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Bikini Atoll coral biodiversity resilience five decades after nuclear testing

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Abstract

Five decades after a series of nuclear tests began, we provide evidence that 70% of the Bikini Atoll zooxanthellate coral assemblage is resilient to large-scale anthropogenic disturbance. Species composition in 2002 was assessed and compared to that seen prior to nuclear testing. A total of 183 scleractinian coral species was recorded, compared to 126 species recorded in the previous study (excluding synonomies, 148 including synonomies). We found that 42 coral species may be locally extinct at Bikini. Fourteen of these losses may be pseudo-losses due to inconsistent taxonomy between the two studies or insufficient sampling in the second study, however 28 species appear to represent genuine losses. Of these losses, 16 species are obligate lagoonal specialists and 12 have wider habitat compatibility. Twelve species are recorded from Bikini for the first time. We suggest the highly diverse Rongelap Atoll to the east of Bikini may have contributed larval propagules to facilitate the partial resilience of coral biodiversity in the absence of additional anthropogenic threats.

Keywords: Marshall Islands; Nuclear testing; Scleractinia; Disturbance; Local extinction; Coral reef biodiversity; Atoll lagoons

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1. Introduction

Understanding the resilience, or capacity for biodiversity to persist after disturbances (Connell, 1997), is crucial to devising appropriate management actions to mitigate biodiversity loss (Hughes et al., 2003; Harley et al., 2006). Current records of long-term to large-scale resilience from disturbances are scant, as there are few opportunities to study large-scale impacts and long-term recovery. Bikini Atoll in the Marshall Islands provides a unique opportunity to investigate such biodiversity resilience because between 1946 and 1958, 23 surface and subsurface thermonuclear experiments were conducted there (Niedenthal, 2001). A thorough taxonomic review of the coral assemblage at Bikini was undertaken prior to the atomic testing programme (Wells, 1954) and this provides an opportunity to investigate the long-term consequences of multiple punctuated to chronic (Chabanet et al., 2005) large-scale disturbances on coral biodiversity, five decades after the event.

In coral reef ecosystems, temporal comparisons using the fossil record indicate coral community composition remains stable on evolutionary timescales (Pandolfi, 1999). These analyses are likely to underestimate the contribution of rare species (i.e. those with restricted ranges and/ or low abundances (Gaston, 1994), because rare members of coral communities are not likely to be well represented in the fossil record. Thus, in taxa such as *Acropora*, where a relatively large proportion of species are listed as rare (Wallace, 1999; Veron, 2000, 2002) there is a high likelihood for the evolutionary changes in biodiversity to be oversimplified. On ecological timescales, community composition is

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disturbance driven and continually in disequilibrium (Connell, 1978; Karlson and Hurd, 1993; Connolly et al., 2005), hence the time required for biodiversity to recover after disturbance is rarely described. Rapid colonization of volcanic flow was observed in Indonesia (Tomascik et al., 1996) and provides an example of rapid recovery and community resilience. Coral communities on the Great Barrier Reef have been reported to remain stable over 10–30 year timeframes (Done, 1992; Lourey et al., 2000; Ninio et al., 2000) however these studies often refer to coral cover rather than changes in coral species composition, and each of these reef systems has nearby larval sources.

The long-term consequences of chronic and large-scale, anthropogenic disturbances for biodiversity are even less understood. In this case, a disturbance is defined as an event that alters the physical environment and/or limits the availability of essential resources (Pickett and White, 1985). It is predicted that, on a regional scale, coral biodiversity will be lost from reefs degraded in this way (DeVantier et al., 2006): however, there are few empirical examples of local or regional coral extinctions in the Indo-Pacific, despite the high likelihood of their occurrence. The large-scale chronic degradation of coral communities also has cascading adverse effects on reef fish assemblages (Graham et al., 2006) and other taxonomic groups in the coral reef ecosystem. There are also few records of coral reef fish extinctions (Munday, 2004), although the vulnerability of restricted-range or conspicuous fishes is widely recognised (Hawkins et al., 2000; Sadovy et al., 2003). Here, we compare biodiversity of the modern coral assemblage at Bikini Atoll to that of the coral assemblage at Bikini Atoll prior to testing (Wells, 1954). We assess the resilience of coral biodiversity and the ability for biodiversity to regenerate after five decades of unimpeded recovery.

1.1. Study location

Atolls of the Marshall Islands span 2, 600, 000 km^2 of ocean and provide some of the most northerly reef habitat in the Central Pacific (Fig. 1). Bikini Atoll is one of the most northerly atolls at 11°N, with 23 islands and approx 187 km^2 of reef. In general, reef habitats at Bikini Atoll and on other Marshall Island atolls include narrow reef flats with spur and groove development, reef crest and steep vertical exposed walls, protected sandy lagoons with patch reef development and inter-reefal sea floor (Pinca and Beger, 2002). Northeast trade winds predominate (Vander Velde and Vander Velde, 2006).

1.2. A brief history

In the northern atolls of the Marshall Islands, 23 nuclear tests with a total yield of 76.3 megatons (TNT equivalent) were conducted across seven test sites located either on the reef, on the sea, in the air and underwater between 1946 and 1958. Five craters were created, the deepest being the Bravo crater at 73 m depth (Noshkin et al., 1997a) (Figs. 2, 3). Post-test descriptions of environmental impacts include: surface seawater temperatures raised by 55,000 °C after air-borne tests; blast waves with speeds of up to 8 m/s; and shock and surface waves up to 30 m high with blast columns reaching the floor of the lagoon (approximately 70 m depth) (Glasstone and Dolan, 1977). Coral fragments were reported to have landed on the decks of the target

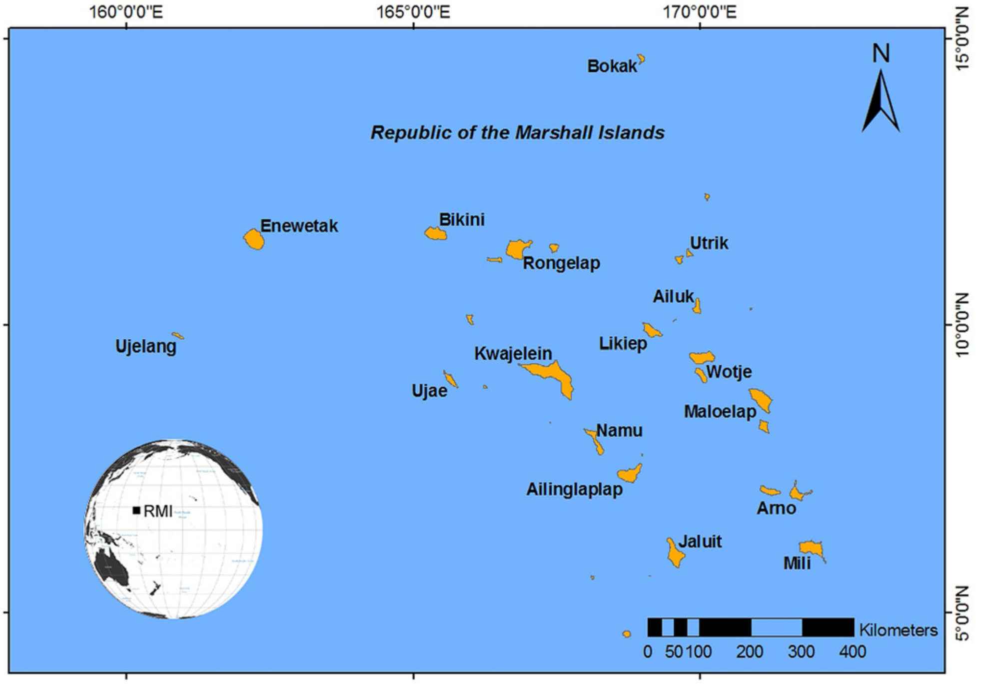

Fig. 1. Map of the Marshall Islands showing the location of Bikini Atoll and its neighbours.

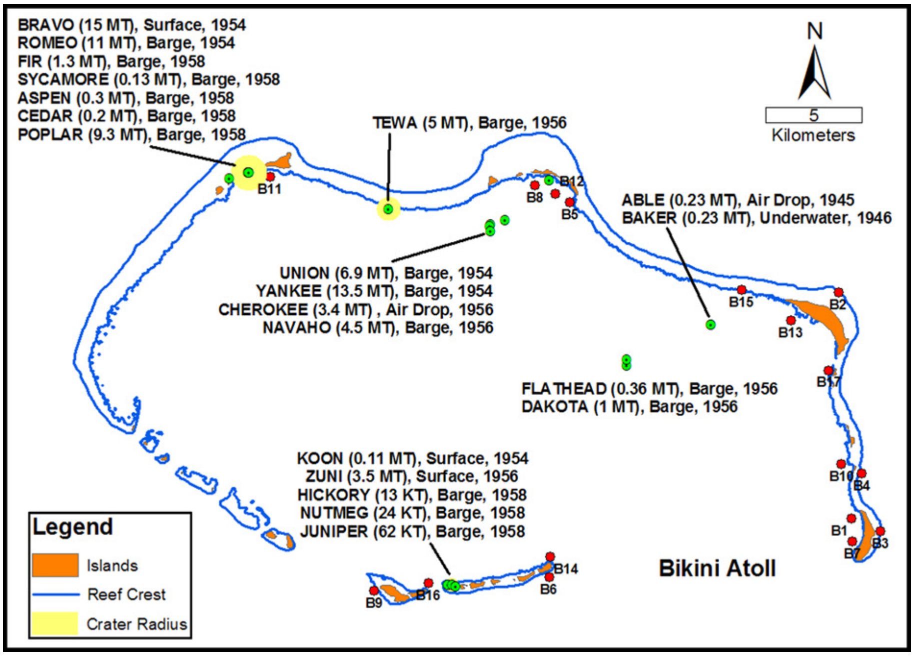

Fig. 2. Location of 2002 survey sites (red spots) and Bikini nuclear testing sites (green spots) indicating test strength (MT - megaton, KT - Kiloton), method, date, and crater radii (Noshkin et al., 1997a). Sites 18 and 19 not included. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 3. Bravo crater (BC) in NW Bikini Atoll Photo: Matt Harris.

fleet deployed within the lagoon. The tests altered the natural sediment distribution by redistributing a higher amount of fine material over the surface of the sediment (Noshkin et al., 1997b). Seawater was contaminated from mixing with fission particles in the atmosphere and through remobilisation from the environment and lagoonal sediments (Noshkin et al., 1997a). Low-level radioactivity was recorded in fouling marine growth and in seawater piping systems (US Defence Nuclear Agency, 1984), fish and clams (Robison et al., 1997), the calcareous algae *Halimeda* spp. (Spies et al., 1981), and coral skeletons (Noshkin et al., 1975).

The retention of radioactive isotopes in the atoll ecosystem has been described in detail (Welander, 1969; Robison et al., 2003). The most publicized of the Bikini tests, 'Bravo', was a 15 megaton hydrogen bomb detonated on a shallow fringing reef in 1954 (Niedenthal, 2001). It destroyed three islands causing millions of tonnes of sand, coral, plant and sea life from Bikini's reef to become airborne. The sediment regime in Bikini was fundamentally altered by the nuclear events because millions of tonnes of sediment were pulverized, suspended, transported and then deposited throughout the lagoon by wind-driven lagoonal current patterns (Van Arx, 1946).

Since the nuclear testing, impacts from pollution and tourism are presumed to have been virtually non-existent in northern atolls of the Marshall Islands. No coral bleaching was reported from the Marshall Islands prior to 2004 and no outbreaks of *Acanthaster plancii* (crown-of-thorns-seastar) or coral diseases were reported prior to 2005 (Abraham et al., 2005; Pinca et al., 2005).

2. Pre-nuclear diversity records

Prior to the main nuclear testing, the coral assemblages of Bikini Atoll were thoroughly investigated via reef walking, snorkel and dredging. Corals were described in Wells (1954) after reference to type material at the British Museum of Natural History and the US National Museum. A comprehensive species list containing 174 scleractinian coral species was established. Wells' 1954 work in the Marshall Islands reshaped coral systematics, describing two new genera, 23 new species and two new varieties as well as placing numerous species in synonomy, based on field observations of variability within species. In the 50 years since Wells, no scientific data have been published about the coral biodiversity at Bikini Atoll. The taxonomic decisions of Wells were revised and/or incorporated into recent revisions of the genus *Acropora* (Veron and Wallace, 1984; Wallace and Wolstenholme, 1998; Wallace, 1999). A partial review of Well's species was undertaken for this project and revealed 46 of the species names regarded as valid by him are now in synonomy (see Appendix 1).

3. Methods

The survey was conducted during 17–29 July 2002 at 19 sites located in the lagoon, passes and on outer reef slopes of Bikini Atoll (Fig. 2; Table 1). These habitats represented a cross-section of typical habitats on Marshall Islands atolls. Reef flat, crest and steep slope habitats were surveyed within slope sites. Sandy inter-reefal areas and submerged patch reefs featuring deep vertical and shallow reef top habitats were surveyed within lagoonal sites (Fig. 4). A 60-min timed swim was conducted by the first author at each site, beginning at 30 m deep and continuing throughout the ascent into shallow water. The majority of each dive was spent in shallow habitats (<8 m). Each coral was given a relative abundance rating ranked by six ordinal categories (dafor scale: 0 = not present; 1 = rare, 1 or 2 colonies; 2 = occasional, 2–5 colonies; 3 = frequent, 6–10 colonies; 4 = common, 11–25 colonies; 5 = dominant, >25 colonies) (DeVantier et al., 1998). Voucher specimens for species identifications were deposited in the Museum of Tropical Queensland. Corals were identified by Richards; with specialist advice from Wallace, Fenner, Turak and Pichon. Known distribution ranges for the species were interpreted from (Veron, 2000, 2002).

4. Results

A total of 183 species of Scleractinian coral was recorded from the survey sites (Appendix 1). This compares with 126 species in the amended species list from (Wells (1954)) Bikini Atoll study (Appendix 1), a reported total of 168 species for the northern RMI atolls (Maragos, 1994), and a possible total of 284 species for the entire RMI (Richards, unpublished data).

Table 1
Characteristics of the 2002 survey sites at Bikini Atoll, HC – hard (scleractinian) coral

Site Number	Coral diversity	Location	Description	Mean Cover HC ± SE
B1	35	South Lagoon	Enyu Island lagoonal patch reef	8.5 ± 1.5
B2	41	North Wall	Bikini Island exposed reef slope	36.3 ± 23.5
B3	33	East Wall	Enyu Island exposed reef slope	12.2 ± 9.0
B4	27	East Wall	Lonchebi Island exposed reef slope	7.4 ± 2.1
B5	43	North Lagoon	Aomoen Island lagoonal patch reef	16.3 ± 7.1
B6	50	South Wall	Airukiiji Island outer reef slope/ wall	25.5 ± 9.3
B7	38	East Lagoon	Enyu Island lagoonal patch reef	7.4 ± 1.5
B8	39	North Lagoon	Aomoen Island lagoonal patch reef	22.4 ± 5.3
B9	43	South Wall	Chieerete Island outer reef slope/ wall	15.3 ± 3.6
B10	42	South Lagoon	Eniairo Island lagoonal patch reef	36.7 ± 26.0
B11	50	West Lagoon	Namu Island lagoonal reef, on H-bomb crater	61.5 ± 18.5
B12	44	North Lagoon	Aomoen Island lagoonal patch reef	65.3 ± 16.4
B13	44	East Lagoon	Bikini Island lagoonal patch reef	56.8 ± 15.3
B14	34	South Pass	Eniiriku Pass	5.4 ± 2.5
B15	0	East Lagoon	Lagoon slope	No data
B16	47	Lagoon, South Pass	Reere Island lagoonal reef near pass	25.8 ± 26.8
B17	31	East Lagoon	Bokonfuaaku Island lagoonal slope	50.3 ± 29.8
B18	17	Intertidal exposed	Bikini Island intertidal reef flat	40[a]
B19	21	Intertidal exposed	Bikini Island limestone excavation site	10[a]

[a] Visual estimates of coral cover.

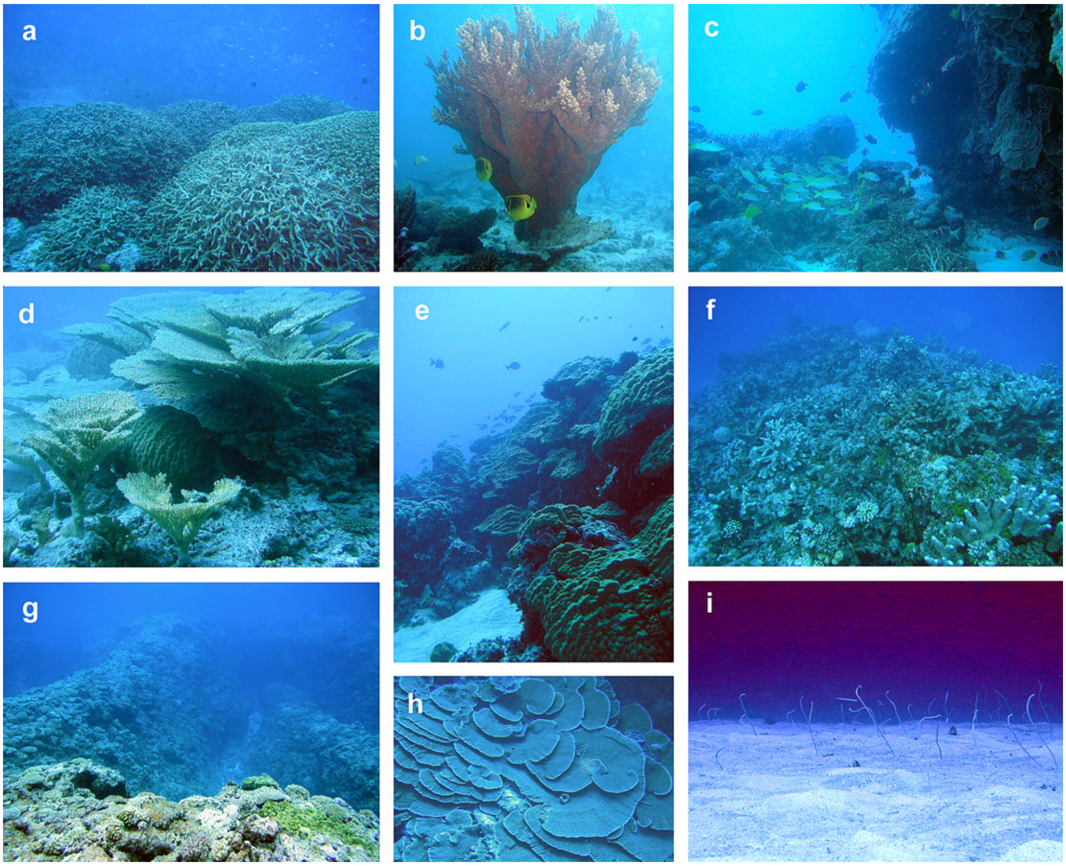

Fig. 4. Bikini Atoll coral communities 2002, (a) lagoonal monospecific *Porites cylindrica* community near the Bravo crater; (b) *Acropora striata* "tree" in the northern lagoon; (c) base of a typical patch reef in the southeast lagoon; (d) *Acropora cytherea* communities dominate some lagoonal reefs; (e) oceanic walls feature drop-offs with communities of massive growth forms; and (f) *Isopora* spp. dominated reef crest with *Halimeda* spp. algal growth; (g) eastern exposed reef crests support a spur and groove habitat with sparse coral growth; (h) dense foliose *Montipora* spp. grow on some walls, and (i) passes often feature sand chutes with sand eels and sparse small coral colonies.

Distribution range was extended to the Marshall Islands for 11 species from the genera *Acanthastrea*, *Acropora*, *Lithophyllum*, *Montastrea*, *Montipora*, *Pectinia* and *Seriatopora* (Table 3). Six of the newly recorded species were locally rare (present at two or less sites across Bikini Atoll). Four species are considered, on current records, to be regionally restricted to Bikini Atoll, although occurring at other locations to the west of the Marshall Islands:

Table 2
Species recorded by Wells (1954) and absent in the 2004 survey

Bikini LOSSES	Habitat	Bikini LOSSES	Habitat	Bikini LOSSES	Habitat
Acropora echinata	Lagoon	*Acropora millepora*	Lagoon/exposed	*Favia russeli*	Lagoon/exposed
Acropora tenella	Lagoon	*Acropora micropthalma*	Lagoon/exposed	*Montipora foveolata*	Lagoon/exposed
Cycloseris distorta	Lagoon	*Acropora spicifera*	Lagoon/exposed	*Acropora palmera*[a]	Exposed
Echinophyllia orpheensis	Lagoon	*Anacropora forbesi*	Lagoon/exposed	*Acropora spicifera*	Lagoon/exposed
Diaseris distorta	Lagoon	*Cyphastrea chalcidium*	Lagoon/exposed	*Montipora hoffmeisteri*	Lagoon/exposed
Goniopora lobata	Lagoon	*Cyphastrea micropthalma*	Lagoon/exposed	*Montipora informis*	Lagoon/exposed
Hydnophora rigida	Lagoon	*Diploastrea heliopora*	Lagoon/exposed	*Montipora undata*	Lagoon/exposed
Leptoseris gardineri	Lagoon	*Fungia fungites*	Lagoon/exposed	*Montipora venosa*	Lagoon/exposed
Pocillopora elegans	Lagoon/exposed	*Montipora folveolata*	Lagoon/exposed	*Montipora granulosa*	Lagoon/exposed
Leptoseris incrustans	Lagoon	*Pocillopora verrucosa*	Lagoon/exposed	*Favia helianthoides*	Lagoon/exposed
Leptoseris mycetoceroides	Lagoon	*Pavona minuta*	Lagoon/exposed	*Fungia fungites*	Lagoon/exposed
Leptoseris scabra	Lagoon	*Plesiastrea versipora*	Lagoon	*Leptastrea corymbosa*	Lagoon/exposed
Oxypora lacera	Lagoon	*Madracis* sp.	Lagoon	*Acropora squarrosa*	Lagoon/exposed
Astreopora suggesta	Lagoon	*Leptoseris solida*	Lagoon	*Porites murrayensis*	Lagoon/exposed

Pseudo-losses that may be attributable to taxonomic inconsistencies or alternative synonomies are shaded in grey.

[a] Bikini Atoll is the type locality for *A. palmerae* however we consider it is a pseudo-loss because it occurred on the exposed algal ridge that was more thoroughly sampled by Wells.

Table 3
Range extensions were recorded from Bikini Atoll in this survey

Regional GAINS	Former records	Local distribution ($n = 19$)	Local abundance
Acanthastrea brevis	No records from RMI	11 Sites	Rare to infrequent
Montastrea salebrosa	No records from Micronesia	9 Sites	Rare to frequent
Pectinia africanus[a]	No S.E. Asia or Pacific Records	1 Site	Rare to infrequent
Acropora kimbeensis[a]	No central Pacific records	1 Site	Rare to frequent
Acropora chesterfieldensis[a]	No central Pacific/N. Hem records	4 Sites	Rare to infrequent
Acropora lovelli[a]	No records from RMI	4 Sites	Rare to infrequent
Lithophyllum undulatum	No central Pacific records	1 Site	Rare
Montipora cocosensis	No central Pacific records	1 Site	Infrequent
Montipora angulata	No records from Micronesia	2 Sites	Rare to infrequent
Seriatopora aculeata	No central Pacific records	2 Sites	Rare to Frequent
Seriatopora dentritica[a]	No central Pacific records	9 Sites	Rare to Common

"Pseudo-gains" which may be attributable to taxonomic inconsistencies or cryptic synonymies are shaded in grey.

[a] Species newly described since the Wells survey.

Acanthastrea hillae, *Acropora bushyensis*, *Montipora cocosensis*, *Polyphyllia talpina* (Richards, unpublished data). Two species (*Acanthastrea brevis* and *Montastrea salebrosa*) were found to be locally abundant and distributed widely at Bikini Atoll in the current survey and were not recorded by Wells, possibly because his sub-tidal sampling was restricted to shallow depths. Of the 28 species missing from the assemblage today that are considered to be genuine losses, 16 species are obligate lagoonal specialists (e.g. *Leptoseris gardineri*, *Oxypora lacera*, *Goniopora lobata*, *Diaseris distorta*) and 12 have wider habitat compatibility (e.g. *Acropora micropthalma*, *Acroproa millepora*, *Cyphastra micropthalma*, *Diploastrea heliopora*) (see Table 2).

5. Discussion

Although the overall coral species richness at Bikini Atoll appears to have remained approximately the same over a 50 year period, transitions have occurred, with losses and gains of species. This study indicates that 42 previously recorded species are absent from Bikini Atoll today (Table 2). Up to 14 of these losses may be explained by alternative synonymies or taxonomic inconsistencies (shaded in grey, Table 2); however we consider 28 species to be genuine losses, because our surveys using SCUBA were locally extensive, and these species were detected at other Marshall Island atolls between 2002 and 2006 (Richards, unpublished data). Sixteen missing species are obligate lagoonal or calm-water specialists (e.g., *Leptoseris gardineri*, *Oxypora lacera*, *Goniopora lobata*, *Diaseris distorta*), the other 12 have wider habitat compatibility. These results indicate that loss and failure to recover from nuclear explosions is concentrated in the lagoon of Bikini Atoll, with other locations showing a similar diversity to that recorded before the nuclear testing.

Through the series of nuclear tests, the coral communities at Bikini Atoll experienced repeated exposure to significant physical disturbance through substrate removal, extreme waves, light/heat exposure and increased sediment loading, all of which are known to be detrimental to coral survivorship (Madin et al., 2006; Goffredo et al., 2007; Puotinen, 2007). Nuclear tests also lead to long-term raised levels of radio-nucleotides such as ^{54}Mn, ^{57}Co, ^{60}Co, ^{65}Zn, ^{90}Sr, ^{144}Ce, ^{155}Eu in invertebrate tissues (Donaldson et al., 1997) and ^{241}Am, and ^{239,240}Pu in sediments (Nevissi and Schell, 1975). Although there were no reported measurements of these factors for the nuclear tests at Bikini, we infer that the strength of the physical events by far exceeded normal atoll conditions, particularly in the lagoon, therefore forming a large-scale disturbance.

The short- or long-term effects of nuclear testing on coral biodiversity and carbonate structures have not been described previously. Nuclear tests performed at Mururoa Atoll had significant impacts on the reef structure at a meso-scale level whereby cracks appeared in lagoonal patch reefs and part of the reef rim collapsed due to the explosion shock wave (Bouchez and Lecomte, 1995). At Bikini, the "Bravo' test created a large crater in the rim of the lagoon, representing material removed from the island and, presumably, redistributed within the lagoon and creating new lagoonal space (Fig. 3). The formation of this crater, and the additional 20 disturbances created by nuclear tests in and on the edge of the lagoon (1945–1946, 1954–1958), constitute the primary physical impact of the series of tests on the coral assemblage which had been present and recorded immediately before this testing (Wells, 1954). The proportion of fine particles in the Bikini lagoon approximately doubled, causing a shift in spatial particle distribution (Noshkin et al., 1997a). The cumulative impacts appear to have pushed lagoonal specialists beyond their capacity for recovery.

Unfortunately, the immediate extent of coral defaunation and rate of subsequent recovery at Bikini Atoll were not reported. It is reasonable to assume that the direct physical impacts, shock waves, temperature rises and ongoing sediment and nutrient suspension would have had significant detrimental effects on lagoonal and shallow exposed corals and are likely to have severely impacted the overall abundance and health of adult colonies and the capacity for coral recruitment, growth and reef accretion for at least the 13 years of testing between 1945 and 1958. It is also likely that the lasting effects of radiation and sediment would have severely affected survivors and colonists for many years after the cessation of testing in 1958. Corals growing in unconsolidated substrate have been shown to be vulnerable to tsunami damage (Baird et al., 2005). Increased turbidity and prolonged periods of low light are also known to cause coral bleaching and mortality (Fabricius et al., 2005), and the suspended sediment would have impeded larval settlement and survival (Hunte and Wittenberg, 1992).

We found that approximately 10% of former Scleractinian coral diversity was absent from the post-nuclear assemblage. Whether this level of biodiversity transition is unusual compared to that expected from natural stochasticity remains to be addressed. Coral communities are known to recover relatively quickly from acute disturbances but not from chronic disturbances, which lead to gradual decline (Connell et al., 1997). Given the large and unpredictable nature of the series of disturbances at Bikini Atoll, long-term community decline over the period of the tests would be expected. Specialists are highly vulnerable to extinction in a disturbance regime (Munday, 2004) because of their fragmented and small populations. Almost half of the corals lost from Bikini are lagoonal soft-sediment specialists. It is possible and likely that nuclear detonations had a severe effect on lagoonal coral populations, making them locally extinct. Many lagoonal coral species are likely to recruit infrequently from larval (sexual) recruitment, relying on indeterminate growth and asexual reproduction for population increase (Wallace, 1985) and thus their populations may not yet have recovered following such an event.

The composition of a community at any point in time is highly stochastic (Paine and Levin, 1981), and range expansions and contractions over decadal time scales are not unusual in marine environments (Scheibling et al., 1999; Wolff and Mendo, 2000). Metapopulation dynamics predicts that environmental stochasticity will drive some subpopulations towards extinction and unoccupied areas towards colonization. However, the timescale on which species diversity is replenished after anthropogenic disturbances is variable and relates to the scale and components of disturbance, geographic location, habitat type and distance from source populations. Recovery is expected to be slow in situations where the physical environment is altered (Connell et al., 1997), such as at Bikini Atoll: however, we show that five decades is a suitable timeframe for the majority of the Bikini Atoll Scleractinian coral assemblage to re-establish after long-term, chronic localised anthropogenic disturbances.

Resilience in the Bikini Atoll reef coral assemblage might be correlated with tolerance of turbid conditions, however a number of species tolerant of turbid conditions appear to have been lost from the community (e.g., *Anacropora forbsei*; *Goniopora lobata*). Even if some mature corals survived, survival of juvenile coral recruits would have been severely impacted by scouring by suspended sediment (Hunte and Wittenberg, 1992). Furthermore, partial mortality and colony weakening by lowered rates of calcification would have favoured pathogen infestation and reduced the reproductive potential of survivors (Hall, 2001; Nugues and Roberts, 2003).

The modern Bikini Atoll community may have been replenished by self-seeding from brooded larvae from surviving adults (e.g. in genera *Pocillopora*, *Stylophora*, *Seriatopora* and *Isopora*), survival of fragments of branching corals, and/or migration of new propagules from neighbouring atolls. The patchy nature of impacts may have mitigated the overall effect of disturbance at Bikini Atoll, with some patches surviving after each impact. Corals living on deep exposed reefs on Bikini Atoll may also have escaped some of the direct impacts, and thus have played an integral role in mitigating the overall effect of the disturbance event. We consider the extremely large and highly diverse Rongelap Atoll is likely to have contributed a significant proportion of new propagules to enable recovery of the Bikini coral community, as Bikini Atoll lies downstream of the prevailing surface current from Rongelap.

The case of Bikini Atoll demonstrates that coral reef communities can recover from and exhibit resilience to major disturbance events. In this situation, the visible impact and recovery of the reefs from the anthropogenic impact of atomic testing can be compared to those following natural disturbance events such as cyclone/hurricane damage. Bikini Atoll's reefs undoubtedly benefited from the post-testing absence of human disturbance, the presence of uninhabited and non-impacted neighbouring atolls, and a supportive prevailing hydrodynamic regime for larval import (Van Arx, 1946). Caution should be taken in generalising our findings to other atolls or coral reef communities that experience a different set of conditions. In most parts of the world, human influences are always present, and chronic disturbances (such as long-term overfishing, coral-harvesting, or multiple coral bleaching events) are likely to be more extensive. Additionally it is becoming less likely that relatively unimpacted reefs are available to act as a source of propagules. These considerations illustrate the crucial role of marine reserve networks which may represent the low-impact source reefs of the future.

Bikini Atoll provides a rare opportunity to examine the long-term impacts of nuclear testing on coral biodiversity. The scale and local intensity of this violent historical event are profound. If the disturbance event were to be repeated in the modern day, recovery would not be expected to be as high, due to the combination of additional stressors associated with climate change (Anthony et al., 2007; Lesser, 2007) and a possibly much altered atoll environment due to an additional 50 years of human occupation. Thus, in a twist of fate, the radioactive contamination of northern Marshall Island Atolls has enabled the recovery of the reefs of Bikini Atoll to take place in the absence of further anthropogenic pressure. Today Bikini Atoll provides a diverse coral reef community and a convincing example of partial resilience of coral biodiversity to non-chronic disturbance events.

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Appendix 1

Comparison of coral species (listed alphabetically) recorded from atolls surveyed at Bikini Atoll in 2002 (this paper), and 1948–1952 (Wells, 1954).

Species	This study	Wells (1954)	Synonyms used in Wells (1954)
Acanthastrea hemprichii	x^*		
Acanthastrea brevis	x^*		
Acanthastrea echinata	x^*	x	
Acanthastrea hillae	x		
Acropora chesterfieldensis	x^*		
Acropora vaughani	x	x	
Acropora abrotanoides	x	$2x$	*A. rotumana*, *A. danai*
Acropora abrolhosensis	x^*		
Acropora aculeus	x^*		
Acropora acuminata	x^*	x	
Acropora aspera	x^*		
Acropora austera	x^*		
Acropora bushyensis	x^*		
Acropora cerealis	x^*	$3x$	*A. cymbicyathus*, *A. hystrix*, *A. tizardi*
Acropora cytherea	x^*		*A. reticulata*, *A. corymbosa* (unres)
Acropora digitifera	x^*	x	
Acropora divaricata			
Acropora donei	x^*		
Acropora echinata		x	
Acropora florida	x	x	*A. polymorpha*
Acropora gemmifera	x^*		
Acropora grandis	x		
Acropora granulosa	x^*		
Acropora horrida	x		
Acropora humilis	x^*	x	
Acropora hyacinthus	x^*	x	*A. conferta*, *A. surculosa*
Acropora kimbeensis	x^*		
Acropora latistella	x^*		
Acropora loisetteae	x^*		
Acropora longicyathus	x^*	x	*A. syringodes*
Acropora loripes	x^*	$2x$	*A. Rosaria* (unres) and *A. ramiculosa* (unres)
Acropora lovelli	x^*		
Acropora lutkeni	x^*		
Acropora microclados	x^*		
Acropora microphthalma		x	
Acropora millepora		x	
Acropora monticulosa	x		
Acropora muricata	x^*	$3x$	*A. Formosa*, *A. virgata*, *A. arbuscula* (unres)
Acropora nana	x		
Acropora nasuta	x^*	x	

Appendix 1 (*continued*)

Species	This study	Wells (1954)	Synonyms used in Wells (1954)
Acropora palmerae		x	
Acropora paniculata	x^*	x	
Acropora robusta	x^*	x	*A. nobilis*
Acropora samoensis	x^*		
Acropora secale	x	x	*A. diversa*
Acropora selago	x	x	*A. delicatula*
Acropora speciosa	x^*	2x	*A. rayneri*, *A. rambleri*
Acropora spicifera		x	
Acropora squarrosa		x	
Acropora striata	x^*	x	
Acropora subglabra			
Acropora subulata	x^*		
Acropora tenella		x	
Acropora tenuis	x^*		
Acropora tortuosa	x^*	x	*A. implicata*
Acropora valida	x^*	2x	*A. variabilis*
Acropora vaughani		x	
Acropora millepora		x	*A. prostrata*
Acropora solitaryensis	x		
Alveopora fenestrata	x^*		
Anacropora forbesi		x	
Astrepora expansa	x		
Astreopora gracilis	x	2x	*A. tabulata*
Astreopora listeri	x	x	
Astreopora myriophthalma	x	x	
Astreopora ocellata	x	x	
Astreopora suggesta		x	
Barabattoia laddi	x		
Caulastrea furcata	x^*		
Coscinarea columna	x^*	x	
Ctenactis crassa	x		
Cycloseris vaughani	x	2x	*C. hexanogalis*
Cycloseris distorta		x	
Cycloseris echinata	x		
Cyphastrea agassizi	x^*		
Cyphastrea chalcidicum		x	
Cyphastrea microphthalma			
Cyphastrea serialia	x^*	x	
Diaseris distorta		x	
Diploastrea heliopora		x	
Distichopora distichopora	x	2x	
Echinophyllia orpheensis		x	
Echinophyllia aspera	x^*	x	
Echinophyllia patula	x^*		
Echinopora lamellina	x^*	x	
Euphyllia glabrescens	x	x	
Favia speciosa	x	x	
Favia favus	x	x	
Favia helianthoides		x	
Favia matthaii	x		
Favia pallida	x^*	x	
Favia rotumana	x	x	
Favia rotundata	x		

(*continued on next page*)

Appendix 1 (*continued*)

Species	This study	Wells (1954)	Synonyms used in Wells (1954)
Favia stelligera	x^*	x	
Favites danae	x		
Favites flexuosa	x	$2x$	*F. virens*
Favites halicora	x		
Favites russelli		x	*Plesiastrea russelli*
Favites abdita	x	x	
Favites bestae	x		
Favites chinensis	x^*		
Favites complanata	x		
Favities russelli	x		
Favites pentagona	x		
Fungia concinna	x^*		
Fungia fungites		$3x$	*F. dentate*, *F. haimei*, *F. stylifera*
Fungia horrida	x		
Fungia granulosa	x		
Fungia paumotensis	x	x	
Fungia repanda	x		
Fungia scruposa	x^*		
Fungia scutaria	x^*	x	
Fungia danai	x		
Galaxea astreata	x		
Galaxea horrescens	x		
Gardinoseris planulata	x		
Goniastrea aspera	x		
Goniastrea edwardsi	x^*		
Goniastrea pectinata	x^*	x	
Goniastrea retiformis	x	x	
Goniopora columna	x^*		
Goniopora fascicularis	x		
Goniopora lobata		x	*G. traceyi*
Goniopora minor	x		
Goniopora somaliensis	x^*	x	
Halomitra pileus	x		
Heliopora coerulea	x^*	x	
Herpolitha limax	x	x	
Herpolitha weberi	x^*		
Hydnophora exesa	x^*		
Hydnophora microconos	x	x	
Hydnophora pilosa	x		
Hydnophora rigida		x	
Isopora cuneata	x	x	
Isopora palifera	x^*	x	
Leptastrea pruinosa	x^*		
Leptastrea purpurea	x	x	
Leptoseris explanulata	x		
Leptoseris gardineri		x	
Leptoseris hawaiiensis	x	x	
Leptoseris incrustans		x	
Leptoseris myceteroides	x	x	
Leptoseris scabra		x	
Leptoseris solida		x	
Lithophyllum undulatum	x^*		
Lobophyllia hemprichii	x^*	$2x$	*L. costata*
Lobophyllia corymbosa		x	

Appendix 1 (*continued*)

Species	This study	Wells (1954)	Synonyms used in Wells (1954)
Lobophyllia pachysepta	*x*		
Madracis sp.		*x*	
Merulina ampliata	*x*		
Millepora millepora	*x*	3*x*	
Montastrea curta	*x**		
Montastrea salebrosa	*x**		
Montastrea valencienesi	*x*		
Montipora verrucosa	*x*		
Montipora aequituberculata	*x**	*x*	*M. composita*
Montipora caliculata	*x**	*x*	
Montipora capitata	*x*		
Montipora cocosensis	*x**		
Montipora crassituberculata	*x**		
Montipora danae	*x*	*x*	
Montipora efflorescens	*x**		
Montipora foliosa	*x**	*x*	*M. minuta*
Montipora folveolata		*x*	*M. socialis*
Montipora granulosa		*x*	
Montipora hoffmeisteri		*x*	
Montipora incrassata	*x**		
Montipora informis		*x*	*M. granulata*
Montipora nodosa	*x*		
Montipora tuberculosa	*x**	*x*	
Montipora turgescens	*x*	*x*	
Montipora undata		*x*	*M. colei*
Montipora venosa		*x*	
Montipora verrucosa	*x**	*x*	
Oulphyllia crispa	*x**	*x*	
Oxypora lacera		*x*	
Pachyseris speciosa	*x*	*x*	
Pavona cactus	*x*		
Pavona clavus	*x*	*x*	
Pavona duerdeni	*x**		
Pavona maldivensis	*x**		
Pavona minuta		*x*	
Pavona varians	*x**	*x*	
Pectinia africanus		*x*	
Platygyra daedelea	*x*	*x*	*P. rustica*
Platygyra pini	*x**		
Platygyra ryukyuensis	*x**		
Platygyra sinensis	*x*		
Platygyra sinuosa	*x*		
Plesiastrea versipora		*x*	
Pocillopora verruosa	*x*		
Pocillopora damicornis	*x**	2*x*	*P. brevicornis*
Pocillopora elegans		*x*	
Pocillopora eydouxyi	*x*	*x*	
Pocillopora meandrina	*x*	*x*	
Pocillopora verruosa		2*x*	*P. danae*
Polyphyllia talpina	*x**		
Porites vaughani	*x**		
Porites australiensis	*x*	*x*	
Porites cylindrica	*x*	*x*	*P. andrewsi*

(*continued on next page*)

Appendix 1 (*continued*)

Species	This study	Wells (1954)	Synonyms used in Wells (1954)
Porites horizontalata	*x**		
Porites lichen	*x*	*x*	
Porites lobata	*x*	*x*	
Porites lutea	*x**	*x*	
Porites rus	*x**	*x*	*Synarea hawaiiensis*
Porites murrayensis		*x*	
Psammocora explanulata	*x*	*x*	
Psammocora haimeana	*x*	*x*	*Plesioseris haimeana*
Psammocora profundacella	*x**		
Psammocora nietzeri	*x**	*x*	
Pseudosiderastrea tayami	*x*		
Scapophyllia cylindrica	*x**		
Scolymia australis	*x*	*x*	*Culicia sp.*
Seriatopora calendrium	*x*		
Seriatopora hystrix	*x*	2*x*	*S. angulata*
Stylaster stylaster	*x*	2*x*	
Stylocoeniella armata	*x**	*x*	
Stylocoeniella guentheri	*x**		
Stylophora pistillata	*x*	2*x*	*S. mordax*
Stylophora subseriata	*x*		
Symphyllia radians	*x*		
Symphyllia recta	*x*	*x*	*S. nobilis*
Symphyllia valencienessi	*x*		
Tubipora musica	*x*	*x*	
Turbinarea retiformis	*x**		
Turbinarea stellulata	*x*	*x*	
Total	183	148	

* Indicates a voucher specimen was collected.

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