Coral reef research: advances through the use of SCUBA

Michael A Lang
Smithsonian Institution, Office of the Under Secretary for Science, 1000 Jefferson Drive SW, Washington, DC 20560, USA

Abstract
Coral reefs are, per unit area, the most productive and diverse ecosystems on the planet. Their complexity and, in some places, fragility provide many complications to scientists conducting high quality research in these environments. Scientific diving has been, for the past six decades, a highly cost-effective and productive tool in coral reef research. Using high impact outputs and based mainly on the research supported through the diving programmes of the Smithsonian Institution, this review outlines some major scientific advances that have been made in coral reef research because of the support or use of SCUBA. The main areas of interest reported here are: algal sexual reproduction on coral reefs, coral spawning, conservation biology, coral diseases and declines, biodiversity, keystone species, biogeography of reef fishes, and DNA barcoding. The review concludes that significant advances in many areas of coral reef research were only achievable through diving-based approaches.

Keywords: SCUBA, coral reef research, biogeography, biodiversity

1. Introduction
Scientific diving allows scientists to closely observe marine organisms and ecosystems, and to systematically study the complexities of marine environments, such as coral reefs. Generally considered globally to be the most biologically diverse and productive ecosystems per unit area, the health of coral reefs is sensitive to human activities and environmental impacts (e.g. Gardner et al., 2003; Pandolfi et al., 2003; Crabbe, 2011). In the face of the global biodiversity crisis, the need for urgency could not be greater to discover, describe and classify the species of the planet in order to allow the conservation, management, understanding and enjoyment of the natural world (e.g. Thomas et al., 2004; Wernberg et al., 2012). As stated by Wheeler et al. (2004), “our generation is the first to fully comprehend the threat of the biodiversity crisis and the last with the opportunity to explore and document the species diversity of the planet”.

Coral reefs can present extremes in factors such as structural complexity and biodiversity (Carr et al., 2002); at the same time many are fragile environments and may be protected by local, regional, national or international laws. This presents many challenges for conducting methodical and productive scientific study. SCUBA presents a mobile, safe and cost-effective methodology for conducting coral reef research. It does, however, have its limitations as a research tool mainly in terms of the physiological constraints of scientists, which in turn restrict operational dive depths and durations. This can be overcome through use of underwater habitats and saturation diving techniques (e.g. Lindholm et al., 2005), but these are expensive and limit the underwater range of the diving scientists.

The coral reef literature is substantial. For this review, most examples represent significant, high-impact advances made in biodiversity-related research over the past few decades where the studies have been totally dependent on the use of SCUBA. In most cases, the examples are drawn from outputs achieved by the Scientific Diving Program of the Smithsonian Institution (Lang, 2005).

2. Geological history of coral reefs
Coral reefs are unique biogeological structures that thrive in clear, nutrient-poor (oligotrophic), tropical oceans and support a rich, diverse biological community. Reef systems are driven by the symbiosis between scleractinian corals and microscopic dinoflagellate algae (zooxanthellae) as their chief energy source. The largest, best developed, least polluted and least commercially exploited coral reef in the Atlantic region is the Mesoamerican barrier reef (Rützler and Macintyre, 1982; Macintyre and Rützler, 2000).

In 1998 the highest sea surface temperatures yet recorded caused severe bleaching of corals worldwide. This thermal anomaly induced mass mortality of scleractinian corals on lagoonal reefs in Belize, the first time that a coral population in the Caribbean had collapsed completely from bleaching,
Cores from these reefs were extracted with a diver-operated drill (MacIntyre, 1996) and showed that these events were unprecedented for at least the past 3000 years (Aronson et al., 2000). The coral reef cores also produced valuable data on reef community succession, rate of framework construction and post-depositional processes for interpretation by coral reef geologists.

3. Algal sexual reproduction on coral reefs
A remarkable spectacle was observed by Clifton (1997) while studying damselfish reproduction in Panama. Diving twice daily (pre-dawn and early afternoon) nearly continuously for 13 months, Clifton documented over 850 natural spawning events involving 24 different algal species off the Caribbean coast of Panama. These observations provided the first intimate details of a seaweed reproductive cycle.

Common tropical seaweeds, such as Caulerpa sp., are a familiar sight to divers on coral reefs. With their relatively large size and abundant distributions, these calcified green algae have long been recognised as an important source of food, shelter, competition and sediment within reef and seagrass communities. Green seaweeds, like some invertebrates (including corals), regularly undergo bouts of mass spawning, which result in clouds of sperm and eggs often shrouding the reef in a pall of green. Synchronous gamete release among neighbours boosts the concentration of eggs and sperm, increasing the likelihood that gametes from different individuals will meet. Each species has a highly specific time of gamete release, and more closely related species spawn at different times (reducing the likelihood that similar, but potentially incompatible, gametes will encounter one another).

As primary producers, these algae contribute significantly to nutrient flux on reefs and help sustain many reef-associated herbivores. As relatively large, structurally complex members of the benthic community, green algae compete directly with corals and other sessile marine organisms for space on reefs while simultaneously providing shelter for a myriad of others. Correlation between increasing green algal abundance, and declining coral cover and reef biodiversity emphasises their importance as a trophic node within the reef community. These algae also produce complex defensive compounds that alter the foraging habits of herbivorous fishes and invertebrates, and have potentially useful biomedical properties. Even in death, the heavily calcified thalli of the Udoteaceae contribute to sand production, reef building and other important geologic processes.

4. Coral reef research
4.1. Coral spawning
Corals are the building blocks of coral reefs and are renowned for the diversity of organisms they shelter. The most abundant and studied coral ‘species’ (Montastraea spp.) of the Caribbean is in fact a complex of at least three species: M. annularis, M. franksi and M. faveolata. All three species spawn in approximate synchrony, typically seven to eight days after the full moon in August (Knowlton et al., 1992). Even more surprisingly, these species each host a diverse array of symbiotic algal partners, so that the combinatorial diversity of Caribbean reefs is an order of magnitude greater than previously assumed.

The ecological importance of this diversity was highlighted during an episode of coral bleaching caused by a Caribbean-wide temperature increase in the summer of 1995. Only certain corals, and parts thereof, were bleached, and the pattern could be predicted by using diving surveys and interventions to work out which algae occurred where (Rowan et al., 1997). Thus, basic research on patterns of biodiversity led to important insights into the likely consequences of global warming.

In the recent past, Montastraea and several other corals have declined in abundance, which poses a threat to reefs both now and for future generations of corals. Montastraea does not fragment prolifically and, thus, sexual reproduction is critical for its long-term survival. It is not known what critical densities are needed to ensure fertilisation success during mass spawning events. This phenomenon of reduced population growth at low population size can place endangered species in a downward spiral from which they may not recover. Corals are long-lived organisms, making it difficult to assess how present reproduction will affect future abundance.

4.2. Conservation biology: coral reproduction and cryopreservation
Conservation biology research on coral reproduction and cryopreservation starts with coral recruitment, consisting of a cycle of spawning and fertilisation, swimming larvae, settlement and metamorphosis, growth and adulthood. Coral reproduction comprises individual polyps producing an egg bundle that exits through the pharynx. The work of Hagedorn et al. (2009) on sexual reproduction entailed frozen sperm fertilisation of live eggs. The asexual reproduction experiments utilised frozen whole segments of coral and stem-like cells from coral embryos.

Field monitoring for succession and coral settlement was conducted by SCUBA where settlement

22
plates were unscrewed from the benthos, the undersides photographed to monitor succession, and half of the plates were temporarily removed for microscopy to monitor for coral settlement and survival. The world’s first coral cryobank is held at the Smithsonian Institution. It contains 450 samples of endangered coral sperm and is maintained in liquid nitrogen at three locations worldwide. A. _palmata_ was one of the first corals listed as threatened under _Endangered Species Act_ 2006.

4.3. Coral declines and diseases

To monitor coral declines, a programme was established to quantify the long-term temperature change effects on the distribution and progress of black-band disease in reef corals. A bleaching event in 1998 killed almost all corals in the Pelican Cays, Belize, and those in the surrounding lagoon area (Aronson et al., 2000). A two-year scientific diving project at Cayos Cochinos, Honduras, documented the vigorous recovery process of coral reefs after Hurricane Fifi and the enforcement of a ban on all types of indigenous fishing pressures (Guzman, 1998). Other stressors include impacts such as coral lethal orange disease (CLOD) pathway from South Pacific coral reefs, as described by Littler and Littler (1995).

Marine environments are subject to man-made disasters such as oil spills on reefs. The escape of 100,000 barrels of oil into the mangroves and reefs of Bahia Las Minas (Caribbean) has had unexpectedly prolonged effects (Jackson et al., 1989). Oil seeped into the sediments around mangroves and returned to coat the coral reefs year after year during periods of heavy rain fall (exacerbated by the effects of deforestation), which slowly washed it out. Injury, post-impact regeneration and growth of corals were monitored by scientific divers at this oil spill site (Guzman et al., 1994). The skeletons of corals record the history of acute disasters as well as chronic stresses. X-ray analyses of corals done in response to the oil spill document a worrying decline in coral growth over the past century.

4.4. Coral reef biodiversity inventories

The _Natural History of the Pelican Cays, Belize_ was one of several diving-based coral reef biodiversity assessments (Macintyre and Rützler, 2000). Species richness is a good indicator of environmental quality, but it cannot be evaluated without substantial knowledge of the animals and plants inhabiting a particular ecosystem. Notwithstanding 50 years’ worth of detailed scientific diving observations, sample collections and studies of species interacting with one another and their environments, the biodiversity and interactive processes in the sea are much less visible and less well understood than those in terrestrial systems. The public, therefore, remains ill equipped to protect coastal environments and manage marine resources.

The dimensions of the problem are particularly evident in the Caribbean region, where population pressures, poor data on environmental quality, limited protective legislation or enforcement and recent natural disasters have all contributed to the degradation of important coastal habitats. The Pelican Cays are different from other mangrove islands (Macintyre et al., 2004) in that a red mangrove is anchored on top of a live and lush coral reef, not in mud. In addition, several of the cays exhibit unique physical characteristics such as deep blue lagoon-like ponds encircled by steep, lush coral ridges. The Pelican Cays archipelago biodiversity inventory (Table 1) uncovered species richness and live surface cover that is unparalleled in the Caribbean. The causes of this unusually high biological diversity are not well understood, but there is significant concern for its future.

Similar inventories were made at Bocas del Toro, Panamá, where diving was employed to collate lists of the major marine faunal and floral groups (Collin, 2005; Collin et al., 2005). This was accomplished through a series of marine workshops, resulting in photographic identification guides and species lists.

4.5. Coral reef monitoring

The Panama Coral Reef Monitoring Network was an outgrowth of the Galeta Oil Spill Project in 1985. Oil pollution, temperature (Guzman and Cortes, 2007), nutrient pollution and sedimentation are the primary stressors that triggered coral reef decline. The Smithsonian Tropical Research Institute’s network presently monitors 33 reefs, including 17 in the Pacific (13 inside marine protected areas) and 16 in the Caribbean (six inside marine protected areas).

Monitoring of the Las Perlas Archipelago Marine Reserves Network in the Pacific started with a diving-based mapping initiative of the distribution

| Table 1: Diversity inventory of select Pelican Cays fauna and flora (Macintyre and Rützler, 2000) |
| --------------------------------- | ----------------- |
| Ascidians                        | 70 spp., 60% of all Caribbean spp. |
| Echinoderms                      | 52 spp., 10 reported for first time in Belize |
| Sponges                          | 147 spp., consisting of 45% of new spp. or variants |
| Encrusting Forams                | 7 spp., including 2 new spp. |
| Macrophytes                      | 148 spp. of algae and 4 spp. of vascular plants |
| Microplankton                    | 110 spp. |
| Bryozoans                        | 31 spp. |
| Corals                           | 8 spp. |
of reef coral diversity, reporting a total of 56 species (19 hard and 37 soft corals) and giving the descriptions of key hotspots (Benfield et al., 2007; Mair et al., 2009). Other objectives included the identification of 37 nesting sites of five species of sea turtles, and whale shark research by acoustic and satellite tracking for connectivity in an attempt to understand migration patterns and basic ecology. Protection of megafauna triggers a trickle-down conservation effect for vulnerable species protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), with monitoring of the potential impact from tourism, and the establishment, in this case, of local legislation.

5. Black sea urchins in the Caribbean
Tropical marine environments are highly dynamic on many temporal scales. Perhaps the most dramatic revelation of long-term major changes was the demise of the long-spined sea urchin (*Diadema antillarum*) throughout the western Atlantic (Lessios et al., 1984). This once abundant organism had 95% of its population disappear over the course of two years caused, apparently, by a disease originating near the mouth of the Panama Canal in 1983. Notwithstanding the high reproductive output of this urchin, recovery largely failed to occur, and many over-fished reefs throughout the Caribbean have been smothered under algae because of reduced urchin grazing.

Diving research showed how over-fished reefs persisted for years with high coral cover prior to the urchin die-off, but then rapidly succumbed once numbers of this single keystone species declined. It therefore showed that synergy between multiple stresses on marine environments can have unpredictably severe consequences. The sea urchin saga (the most severe, widespread epidemic ever documented for a species of marine animal) also demonstrates how even extraordinarily abundant organisms (>70 animals/m²) are potentially vulnerable to rapid elimination by disease.

*Diadema* is the first marine species affected by mass mortality to have been monitored continuously for over 20 years (Lessios, 1995; Lessios, 2005). The data, both from Panamá and Jamaica, indicated that a one-time historical event cannot only reduce the density of a previously abundant species throughout a whole region, but it can also maintain it at constant low levels for a long time. This occurred even though the affected species is known for high fecundity and planktonic larvae. These characteristics were thought to reduce the chance of catastrophic mortality and extinction.

It is possible that the high pre-mortality effects on *Diadema* densities may be a recent phenomenon that has been caused by over-fishing predators and competitors. However, historical information on the composition of most communities is lacking. Therefore, no one can be sure that rare species may not be rare. This may not be caused by any continuing process (such as competition or predation), but because of some similar catastrophe in its past. The only way to evaluate the potential importance of historical events is through long-term studies of their consequences, so that their persistence can be assessed. In the end, the mass mortality of a keystone species like the black sea urchin resulted in altered ecosystems.

6. Biogeography of reef fishes
Populations of individual species of most reef fish are generally thought to function on large spatial and temporal scales, because of a fundamental characteristic of their life cycles – the production of pelagic larvae. The larval life lasts weeks to months and begins as a relatively passive particle (an egg or a 1–2mm swimming larva that has every chance of being carried well away from its natal reef). Consequently, larvae from one reef seem likely to seed populations on other reefs, and populations of reef fish that are tens to hundreds of kilometres apart may have strong demographic and genetic connections.

While most species of coral reef fishes have broad distributions (hundreds of thousands of square kilometre), a very few occur only on single, small, isolated tropical islands (Robertson, 2001). Such small-island endemics may provide important information about the long-term maintenance of reef fish biodiversity precisely because they exist on mere specks of habitat for very long periods of time (hundreds to millions of years). If such species (or their island environments) do not have special life-history attributes that facilitate long-term persistence, then reef fishes, whose populations operate on large spatial scales, may also be quite capable of surviving severe, widespread population declines and habitat stress. Investigations of the biological characteristics of small-island endemics in the eastern tropical Pacific have predominantly included scientific diving in the Revillagigedos Islands, Clipperton Island, Cocos Island, Galapagos Islands and Malpelo Island (Allen and Robertson, 1994).

Clipperton Island, the only atoll and the largest coral reef in the eastern Pacific, is the most isolated reef in the tropical Indo-Pacific (950km from the nearest shoals). It has a depauperate fish fauna
(98 shorefish species), including a relatively large number of endemics: eight species from seven families (squirrelfishes, groupers, angelfishes, damselfishes, wrasses, blennies, and gobies) that have a range of adult and larval ecologies. Population sizes of adult Clipperton endemics were estimated to range between 100,000 and 3 million. These are remarkably small populations for short-lived marine organisms that produce pelagic larvae. In comparison, mainland congeners of the endemics probably have populations about 1000 times as large.

Recruitment of pelagic larvae of reef fishes often fluctuates considerably over time. Populations of short-lived species are more susceptible to local extinction from short-term recruitment failures. Interestingly, most Clipperton endemics were relatively small and thus appeared to be short-lived. The loss of larvae from Clipperton represents an extinction risk. Successful endemics have adaptations that aid the retention of their larvae near the island. Unique oceanographic characteristics may also aid in larval retention. For species with planktonic eggs, this problem is most acute in that released eggs are completely passive for the first 24 hours of their pelagic life. Species that have benthic eggs, on the other hand, release swimming larvae that should have some ability of resisting offshore loss.

7. DNA barcoding and fish diversity

Another biodiversity research tool that is increasingly used in conjunction with scientific diving is DNA barcoding. This technique has proven useful in identifying (or corroborating previous identifications of) marine fish larvae. It has also assisted in identifying range extensions, revealing taxonomic problems, clarifying species diversity and serving as a source of information that directs subsequent morphological work. Collecting voucher specimens and colour photographs of vouchers is critical. Large faunal barcoding studies result in a large amount of basic taxonomic data management needs. Baldwin et al. (2009) reported 47 tropical fish larvae identified through rearing from 1992 to 2003, and 70 new larvae identified through DNA barcoding from 2004 to 2006.

8. Transisthmian biodiversity

The rise of the isthmus of Panama occurred 3 million years ago, linking North and South America and forever changing ocean currents by forming a barrier between the Caribbean and the Pacific. With only 80km of separation, this is one area where scientists can dive in two oceans in one day. Twenty transisthmian sibling pairs of snapping shrimps have been described from among 45 worldwide speciose genera of over 1000 species (Alpheus: 300-plus spp; Synalpheus: 150-plus spp.).

A careful underwater study of a sponge-inhabiting shrimp (Synalpheus regalis) confirmed its eusociality, an advanced social structure, for the first time in a marine animal (Duffy, 1996). This marine model provides competition for landbound ants and airborne bees for studying cooperative animal societies where queens rule. The apex of animal social organisation is eusociality, characterised by overlapping generations, reproductive division of effort and cooperative care of young.

This sponge-dwelling shrimp lives in colonies of up to 300 individuals, each containing only a single reproductive female. Direct-developing juveniles remain in the natal sponge and larger, non-breeding individuals defend the colony against heterospecific intruders.

9. Conclusions

SCUBA has been a research tool available to the science community for over 60 years. In the early days of its use, there were many discoveries associated with man’s first cost-effective interventions into the underwater environment. It could be argued, however, that in the last two decades SCUBA has become an essential and very productive means for conducting research in shallow, coastal and complex environments.

Coral reefs are extremely important marine ecosystems, but are highly vulnerable to even minute fluctuations to ambient physicochemical conditions. Climate change may produce a series of challenges for coral reef systems, and research programmes using SCUBA have not only provided baseline information against which to measure change, but have also provided the experimental framework to best detect and monitor those changes. Coral bleaching is the most profuse occurrence to be first associated with the potential effects of thermal change. Following from the first few isolated suggestions of a link, there are now thousands of publications on coral bleaching. In most cases, the published research was dependent on the use of SCUBA (e.g. Kushmaro et al., 1996; Fine and Loya, 2003; Reshef et al., 2006; Winters et al., 2009a,b).

This short review provides examples of several high-impact works that employed SCUBA for conducting coral reef research. SCUBA must continue to provide essential support for conducting excellent science in complex environments.
Acknowledgments

The Smithsonian Scientific Diving Program and Marine Science Network are supported in part by funding provided by the Johnson and Hunterdon Oceanographic Research trust endowments of the Smithsonian Institution’s Office of the Under Secretary for Science. Thanks go to the following scientific divers for their sustained efforts in contributing to our understanding of marine biodiversity and ecology: Carole Baldwin, Biff Bermingham, Ken Clifton, Rachel Collin, Emmett Duffy, Rob Fleischer, Hector Guzman, Tuck Hines, Nancy Knowlton, Haris Lessios, Mark Littler, Diane Littler, Ian Macintyre, Valerie Paul, Ross Robertson, Greg Ruiz, Klaus Rützler and Phil Taylor.

References


