr⁻¹ in *Acropora microphthalma*. Similar results and photographs were published by Nilsen (1992) for a variety of acroporid corals maintained in Norway. Atkinson *et al.* (1995) reported extension rates of 12.7 cm yr⁻¹ for *A. elseyi* and 20.6 cm yr⁻¹ for *A. pulchra* for corals at the Waikiki Aquarium.

Even though corals in aquariums may calcify and grow at rates close to those in the wild, some aquarists have reported that the skeletons appear to be less dense and quite fragile. To test this observation, we compared the density of captive grown *A. microphthalma* with a similar sized fragment taken from a wild colony. Both the wild and captive reared specimens originated in Fiji, but the captive specimen grew in an aquarium for six years. All fragments were thoroughly cleaned and dried, and then weighed on a metric balance. The volume of each specimen was determined by measuring the displacement of water in a graduated cylinder. To reduce the possibility of error due to air trapped within the skeleton, we used the mean value of five consecutive measurements. The density was then calculated as the weight/volume. The specimen from the wild had a density of 1.16 g cc⁻¹ while the captive grown specimen had a density of 0.61 g cc⁻¹.

A similar test was conducted on specimens of *A. pulchra* from Tumon Bay, Guam. Specimens collected from Tumon Bay had a density of 1.23 g cc⁻¹, but after six years in captivity at the Waikiki Aquarium, the cultured coral had a density of 0.81 g cc⁻¹. To date, these are the only such mea-

TABLE 1. Change in wet-weight of corals over a 37-month period in the Waikiki Aquarium "surge corals" exhibit.*

Species	Weight 1993 (kg)	Weight 1996 (kg)	Δ (kg)
<i>Pocillopora eydouxi</i>	2.50	4.27	1.77
<i>P. meandrina</i>	0.23	0.36	0.13
<i>Stylophora pistillata</i>	0.36	1.24	0.88
<i>Acropora formosa</i>	0.22	2.46	2.24
<i>A. sarmentosa</i>	0.09	0.82	0.73
<i>A. pulchra</i>	0.58	2.89	2.31
<i>A. secale</i>	0.13	2.08	1.95
<i>A. microphthalma</i> + <i>A. elseyi</i>	4.44	14.88	10.44
<i>Galaxea fascicularis</i>	0.11	0.37	0.26
<i>Lobophyllia hemprichii</i>	1.00	2.34	1.34
<i>L. hemprichii</i>	0.42	1.58	1.16
<i>L. hemprichii</i>	0.34	1.24	0.90
<i>L. hemprichii</i>	2.10	6.07	3.97
<i>Platygyra lamellina</i>	1.50	2.62	1.12
<i>P. lamellina</i>	0.48	0.48	0.00
<i>Leptoria phrygia</i>	0.21	0.23	0.02
<i>Diploastrea heliopora</i>	0.26	0.64	0.38
<i>Goniastrea retiformis</i>	0.50	0.67	0.17
<i>Favia pallida</i>	0.36	0.70	0.34
<i>F. speciosa</i>	0.46	0.92	0.46
<i>Euphyllia glabrescens</i>	0.31	4.88	4.57
Totals	16.60	51.74	35.14

Calcification rate = $[35.14 \text{ kg CaCO}_3 \times 3.08 \text{ yr}^{-1} \times .8] \times 1.4 \text{ m}^{-2} = 6.5 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$.

* Corals were weighed in air after removal of excess water. The magnitude of weight changes reflects the initial size of the corals, and their morphology, e.g., branching vs. massive. To calculate the calcification rate, 80% of the wet weight was attributed to the calcium carbonate skeleton; the surface area of the reef was 1.4 m².

surements taken on captive grown corals compared to those from the wild and they do support the observation that captive grown corals are less dense.

DISCUSSION

Walter Adey has long advocated the use of coral reef mesocosms as tools to provide insight into complex reef communities (Adey, 1983, 1987). However, surprisingly few researchers have taken advantage of reef aquarium systems to study the responses of corals and reef communities to environmental perturbations. The purpose of this review has been to offer a different perspective on the tolerance of corals to changing environmental conditions, and also to stimulate an interest among coral biologists to use aquarium systems to test hypotheses related to coral biology. Presently, aquarium science is in a "natural history" phase of observation, description and hypothesis development, but actual hypothesis testing using aquariums as tools has been rare.

Within the context of this symposium, it is eminently possible to develop aquarium systems to directly test hypotheses relating to the responses of corals to increasing levels of atmospheric carbon dioxide, temperature, nutrients, ultraviolet radiation and other environmental factors. Langdon (this symposium) has already demonstrated the feasibility of such an approach in the Biosphere II system, although his aquarium system was deficient in coral and is very large. Atkinson *et al.* (1995), using aquariums, have shown that corals can grow in seawater with relatively high levels of inorganic nutrients and also very high levels of dissolved CO₂ gas. The fact that corals thrived in this water seems to contradict conclusions advanced in this symposium that high CO₂ may inhibit calcification. Is this an artifact of the aquarium conditions, or some other peculiarity of the aquarium water, or can corals in fact acclimate to these unusual environmental conditions? More research on the relative effects of

light, nutrients and $p\text{CO}_2$ is warranted, and small, easily managed aquarium systems are practical for conducting this kind of research. Furthermore, wild-caught corals are readily available in pet stores in nearly every large city in the United States, and cultured corals are also becoming available allowing replicate tests on genetically identical clones.

Reef aquariums are not complete simulations of nature. Compared to coral reefs, aquarium systems are very small; they are low in diversity; they are deficient in plankton, larvae, corallivores, parasites and pathogens; they are relatively high in nitrate and dissolved organic nutrients; and significant effort is usually required to maintain calcium, pH and alkalinity levels. Furthermore, light intensity is low, ultraviolet light is virtually absent, and the light field is usually unidirectional and unvarying, with no lunar cycles or seasonality. Flow rates, which average around 3 cm/sec are very low, consistent with deep fore-reef environments (Sebens, 1997).

The fact that an aquarium is not, and probably never will be, an exact simulation of nature, should not detract from its potential power to detect biological responses to extreme environmental changes. In this respect, aquariums are analogous to mathematical models which also are not exact simulations of nature but nonetheless can offer predictive power and insight into the nature of biological systems.

Corals do survive and often thrive in these artificial environments. This opens up a wide range of opportunities, including the culture of genetically identical colonies (clones) for bioassay studies (potentially the same genetic strain might be available for decades or perhaps indefinitely); "designer colonies" may be developed for medicinal purposes such as bone transplants, particularly as we learn more about the factors affecting the shape and density of the skeleton; if reefs continue to disappear, genetic diversity of some species may be maintained in thousands of public aquariums, home aquariums, and research laboratories for possible future reintroduction to the wild when environmental conditions improve; and the rapid recolonization of de-

nuded reefs might be facilitated by the mass culture of corals on coral farms. Coral farms may also produce much of the coral in demand for home aquariums and thereby reduce the negative effects from over-harvesting on coral reefs.

Hobbyists rarely analyze the environmental conditions in their aquariums, but enough is known to present an overview of their experiences. What is most surprising is that corals appear capable of surviving the rigors of collecting, shipping, and transfer to totally artificial conditions. Clearly corals are not as delicate as is widely believed. Furthermore, aquarists report that they rarely provide any acclimation period for their corals. They are transferred directly from shipping containers to aquariums with artificial seawater and artificial lights. But the maintenance of living corals in aquariums requires considerable diligence and knowledge, particularly in the management of lighting, water flow, and water chemistry, and beginning aquarists may have considerable difficulty understanding and meeting these requirements.

During the preparation of this paper, many of the aquarists cited herein shared the following conclusions over the Internet, based on their collective experiences with corals in aquariums. These comments are not universally agreed upon, but I offer them here as an indication of the range of observations that aquarists have made, and which could lead to stimulating future research. For now, these observations suggest that corals are capable of a wide range of responses that may never be observed *in situ*.

1. The growth forms of corals may change dramatically in aquariums often making them unrecognizable even to coral taxonomists (Carden Wallace and John Veron, personal communications). Corals may also grow in unusual directions, or the polyps may extend well beyond the corallum (coral taxonomists are often unable to identify aquarium-grown corals).
2. The skeletal density of corals in the aquarium may be significantly less than their wild counterparts, and in some

- circumstances may be so soft that it crumbles when touched.
3. Relatively high inorganic nutrients do not appear to limit the growth of corals in aquariums (see Atkinson *et al.*, 1995).
 4. Small coral colonies acclimate more successfully to aquariums than do larger colonies.
 5. Corals appear to be highly sensitive to changes in lighting. What may appear to the human eye to be a subtle change in lighting, *e.g.*, changing a lamp, may result in bleaching.
 6. Most corals can tolerate exposure to air for 18–24 hours provided they remain damp.
 7. Bacterial infections are common in captive corals but can often be cured with antibiotics such as chloramphenicol (Craig Bingman, personal communication).
 8. Rapid tissue necrosis is common among captive corals usually starting at the base of the coral and working its way to the tips of branches.
 9. The addition of plankton is not required to maintain zooxanthellate corals in most aquariums.
 10. Corals that ordinarily live in turbid and virtually stagnant lagoons, *e.g.*, *Plerogyra sinuosa*, will coexist in the same aquarium with corals obtained from wave-swept fore-reef environments, *e.g.*, *Acropora grandis*.
 11. Corals from the Caribbean and the Pacific will coexist in the same aquarium.
 12. Corals do not require the presence of any other animals in the aquarium to survive, with the exception of herbivores to control algal growth.
 13. Spawning among corals in aquariums has been reported but is rare, although asexual planulation is not uncommon in corals such as *Pocillopora damicornis* and *Tubastrea* spp.
 14. Brightly colored corals often lose these pigments within a week after being imported, although they may simply be masked by zooxanthellae.

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