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'A CLOSE AND FRIENDLY ALLIANCE': BIOLOGY, GEOLOGY AND THE GREAT BARRIER REEF EXPEDITION OF 1928–1929

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Abstract The 1928–1929 Great Barrier Reef Expedition marks an important milestone in the evolution of modern coral reef science, from its nineteenth-century theoretical and deductive foundation – so clearly exemplified in Darwin's coral reef theory – to the twentieth-century focus on empirical and analytical studies. Here, we consider the anatomy of the expedition, its antecedents, its immediate scientific achievements and its longer-term legacy. This truly interdisciplinary expedition differed from its ship-borne or short-stay reef reconnaissance predecessors, being housed on a single reef and sand cay (Low Isles, northern Great Barrier Reef) for a period of 13 months. Its intensive, rather than extensive, investigations involved meticulous microscopic work and painstaking laboratory and field observation, measurement and experimentation, cataloguing linkages between reef habitats, tidal processes and physical and chemical properties of water, as well as a quantitative inventory of reef-flat and reef-front biota spatially grounded in accurate transect surveys and planimetric controls. Results were published in the Expedition's exhaustive Scientific Reports over the next three decades, as well as in a host of other scientific journals.

We assess the Expedition's major achievements: highlighting the importance of the carnivorous diet of corals; describing a natural coral bleaching event and mechanisms of algal loss; determining how corals survive submerged within variably oxygenated and turbid waters; estimating adult and juvenile coral growth rates and the effects of transplanting corals; understanding relationships between lunar periodicity and mass spawning of corals; and recognizing the commonalities and differences in reeftop sediments and landforms and their indicative role of past storms and sea levels and contemporary morpho-dynamic changes. Finally, we argue that these and many other topics explored during the expedition continue to be relevant in modern reef science, not least in providing an exceptional set of ecological and geomorphological benchmarks against which it has been possible both to measure one hundred years of ecological and morphological change and to provide a dynamical environmental envelope against which to assess potential future changes.

Keywords: Coral Physiology; Coral Growth; Coral Bleaching; Reef Flat Ecology; Low Wooded Islands; Reef Island Mapping

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Introduction

'but the time has come when a close and friendly alliance between workers in all sciences concerned with coral reefs is not only desirable but necessary' J.A. Steers (1930, 2) in A Geographical Introduction to the Biological Reports, Scientific Reports of the Great Barrier Reef Expedition 1928–1929, Volume III.

'*results were pooled and compared, so that the surveyor was forced to understand that a reef is a living organism and the biologist was made to realise that he must measure his environment. Each group kept the other in mind'*. Comments by Michael Spender in answer to questions during discussion at the Royal Geographical Society (RGS) following publication of 'The Coral Islands and Associated Features of the Great Barrier Reefs': Discussion' by Balfour et al. (1937, 141).

Almost 100 years ago, in 1922, steps were taken to initiate the 1928–1929 Anglo-Australian Great Barrier Reef Expedition (Brown 2007a). As this centenary, and that of the expedition itself approaches, it is worth re-examining the role that this interdisciplinary research effort played in defining a new era of reef science and its relevance to coral reef studies today. Stoddart (1969, 433–434) noted 'that the work of the Great Barrier Reef Expedition of 1928–1929 emphasized for the first time the relationships between reef growth and environment and the critical importance for their study in the field' while Mather (2002, 459) viewed the expedition as having 'a profound effect on coral science for the next 45 years'. The continued significance of this expedition is marked by the numerous recent citations of this pioneering research over 90 years since its first execution (Edmunds and Gates 2003, Holmes 2008, Todd 2008, Downs et al. 2009, Goodkin et al. 2011, Wijgerde et al. 2011, Hoegh-Guldberg et al. 2017, Coles et al. 2018, Nelson & Altieri 2019). In this chapter, we revisit and emphasize previously unacknowledged important findings of the Expedition and contextualize their significance and legacy, with both a retrospective awareness of subsequent Australian and international research pertaining to coral reefs and for those discovering these achievements for the first time.

Background

The 1928–1929 Expedition marks an important step in the evolution of modern coral reef science, from nineteenth-century concerns with theorizing and deductive reasoning, based on generalized mapping and the interpretation of hydrographic charts, to a twentieth-century focus on empirical studies with a strong emphasis on field observation, measurement and experimentation. The drivers for this shift came from the widening geographical exploration of reef systems, the growth of seasonal and then permanent field stations, and the move from largely individual inquiry and exploration to programmes of research framed by national and international scientific agendas set by Academies of Science and their Committees (although often driven by committed scientific visionaries) (Spencer et al. 2008).

The long sequence of events that led to the Expedition's arrival at Low Isles on the northern Great Barrier Reef in July 1928 has been set out by Hopley et al. (2007), Brown (2007a) and, in some detail, by Hill (1984) and Bowen & Bowen (2002). These authors identify a set of key milestones: Charles Hedley's paper on biological field stations at the Pan-Pacific Union in Honolulu in August 1920; Henry Richards' presentation on the 'Problems of the Great Barrier Reef' to the Queensland Branch of the Royal Geographical Society of Australasia in April 1921; the formation of the Society's Great Barrier Reef Committee in September 1922; and Richards' paper on 'The Great Barrier Reef of Australia' at the Second Pan Pacific Science Congress, held in Melbourne and Sydney in August 1923. These signal events need to be seen, however, in the context of not only the loosening of the old colonial ties (albeit with the maintenance of the historical linkages to the major London institutions for science and exploration), the parallel scientific engagement with emerging US interests in the Pacific (exemplified in a coral reef context by the roles taken by W.M. Davis, T. Wayland Vaughan and A.G. Mayor) but also both scientifically and politically, through the 'emerging self-image of science in Australia' (MacLeod & Rehbock 2000, 209).

Much of the stimulus for a renewed interest in Pacific coral reef research at the beginning of the twentieth century came from the leading geomorphologist of the day, William Morris Davis. Davis wrote his first paper on coral reefs in 1913, to celebrate the centenary of the birth of James Dana, geologist and mineralogist on the United States Exploring Expedition (1838–1842) (Davis 1913); it was Dana's highly popular *On Coral Reefs and Islands* (1872) that established coral reefs as a legitimate object of scientific inquiry in North America (Appleman 1985). This was a field of research that then consumed Davis for the next 15 years,[1] culminating, at the age of 78, in his major publication, *The Coral Reef Problem* (Davis 1928). Like many of the theorists before him, Davis' physical engagement with the Great Barrier Reef was remarkably slight. Following the British Association for the Advancement of Science 'imperial meeting' in Melbourne and Sydney in August 1914, he spent one night on Green Island, near Cairns (Figure 1), 'an entertaining experience' but 'entirely fruitless as far as the origin of the reef is concerned' (Davis 1928, 347). However, when he returned to the USA, he proposed that more extensive coral reef work should be organized by all interested Pacific nations; this was taken up by the American Association for the Advancement of Science and folded into the plans for a congress of the newly formed Pan-Pacific Union. The Congress took place in Honolulu from 2 to 20 August 1920, with Davis present. The Australian attendees included

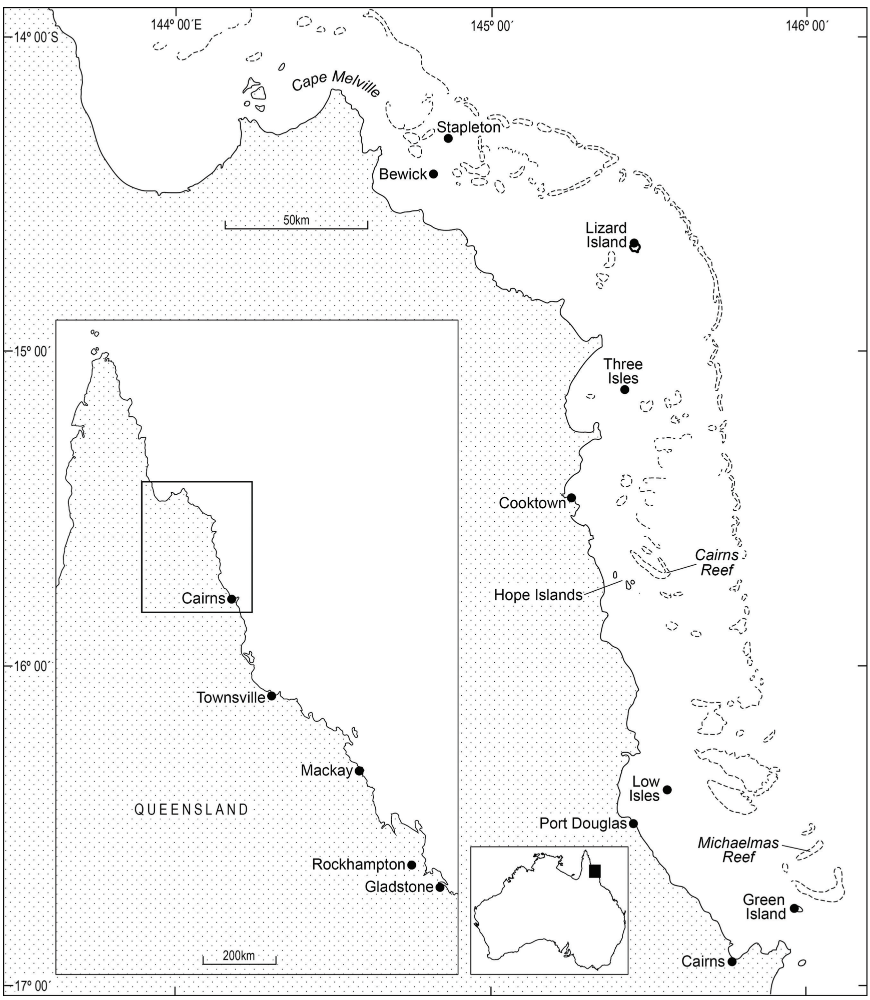

Figure 1 Great Barrier Reef between 14 and 17°S, with locations mentioned in the text.

Ernest Clayton Andrews, senior geologist of the New South Wales Geological Survey (from 1899; and its Director (1920–1930)) (Walsh 1979) who had accompanied Davis to New Caledonia and the New Hebrides ahead of the 1914 meeting; Charles Hedley, conchologist and (then) Acting Director of the Australian Museum, Sydney (Fairfax 1983); and Henry Caselli Richards, the recently appointed (1919) Professor of Geology at the University of Queensland (Hill 1988). Following the 1920 meeting, one of the prime organizers of the conference, the Yale geologist and then Director of the Bishop Museum, Herbert E. Gregory, established a group to determine the location of the next meeting. This group included Andrews and the American geologist Thomas Wayland Vaughan who had entered Harvard University as a graduate student in 1892, two years after Davis' promotion to Professor of Physical Geography (Thompson 1958). In 1919, Gregory had been appointed to chair the newly formed US National Research Council's Committee on Pacific Investigations of which Vaughan became vice-chair. Given the backgrounds of Gregory, Vaughan and Andrews, it is perhaps not surprising that the intellectual rationale for the next gathering – the Pan-Pacific Congress of 1923 – was emphatically geological (MacLeod & Rehbock 2000). This was particularly strongly articulated by Andrews: 'To appreciate the possibility of this community of scientific interests it is necessary to understand the underlying geographical and structural unity of the area, which is shown in the peculiar and symmetrical arrangements of its ocean depths, its volcanoes, its earthquake zones, its mountain ranges, its islands, and its coral reefs. The simplest explanation of this remarkable unity is that the floor of the Pacific Ocean has sagged slightly as a whole, and that the bordering continents have been drawn to it in the form of earth waves, undulations, or crinkles'.[2] And writing to Vaughan a year later, he ventured to suggest 'The more I consider the case for the 'Geographical Unity of the Pacific['] and the attempt to co-ordinate the present state of knowledge of the structure of the continents, the more it seems to me that the sub-oceanic mass of the Pacific appears to exercise a great control on the surrounding continents. It has occurred to me that this work might be undertaken some time by somebody – perhaps myself – who could coordinate all the main facts of structure within the Pacific Region'.[3]

While the determination, and political networking skills, of Henry Richards were critical in general terms in promoting scientific research on the Great Barrier Reef, his energies were strongly directed towards geological problems. Is the Great Barrier Reef 'in a static condition or one of elevation or of subsidence'? Richards asked (1922, 51), highlighting the debates around 'the coral reef problem' that had been circulating since the mid-nineteenth century and which had drawn the Great Barrier Reef's structure and history into their orbit. The theoretical framework for explaining the large-scale structure and distribution of coral reefs had been set by the Darwinian revolution of the 1830s and 1840s yet neither Darwin himself, nor one of his greatest supporters, Dana, ever set foot on any of the reefs of the Great Barrier Reef (Mozley 1964); it was left to Joseph Beete Jukes, geologist on the survey vessel H.M.S *Fly*, to apply the Darwinian model to the Reef (Jukes 1847, Vol 1, 333). Jukes had met Darwin before leaving England in April 1842, sailed with a copy of *The Structure and Distribution of Coral Reefs*, and once in Sydney discussed Darwin's theory with W.B. Clarke (Mozley, 1969), like Darwin and Jukes, a former pupil of Adam Sedgwick, Woodwardian Professor of Geology at the University of Cambridge. It was Clarke who made Jukes aware of Dana's support for the subsidence theory (Stoddart 1988). Jukes' argument was not unproblematic: as elsewhere, the application of Darwin's theory was wholly inferential, the subsidence process being too slow to be demonstrated by observation and the critical test of the presence of great thicknesses of shallow water limestones not amenable to mid-nineteenth century drilling technologies (Stoddart 1989). It was not difficult therefore for Alexander Agassiz, on the basis of minimal fieldwork during the 1896 cruise of the steamer *Croydon*, and with 'free indulgence in speculative interpretation' (Stoddart 2018, 167), to propose an equally untested, and diametrically opposed, history for the Reef. Agassiz argued that the Great Barrier Reef was the product of the 'mere action of erosion and denudation' (Agassiz 1898, 127) leading to 'a comparatively thin veneer of coral rock overlying the denuded land' (Agassiz 1913, 320). When coral boring did become feasible, this was undertaken in an oceanic setting at Funafuti Atoll, 3500 km east of the Great Barrier Reef, over three expeditions between 1896 and 1898. While the first of these expeditions was very much an initiative of the Royal Society of London, the second and third expeditions, a rejection of the old system of imperial dominance (Macleod 1987), were led from Sydney by the charismatic T.W. Edgeworth David and, under Edgeworth David's direction, A.E. Finckh respectively. Drilling across the three campaigns achieved progressively greater depths until terminated, before reaching reef basement, at 340 m (Royal Society 1904). This strong, yet inconclusive, test of Darwin's theory (and the subsequent drilling attempt by Alfred G. Mayor and technician John Mills at Pago Pago, Samoa (Stephens & Calder 2006)) helped underpin the early arguments about where scientific effort on the Great Barrier Reef needed to be focused. Following the establishment of the Great Barrier Reef Committee – 'instituted to investigate the origin, growth and natural resources of the Great Barrier Reef of Australia' (Thomson & Hedley 1925, ix) – in Brisbane on 12 September 1922, Richards moved swiftly to promote geological investigations. He reported on a five-week survey between Cairns and the Torres Strait in June–July 1923 which he had undertaken with Hedley to claim 'submergence on a grand scale has gone on' (Richards & Hedley 1923, 1) and 'the idea of a thick coral mass' (Richards & Hedley 1922–1923, 109). By November 1924, Richards and Hedley (who was by now the Scientific Director of the Great Barrier Reef Committee) began to raise the possibility of a drilling programme both on the outer edge of the Reef and at a series of mid-shelf locations and to draw Vaughan (whom Richards had visited in La Jolla, California in January 1925) and J. Stanley Gardiner, of the Zoological Laboratory at the University of Cambridge and who had been a member of the first of the Funafuti Expeditions (Brown 2007a), into the discussions on possible boring sites. Richards' preference for a boring on the far north of the Great Barrier Reef, at Raine Island,[4] did not meet with Vaughan's approval; conversely, he was 'heartily in favor of one of the Bunker or Capricorn Group'[5] at the southern end of the Reef. And for Gardiner, speaking after the presentation of a paper on the Great Barrier Reef to the Royal Geographical Society (RGS), London, on 23 February 1925 by his close colleague Gerald Lenox-Conyngham (who had sent greetings from the British government, the Royal Society of London and Cambridge University (where he was Reader in the new subject of Geodesy) at the opening of the 1923 Congress and had visited the Great Barrier Reef after the meeting), 'the proper place for the first boring is not at the edge of a reef, but rather halfway across, then there would be less difficulty and more certainty of reaching the underlying rocks, which it is all-important to determine' (Douglas & Gardiner 1925, 332). By 1926, mounting costs had restricted an ambitious drilling programme to just one location, and Oyster Cay, Michaelmas Reef (Figure 1), which could be serviced from Cairns, became the chosen drill site. Drilling began in May 1926, under the supervision of Charles Hedley, who had experience of coral drilling from the first Funafuti Expedition. The stratigraphy of the borehole was, however, confusing, with alternating coral sands and muds, and the operation was abandoned, with funds exhausted, in August at a depth of 183 m without reaching a clear reef basement. Uncharitably, Vaughan told Richards 'I do not feel so much surprise as you and your associates appear to have experienced'.[6] Little of immediate scientific value could be extracted from the exercise; indeed, the full analysis of the core materials was not published until 1942 (Richards & Hill 1942). Drilling was not resumed on the Great Barrier Reef until the Heron Island bore of May 1937, again somewhat inconclusively to a depth of 223 m (Hill 1984, 10).[7] Following these activities in 1926, there was then a serious shift from wholly geological to more broadly biological problems; we now discuss this shift below.

At the beginning of the twentieth century, an 'initial interest in coral morphology and taxonomy extended to embrace more dynamic aspects covering function and ecology' (Yonge 1980, 445). In this regard, Yonge identified Wayland Vaughan, as reef biologist rather than geologist, and Mayor as significant pioneers, through their leadership (1908–1915) of the Florida program from the U.S. Geological Survey and the Carnegie Institution of Washington, respectively. Vaughan carried out pioneering experiments on coral growth rate and observations on the effects of light, and salinity on corals in addition to establishing their food sources and larval biology in southern Florida

(Vaughan 1912). The most thorough set of Vaughan's early measurements were made on corals in the Dry Tortugas. Increments in colony height, diameter and, at times, weight were made for the major reef framework-building corals and other species on the reef. These careful studies revealed considerable variability in growth rates, for both individual colonies over time and between colonies of the same species (Vaughan 1915a, 1915b, 1916). Work by Mayor on Samoa also included research on coral growth (Mayor 1918, 1924), involving transplantation of a variety of corals in the field to assess growth rates, as well as performing experiments on Caribbean coral feeding responses at different temperatures and coral survivorship at extreme temperatures (Mayer 1918b).[8] Mayor had been with Agassiz on the cruise of the *Croydon* and inspired by the high-resolution chromolithographic and photographic plates of emergent reef flats depicted in William Saville-Kent's (1893) *The Great Barrier Reef of Australia*, established a summer field station in October 1913 on the Maer (Mer) reefs of the isolated Murray Island group in the Torres Strait. By monitoring water levels, air and water temperatures, substrate characteristics and sedimentation and the distribution and morphology of coral colonies in squares (measuring approximately 15 m × 15 m) staked out at 60 m intervals along a 500 m long transect – in what might be seen as the first example of modern coral reef ecology – Mayor was able to establish the critical limits to the duration of subaerial exposure and sediment loading that might be tolerated by corals (Mayer 1918a).

Nothing remotely comparable had been undertaken on the Great Barrier Reef up to this time. Charles Hedley had, like Gardiner, accompanied the first of the Funafuti Expeditions; his observations and voluminous collections were published in a series of memoirs of the Australian Museum (Hedley, 1896, 1899a,b,c,d; the first resulting in considerable friction over publication rights with the Royal Society [Rodgers & Cantrell 1988]). On the second Funafuti Expedition, Edgeworth David's second-in-command, the Melbourne geologist George Sweet, compiled maps of all 30 of the islands on Funafuti's reef rim, together with almost 100 geological cross sections identifying 20 different geological units, with notes on unit ages and environment of deposition (Royal Society 1904, Spencer et al. 2008). The observations at Funafuti by Hedley and Gardiner, and these remarkable maps of atoll motus, began to set a very different, yet complementary, agenda to that of the reef theorists. However, none of this work translated into a proper programme of coral reef research on the Great Barrier Reef. In 1901, Hedley and Andrews made descriptions of the continental shelf between 20 and 21°S, revisiting some of the evidence for uplift previously described by Jukes (Andrews 1902); in 1904, Hedley visited Masthead Island in the Bunker-Capricorn Group (Hedley 1906); and in 1906, in what has been described as the first paper by Australians on Australian reefs (rather than reef biota) (Stoddart 1989), Hedley and T. Griffith Taylor, another protégé of Edgeworth David, provided the first reef transects from Hope Island and Cairns Reef, northern Great Barrier Reef, detailing wave-driven transport of carbonates across reef platforms (Hedley and Taylor 1907, Taylor 1958) and made 'a valuable contribution to the scleractinian fauna of the Great Barrier Reef' (Veron & Pichon 1976, 1). But these were merely isolated, brief field visits.

In December 1921, Henry Richards wrote to Sir Matthew Nathan, Governor of Queensland and President of the Queensland branch of the Royal Geographical Society of Australia, to urge 'we should do here what Mayor and Vaughan are doing in the Gulf of Mexico'.[9] Early in 1922, Nathan put out some feelers to the Royal Geographical Society (RGS) in London, writing to the President, Sir Francis Younghusband, 'we should like very much to know that we have the sympathy of the parent Society'.[10] Subsequently, immediately following the formation of the Great Barrier Reef Committee, in October 1922, Nathan wrote a letter to Sir Sidney Harmer, The Director of the British Museum (Natural History) and also to Arthur Hinks, the Secretary to the RGS seeking both interest and cooperation and appending a proof copy of Richards' paper on the 'Problems of the Great Barrier Reef' (Richards 1922). In December, Hinks replied to say 'The Society is in cordial sympathy with your proposal',[11] and in February 1923, Harmer replied to also confirm interest in the project and to list suggestions of additional topics for study[12]; a similarly extensive reply was received from Hinks in the same month.[13] These dialogues, alongside those undertaken with universities, scientific institutions and societies in Australia, fed into Richards' presentation to the Second Pan Pacific Science Congress in August 1923. Entitled 'The Great Barrier Reef of Australia', the presentation outlined a revised plan of research (Richards 1923). Bowen & Bowen (2002, 240) claim that in this paper, Richards 'simply reiterated his plea for more geological research into the still unresolved issue of the formation of the Reef', but careful scrutiny reveals a much broader remit. The research outline covered physiographical, oceanographic, geological, botanical and zoological proposals. Particular reference was paid to detailed topographical and oceanographic surveys of the Great Barrier Reef (including chemical and physical characteristics of seawater); the quantitative study of plankton; the biology of invertebrates of economic importance; and 'pure research' on aspects of the coral reef. In the latter category, the following research concerns were addressed 'the systematic, morphological and embryological study of inadequately known groups, ecological studies – including that of the reef as a living entity, coral charting and observation of growth of the same and different species of coral under varying conditions and the collection and preservation of specimens and the establishment of aquaria' (Richards 1923, 5).

Clearly, the revised programme was ambitious, involving long-term research proposals which would be costly and labour-intensive; the realities could not meet the ambition. Internationally, the impetus for reef ecological studies had waned with the death, from drowning, of Mayor in 1922 and the move of Vaughan from the US east to west coast in 1924 to become the Director of the Scripps Institution, where his focus became directed towards establishing the new science of oceanography. Although Vaughan had been asked after the Third Pan-Pacific Science Congress (Tokyo, October – November 1926) to chair a Committee on Coral Reefs, he only began to get around to this task in July 1927, having first concentrated on establishing the International Committee on the Oceanography of the Pacific.[14] These difficulties were compounded in Australia itself. The Great Barrier Reef Committee was seriously weakened by the loss of both its chair, Sir Matthew Nathan, who had retired as Governor of Queensland in September 1925 and returned to England, and its Scientific Director, Charles Hedley, who died suddenly from a heart attack in September 1926. There continued to be a lack of trained marine biologists from Australia's young universities.

Conversely, in England, the drive to undertake research other than simply reef borings continued to be strongly promoted by Stanley Gardiner. In January 1925, Gardiner wrote to Richards to say 'three-quarters of the value of any boring may well be lost in the Barrier Reef region without a concurrent physical and biological survey of an area of the region much more thorough and comprehensive than was undertaken at Funafuti'.[15] And trenchantly to Hinks 'I'm against boring *without* proper detailed survey *at the same time*, this to be both biological+topographical, both to be *very* thorough'.[16] Representing the University of Queensland, Nathan attended the Third Congress of the Universities of the Empire in Cambridge, England, in July 1926 and there met with Gardiner to discuss suitably trained individuals who could spend a significant period of time, perhaps up to one year, on the Reef. Gardiner proposed his Cambridge colleague, Frank Armitage Potts. Potts had been with Mayor in the Torres Strait in 1913 (and in Fiji and Samoa in 1920) and had described observations and findings from the 1913 expedition in a lecture at the RGS in February 1925, published as Part II of a Great Barrier Reef paper with Lenox-Conyngham (Lenox-Conyngham & Potts, 1925). In the ensuing discussion, Gardiner remarked 'tonight Mr. Potts has shown us how the corals live; how they form the reef; at what rate they grow; what affects their growth; and, finally, what binds them together into a solid rock' (Douglas & Gardiner 1925, 331). Not surprisingly, therefore, the minutes of the meeting of the Great Barrier Reef Committee on 9 September 1926 record that a proposal had been received from Mr. F.A Potts of Cambridge University, England, to carry out a biological expedition to the Great Barrier Reef.[17] The precise brief was 'to study the ecology of a coral cay for a period from July 1927 to July 1928'. The Great Barrier Reef Committee decided that such an expedition would be valuable and proposed that Low Isles on the northern Great Barrier Reef was a suitable location for the investigation. In the Great Barrier Reef Committee, minutes of 23 February 1927 the members of Pott's expedition are listed – they included Dr. H. Graham

Cannon, Professor of Zoology at the University of Sheffield; Mr. F.S. Russell, an assistant naturalist at the Marine Biological Association, Plymouth; and Mr. E.B. Worthington from Gonville and Caius College, Cambridge.[18]

The stakes had been raised, however, by a resolution from the Third Pan-Pacific Science Congress, held in Tokyo, October–November 1926. The Congress was attended not only by Vaughan but also by William Setchell, the Yale botanist who had been appointed to the chair in Botany at UC Berkeley in 1895. An expert in marine algae, he had broadened his interests into coralline algae from accompanying Mayor to Fiji and Samoa in 1920, travelling widely through Polynesia thereafter (Campbell 1945). It was Setchell who framed the seventh resolution at the Congress, calling for the formation of a Committee of biologists, oceanographers and geologists to investigate the coral reefs of the Pacific Ocean because 'coral reefs are symbiotic entities whose origin and growth relations have received too little attention' and where 'methods of investigation are complicated and costly' (Setchell 1928, 153). Bowen & Bowen (2002) argue that this resolution, with its implications for the likely international scrutiny of the expedition that would necessarily take place at the next Pan-Pacific Congress, planned for Java in 1929, caused Gardiner to re-consider whether the proposed expedition was sufficiently well planned with its current leader and personnel. However, a great deal of momentum had been developed for an expedition by this time with the establishment of a British Barrier Reef Committee (with Nathan acting as its Chairman) in January 1927. This Committee subsequently became the Great Barrier Reef Committee of the British Association at their Leeds meeting in September 1927 (Nathan 1927); Yonge (1930a) details its full 25-person strong membership. In addition, the Balfour Trustees in the Department of Zoology at Cambridge, guided by Gardiner (see Morton, 1992 for the full story), offered a Balfour studentship to Dr. C. Maurice Yonge in April 1927, then researching feeding and digestion in the British oyster, *Ostrea edulis*, at the Plymouth Laboratory of the Marine Biological Association, in the anticipation that he would accompany the Potts' expedition. However, following the failed launch of this expedition Gardiner made it clear to Yonge (in a letter of 3 May 1927) that he could follow his marine biological interests in laboratories as far afield as Naples, Woods Hole or Bermuda if he so desired.[19] In July, Gardiner wrote, rather disingenuously, to Vaughan to inform him 'unfortunately Potts who married last year cannot go but I hope we shall be able to find somebody, if not with equal knowledge of coral reefs, quite thoroughly efficient'.[20] But it is clear that Gardiner had already found that 'quite thoroughly efficient' person, appending to the letter a project outline that identified Yonge as 'the leader of the expedition and a comparative physiologist'. By 10 August 1927, Richards wrote to Vaughan 'now I hear from Potts that he will be unable to come next year, but that Dr Bidder [George Bidder, marine biologist who lectured in Cambridge 1920–1927] and Dr Stanley Gardiner were hoping to get away an expedition next year under a marine biologist named Yonge of whom I know very little'.[21] In reply, Vaughan assured Richards that all was well: 'Stanley Gardiner is one of my really old friends. We have known each other personally since January 1898'. He went on to say 'Gardiner's program will be just about as fine as it is at present possible to make it' and 'highly valuable results are assured'.[22] Following the Leeds meeting, and discussions among Nathan, Edgeworth David, Potts and Yonge,[23] a new proposal to send an expedition to the Great Barrier Reef was explored. The programme was formalized in a letter to Sir Matthew Nathan from Gardiner on 24 September 1927.[24] In this letter, the key elements of the proposed research were:

> To examine a sector of the Great Barrier Reef from shore to ocean off Cairns, chart it accurately, survey associations of plants and animals on its surface both qualitatively and quantitatively, study the food and power of lime formation in the same and all other matters as concern the formation and growth of that part of the Reef. In detail it was proposed to undertake an investigation extending through 12 calendar months; this enabling a proper knowledge of the seasonal problems concerning the physical and chemical conditions, the rate of growth, seasonal reproduction of animals and plants and other food organisms, etc. etc. as well as giving time for the necessary work connected with a thorough scientific

> survey of the area. The members of the expedition would be housed in the camp of the Australian Barrier Reef Committee on Low Islands, about 20 miles north of Cairns and it is anticipated that a power boat would be obtained for the purposes of this expedition.

But this was not all. At the meeting of the British Great Barrier Reef Committee on 4 October 1927, 'Mr. Debenham' asked for information as to the extent to which geographical investigations were to be undertaken; in response, the Committee asked him to prepare a memorandum to form the basis of an appeal to the RGS for funds.[25] Frank Debenham had just been promoted from University Lecturer to Reader and Head of the Department of Geography at Cambridge, having been from 1919 RGS Lecturer in Surveying and Cartography, a post previously held (1908–1913) by Arthur Hinks before he moved to the RGS to become Assistant Secretary, and then Secretary and Editor of *The Geographical Journal*, a post he held for 30 years until his death in 1945. Debenham, an Australian, had been trained in petrology at Sydney University by Edgeworth David and had participated in Scott's fateful *Terra Nova* Expedition in 1910–1913, along with Griffith Taylor (Speak, 2008). While in Cambridge, Hinks wrote two influential books, *Map Projections* (1912) and *Maps and Survey* (1913), and Debenham promoted plane table mapping, the use of a mounted drawing board as a solid level surface on which landform positions are plotted in the field. This was, and still is, an efficient approach for rapid field surveys, as captured in Debenham's highly successful handbook, *Map Making* (1936). It is not surprising, therefore, that both Hinks and Debenham were interested in the high-resolution measurement of position and 'changes of level'.[26] But with the biological party in place by the start of 1928, far less progress had been made with the 'geographical investigations'. Gardiner sent a hurry up to Hinks in January 1928 'There remains a Chemist and a Geographer… personally I'm very very keen to have one. Is there any possibility of your providing us such a person?' and '… you know more than I do on what is wanted and clearly Davis, Daly [Professor of Physical Geography at Harvard who had replaced WM Davis in 1912] and Vaughan agree with me in stressing this side and consider that there is real scope'.[27] Hinks shifted the problem away from the RGS onto Debenham who throughout January struggled to come up with a name. But then in February, he wrote to Hinks to put forward the name of J. Alfred Steers who had been appointed to a University Lectureship in Geography the previous year.[28] Debenham extolled the virtues of his young recruit: 'He is extremely adaptable, and has improved in width of outlook, technique etc., tremendously in the last two or three years, but he does need a good long trip, such as this [the Great Barrier Reef Expedition], to make him of first-class value to my department. Of course Steers has never seen a coral reef, but he has the greatest interest in coast lines, and has lectured in considerable detail on the formation of coral reefs. He is also a man who would get up the subject very thoroughly en route to the work. Altogether I rather like the idea'.[29] And so at the Meeting of the British Great Barrier Reef Committee on 23 February 1928, 'Mr Debenham announced that his assistant, Mr Steers, Fellow of St. Catharine's College, Cambridge, desired to accompany the expedition and that he could be spared from his duties from June to December'.[30] At much the same time, a final year undergraduate in Engineering from the University of Oxford, Michael Spender, having seen the notice on the Expedition in the journal *Nature* for 11 February, wrote immediately to Hinks to see if there were 'any junior posts yet to be filled', mentioning, music no doubt to Hinks' ears, that he had 'taken the survey course of the school; which includes a month in the field with the usual instruments and a good deal of work in the drawing office'.[31] References were obtained from the Professor of Engineering at Oxford, Frewin Jenkin, and Spender met with both Hinks and Gardiner. All were impressed; Debenham less so: 'Spender is full of ideas, and active, but I am afraid he has a lot more to learn than he thinks, and must drop some of his Oxford manner when in Australia. Steers should provide a good calming influence'[32] (for insights into the highly complex individual that was Michael Spender see Shipton (1945)). The other member of the Section, for a six-week period, was E. C. Marchant, from St. John's College, Cambridge, who had read Part I of the Geographical Tripos.[33] All that was left was for a programme of 'geographical investigations' to be established. This was provided by Debenham on 14 March 1928 in a Memorandum on work to be carried out by the RGS members of the Barrier Reef Expedition:

> The time seems opportune for beginning a more exact type of investigation, in which the surface changes already suspected in connection with coral reefs shall be the subject of careful measurement. The results and deductions of such measurements will not be available for a period of years, but when available they should be quite conclusive on such subjects as emergence and subsidence, growing and wasting of coral banks, scouring and filling of lagoons.[34]

Debenham went on to outline in detail the types of measurements required, including the determination of mean sea level from a recording tide gauge; establishment of a network of bench marks; depth sounding and collection of bottom sediment samples; and observations on coral growth, marine erosion, solution and storm deposits, with across-reef transects mapped by plane table, theodolite and compass-and-chain.

And so, after a faltering start, the Expedition was finally underway. The leader, Maurice Yonge, and some of his team set off from London on the RMSA ORMONDE bound for Australia on 26 May 1928. The group arrived at Brisbane on 9 July and finally at Low Isles, their headquarters for the next 12 months, on the 16 July 1928. Low Isles is situated at 16°23′S, 145°34′E on the inner shelf, 65 km north-northeast of Cairns and 15 km northeast of Port Douglas on the Queensland coast. The outer barrier of the Great Barrier Reef lies 40 km to the east (Figure 1). A modern image of Low isles is shown in Figure 2; it comprises a small sand cay (0.02–0.03 km^2) and a larger mangrove forest (0.17 km^2 in 1928, 0.46 km^2 in 2017) on top of a horse-shoe-shaped reef platform occupying an area of 1.77 km^2 and typically 2 km in width. The Expedition was housed in six huts, prefabricated

Figure 2 Aerial photograph of Low Isles taken at an oblique angle from the south east on 5 October 2007. Woody Island, the mangrove stand on the exposed side of the reef, can be seen in the foreground, while the smaller, vegetated sand cay where the Expedition was based can be seen in the background (reproduced under licence #2011071, photo credit: David Wall © davidwallphoto.com).

off site and then assembled *in situ* on the sand cay, ready for the arrival of the field party (Figure 3); the laboratory hut had been used on Oyster Reef for the drilling operations there in 1926. This was a meticulously planned and extremely well-equipped expedition: details of the laboratory spaces, aquaria, library facilities, met. station, field equipment and boat support are detailed by Yonge (1930a, 1931a).

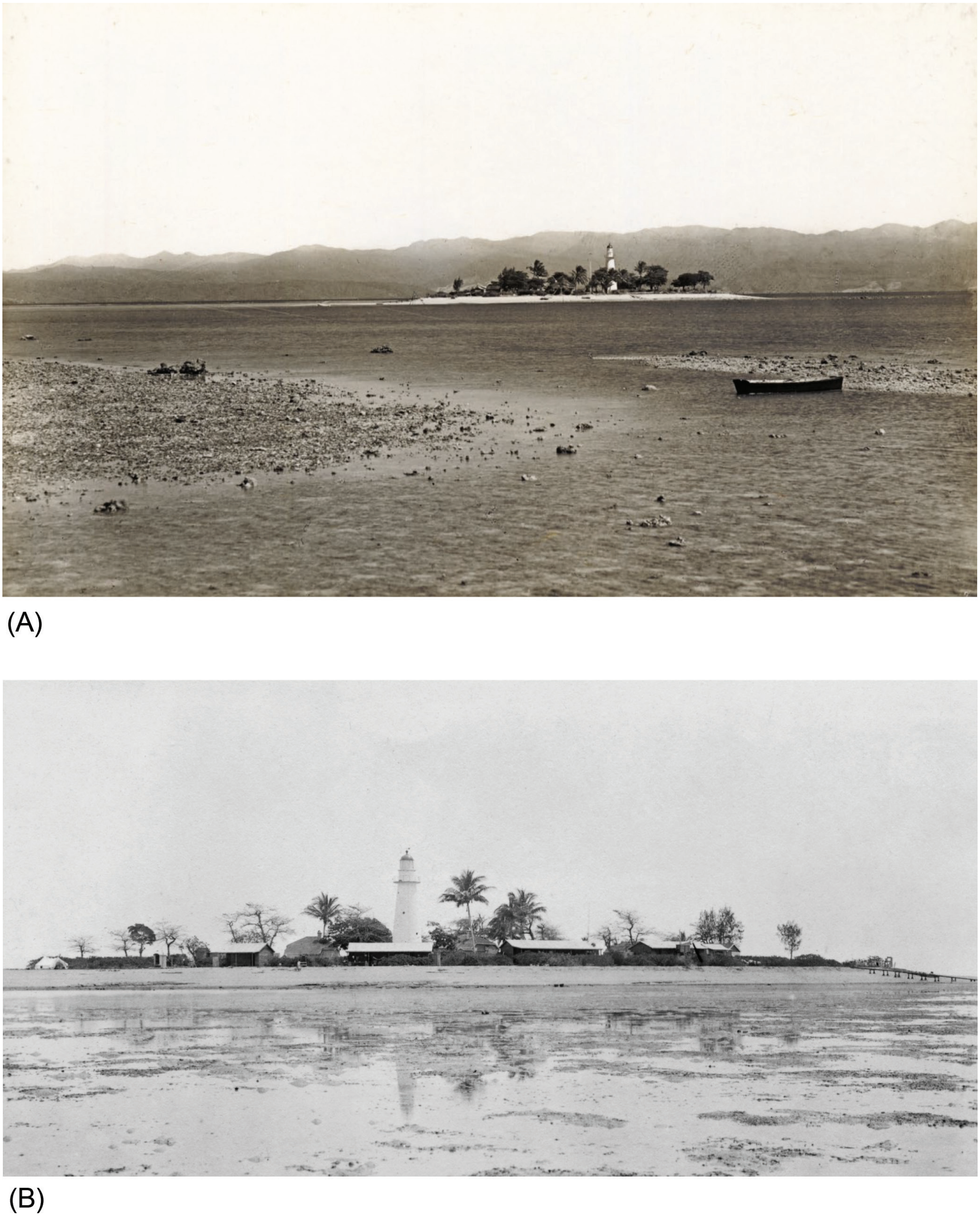

Figure 3 (A) The sand cay at Low Isles at the time of the Expedition (1928–1929) from Tripneustes Spit looking west across the Anchorage; (B) the expedition huts on the Low Isles sand cay (both images by kind permission of the Royal Geographical Society).

Table 1 Personnel of the Great Barrier Reef Expedition at Low Isles, 16 July 1928 to 28 July 1929 (after Yonge, 1930a)

Name	Position	Nature of work	Time on expedition (months)
CM Yonge	Expedition Leader	Physiologist	12.5
FS Russell	Deputy Leader Leader, Boat Party	Zooplankton worker	5
JA Steers	Leader Geographical Section	Geographer	4
TA Stephenson	Leader, Shore Party	Zoologist	11.5
AP Orr		Chemist and hydrographer	12.5
SM Marshall		Phytoplankton worker	12.5
FW Moorhouse		Economic zoologist	12.5
AG Nicholls	Assistant to Leader		12.5
GW Otter		Zoologist	11
G Russell	Assistant to Mr. Russell		5
A Stephenson		Honorary zoologist	11.5
G Tandy		Botanist	5
MJ Yonge	Assistant to Leader	Medical officer	12.5
JS Colman		Zooplankton worker	10.5
EA Fraser		Zoologist	4
SM Manton		Zoologist	4
CE Marchant		Geographer	3
MA Spender		Geographer	11

The Expedition's personnel are detailed in Table 1 and the wider party in November 1928 shown in Figure 4. The advance party consisted of Dr. C. M. Yonge, leader of the Expedition and physiologist, together with his wife, Mrs. M. J. Yonge; Mr. F. S. Russell, second in command and in charge of the Boat Party and a zooplankton worker, also with his wife Mrs. G. Russell; Dr T. A. Stephenson, zoologist and leader of the Shore Party with his wife Mrs. A. Stephenson; Miss S. M. Marshall, a phytoplankton worker; Mr. A.P. Orr, chemist and hydrographer; Mr. G.W. Otter, zoologist; and Mr. G Tandy, botanist. They were accompanied to Low Isles by Mr. F.W Moorhouse of Brisbane described as an 'economic zoologist' and then joined two days later by Mr. A. G. Nicholls, as assistant to the leader, from Perth. Other personnel came out from England during the course of the Expedition while others left; the arrivals included Mr. J.S. Colman, zooplankton worker; Miss E. A. Fraser, zoologist; and Miss S.M. Manton also a zoologist (Yonge 1930a, 1931a). For Manton, arriving at the end of March 1929, 'The amount they've done and the bright and intelligent things they're at is astonishing, and a little overpowering at first when you plunge into the middle of it armed with abysmal ignorance. They work jolly hard too…' (Clifford & Clifford 2020, 57). For four to six weeks in the latter part of 1928, the Expedition was joined by five members of the Australian Museum; one of these members, the conchologist Mr. T. Iredale, was also involved in the Expedition's 1929 fieldwork at Three Isles (Figure 1). There were also some 15 occasional visitors with scientific interests, including Henry Richards and, perhaps the first example of a journalist embedded within an expedition to the reef seas, Charles Barrett of the *Melbourne Herald* (McCalman 2014). For the Geographical Section, Steers and Spender arrived in Townsville in August and were then joined by Marchant at Cooktown in mid-October. Steers left to return to Cambridge in early November 1928 but Spender stayed on to the end of the Expedition, the camp being evacuated on 28 July 1929. The huts were locked up with a plan to maintain them as a permanent field station; unfortunately, that dream ended with the destruction of the buildings in the cyclone of 3 March 1934 and the resignation of Moorhouse, as the Queensland Government's marine biologist and site manager, a year later.

Figure 4 Party at Low Isles, 3 November 1928. From left to right, back row, standing: H.C. Vigden, F.A. McNeill, J.A. Steers (largely obscured), A.P. Orr, H.S. Mort, H.A. Longman, E.O. Marks, M.A. Spender, J.S. Colman, G. Tandy, C.E. Marchant, A.A. Livingstone, T. Iredale; front row, seated: F.W. Moorhouse, A.C. Wishart, Miss S.M. Marshall, F.S. Russell, Mrs. Russell, Professor H.C. Richards, Mrs. Yonge, C.M. Yonge, Mrs. Stephenson, T.A. Stephenson, A.G. Nicholls; seated on ground: Master Iredale, G.W. Otter (photo credit: M.J. Yonge) (by kind permission of the Royal Geographical Society).

While the Expedition was based at Low Isles throughout, there were a series of short visits by smaller groups to the outer barrier and islands inside the barrier for plankton, hydrographic and dredging operations, as far north as 14°30′S (Figure 1) (the activities of the Geographical Section are considered in further detail below). The longest of these visits was the two-week ecological and topographic survey of Three Isles in May 1929 and a similar length visit to Lizard Island and the neighbouring outer barrier (Figure 1) in the following month. In March 1929, A.P. Orr and G.W. Otter used the visit of Commonwealth Lighthouse Service's SS CAPE LEEUWIN to Willis Island in the Coral Sea, 450 km east of Cairns, to undertake open ocean oceanographic sampling and in the period April to May 1929, the Yonges, Nicholls and Moorhouse made an extended visit to Thursday Island and the Murray Group in the Torres Strait. Furthermore, the entire team spent some time on the Atherton Tableland, inland from Cairns, as a respite from the summer heat and there were frequent Sunday excursions to the mainland coast.

Novel aspects of the 1928–1929 Expedition

The Great Barrier Reef Expedition of 1928–1929 was ground breaking in several respects. First, the interdisciplinary nature of the Expedition was a clearly articulated philosophy, from the planning stages right through to publications. Gardiner writing to Hinks in February 1928 set out the necessary interactions: 'fix the places to be so surveyed the biologists must tell us precisely what is the life complex on each – and the exact position (on the geographers survey) of any peculiar complexes or striking groups of corals should be noted. I think that the geographer should make an independent estimation of the wash of the sea (tide, currents waves etc. but not necessarily with extreme accuracy as the use of terms such as tide etc. imply) on each survey reef because the biologist will have 80% of his mind on his organism & the geographer 80% of his on physical conditions'.[35] This was followed up by Debenham, writing to Hinks in March 1928: 'the biologists made a definite request, which I thoroughly agree with, that during the later part of the time, that is when Spender is based at headquarters [i.e. Low Isles] he should, in addition to carrying out such work as is in the memorandum [see above and source no. 33], make a survey of the guiding marks and beacons which the biologists will set up when taking their dredgings and soundings, etc.'.[32] Although the intention of setting up what would have been the first long-term record of water level variations on a coral reef was stymied by a shipping strike, which delayed the arrival of the tide gauge at Low Isles until February 1929, thereafter, after some difficulties in establishing a stable measurement platform, a near continuous water level record was obtained for the period from 8 February to 24 July 1929; subsequent analysis of the tide gauge record by the Liverpool Tidal Institute started to make sense of the water level variations that the Expedition found 'capricious and unreasonable' and 'consistently baffling' (Spender 1932, 203–204). It was possible to relate the different morphological components of the Low Isles reef system to tidal levels and, for example, to study the distribution of coral cover down to 5.5 m, with maximum coral cover being found at ~0.6 m below datum (Spender 1930; Figure 5).

As Steers' time on the Expedition was coming to an end in October 1928, there were discussions between Richards, Debenham, Hinks, Steers and Yonge about how Spender's time might be most usefully deployed. After the fact, and when Steers had been back in England for three months, Yonge wrote to Steers: 'The question of Spender's programme has been difficult…. I want Spender to do all he possibly can to help you but Richards, Stephenson, Spender and myself are in complete agreement that it is far better to do the one job of surveying the island really properly than that scrappy work should be done on a series of surveys and borings none of which could give any satisfactory result'.[36] In purely practical terms, once Marchant left in early January 1929, Anne Stephenson was deployed as 'staff man' for Spender's surveys and 'Spender is learning the animals and plants so that they can do biological survey also'.[37] By April, Spender told Hinks: 'I am still confident that this piece of work will be importantly useful in all these problems – the general coral reef problem, the problem of these unique (?) Low wooded Islands, and the biological problem of this reef. No ecological work comparable has ever been done in coral reef work'.[38] Progress improved significantly once daytime low tides allowed access to the reef flats and in the 'statement of position' on 28 May Spender was able to say 'the mapping of Low Islands is very nearly complete. Several level traverses have been made across the flat, along the ramparts and over the strip sections being ecologically surveyed by Dr Fraser and Miss Manton',[39] summarizing by mid-June 'Geographical work obviously interlocks with the Shore Party work; we have in fact, worked together the whole way through. When Davies [surely a mis-spelling of WM Davis] denies any significance in the biological aspect of the reef, he cannot be anything but exaggerating'.[40] By the time of the publication of the Expedition Reports, Gardiner was able to say 'on the bio-logical side we can now zone the areas downwards & ecology becomes a matter of physiological reactions in waters; this is what interests U.S.A.'[41] (although he was rather more circumspect subsequently[42]).

Second, unlike earlier expeditions on coral reefs, it brought scientists together at a single research site for long-term *in situ* observations and experimentation over a period of nearly 13 months. The chosen location of the Expedition at Low Isles on the northern Great Barrier Reef was a key factor and much was made in early deliberations of selecting a site which satisfied the requirements of using a reef as a natural laboratory (and which could also be sustained by servicing on a regular basis from Port Douglas; Figure 1). Thus, the British Great Barrier Reef Committee reported at the BAAS meeting in Glasgow in 1928 that the 'work of the expedition consists of research on the growth, feeding and reproduction of organisms around the camping island, to a large degree the sea forming a substitute for laboratory tanks'.[43] In this shallow water environment which Yonge also later referred to as 'a natural aquarium' (Morton 1992, 391), a range of scientific activities were carried out that included an assessment of the role of zooxanthellae in sustaining corals; oxygen exchange between corals and surrounding water; sediment cleansing by corals; estimates of coral

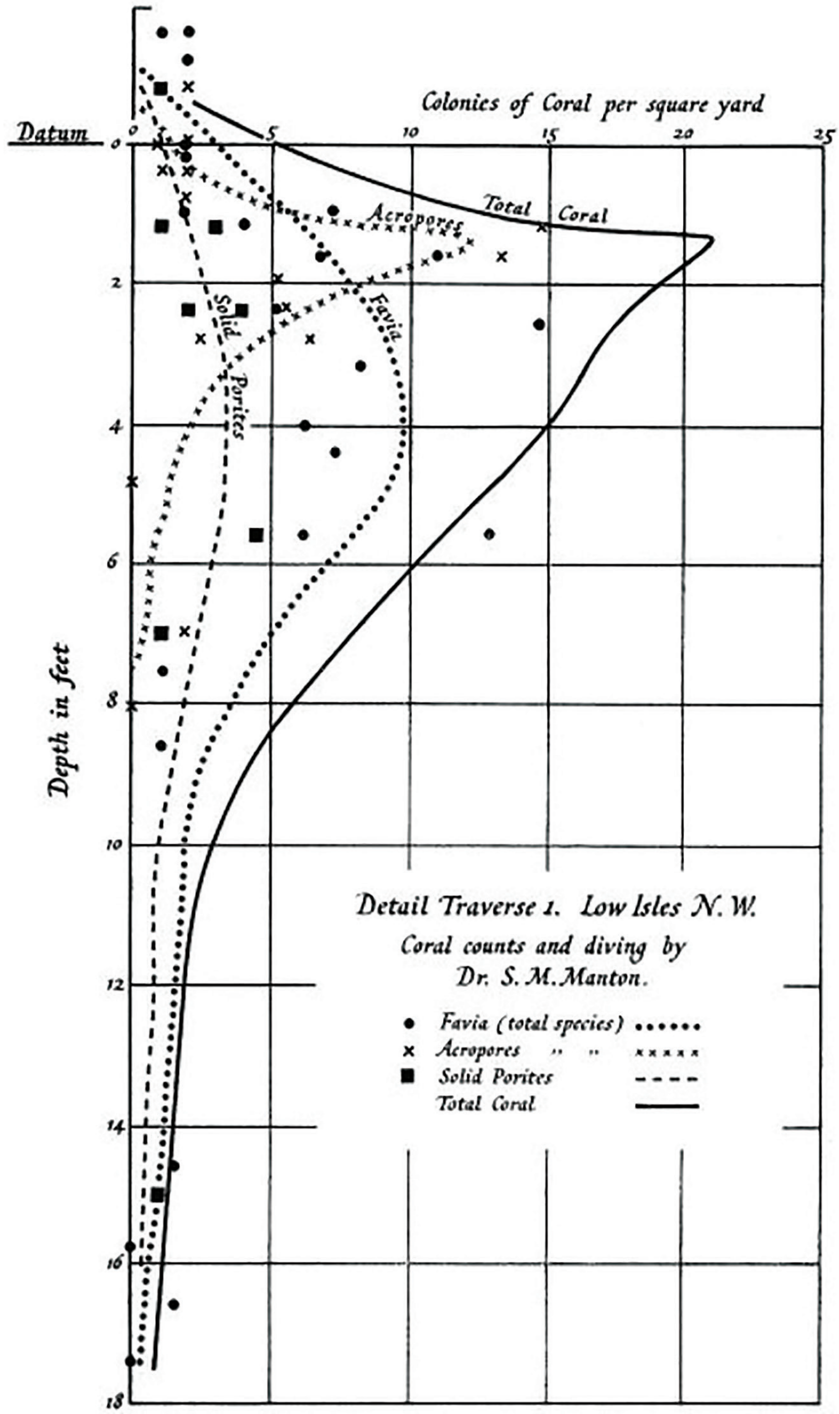

Figure 5 Graph showing relation between abundance of coral growth and depth, seaward of the boulder-zone, Transect I (see Figure 12 for location, Figure 14 for transect bathymetry) (reproduced from Spender, M. 1930. Island-reefs of the Queensland Coast. *The Geographical Journal* **76**, 193–214, 273–293 (Figure 4), by kind permission of the Royal Geographical Society).

growth rates; the effects of transplantation of corals from one site to another; and coral reproduction and development of juvenile corals from planula larvae.

A third novel feature of the Expedition was the introduction of relatively sophisticated (for the time and area of study) experimentation into the scientific programme with Gardiner describing the Expedition members as 'experimentalists' (Brown 2007a) (Figure 6). As we have detailed above, the Expedition was not the first to engage in experimental studies. But the prolonged stay at the Low

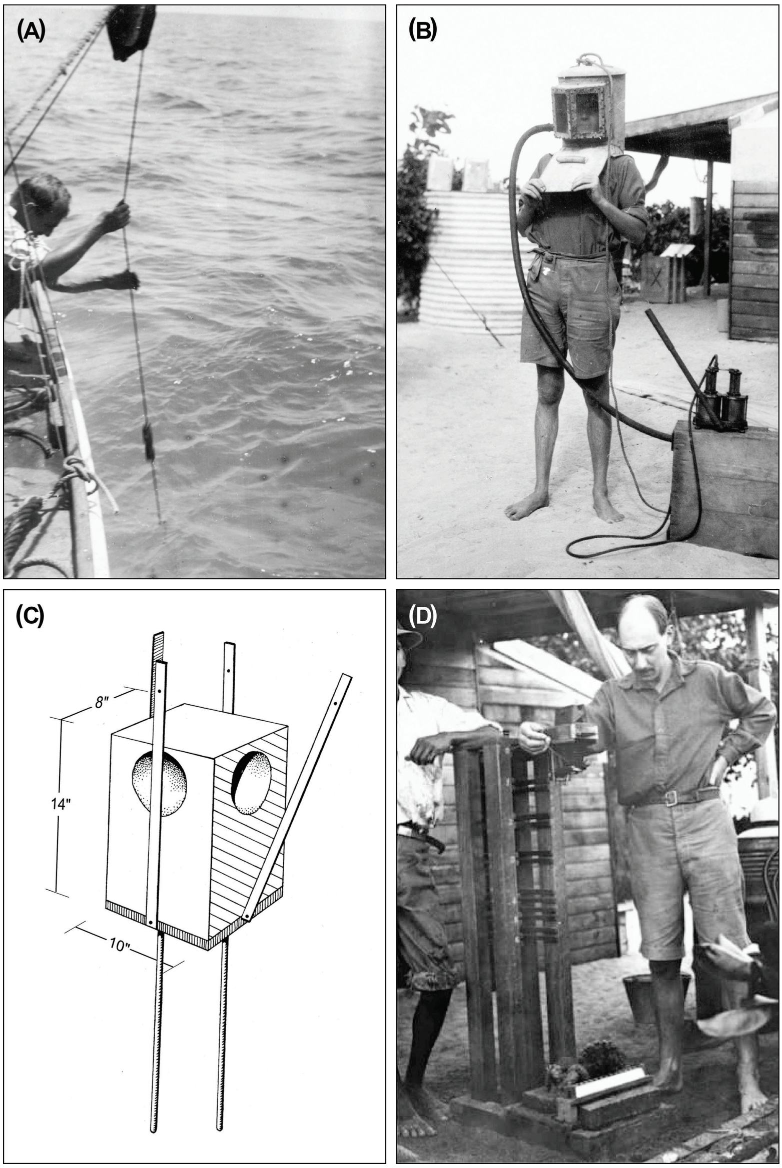

Figure 6 Methods used by the Expedition. (A) hydrographic survey: Freddie Russell sending messengers down the wire to the water sampler (by kind permission of the Royal Geographical Society); (B) demonstrating the Expedition's diving helmet (by kind permission of the Royal Geographical Society); (C) the 'clock-tower' – a structure devised by Alan Stephenson to rear coral planulae on the reef. Re-drawn from Stephenson (1931); (D) Alan Stephenson and apparatus for photographing coral colonies (ANL archives, PIC/11204/349 LOC ALBUM 1115/4, with kind permission of the National Library of Australia).

Isles base and the person power and expertise available meant that experimentation could be taken to a different level and a whole range of physiological experiments were performed in both the field and laboratory, many using the observations of Mayor and Vaughan as their starting point. Indeed, good use was also made of the diving hood developed by Mayor for underwater observations and the 'light- proof live-car' of Vaughan (described by Yonge & Nicholls [1931a] as a 'coffin-shaped box') to test the effects of darkness on selected corals and their zooxanthellae.

The Expedition also took the major innovative step of checking ground observations at Low Isles against aerial photography flown on 24 September 1928 (Figure 7) by the Royal Australian Air Force (RAAF)[44] (Stephenson et al. 1931). This was well ahead of its time: the widespread potential of aerial photography for detailed reef mapping was not realized until towards the end of WWII (Steers 1945, Hamylton 2017). Fittingly, one important case study site at the time of this renewed interest was Low Isles. The reef was overflown by the RAAF on 21 January 1945, with photography and subsequent ground referencing by Rhodes Fairbridge and Curt Teichert[45]; the timing allowed assessment of the impacts of the tropical cyclone of 1934 (Fairbridge & Teichert 1948 [and see also Moorhouse 1936]). By 1968, it was possible for W. G. H. Maxwell to develop an elaborate taxonomy of reef types and to link these types together in an inferred, multistrand evolutionary sequence from the remarkable aerial photography archive of the Great Barrier Reef, funded from 1964 by the Australian Commonwealth Government (Maxwell 1968). In 1982, the Great Barrier Reef Marine Park Authority commissioned the first full inventory of the GBR Marine Park that identified 2904 discrete reefs based on a combination of Landsat satellite imagery and aerial photographs (Hopley et al., 2007). The resulting gazetteer was used for management zoning, and the later re-zoning under the Representative Areas Program, of the Great Barrier Reef Marine Park (Day, 2019). The reef classification scheme at the heart of the gazetteer was based on the evolutionary model proposed

Figure 7 Expedition members and support staff meet the aircrew and inspect the aircraft at The Anchorage, Low Isles during the aerial survey of 24 September 1928 (source: James Cook University Library Special Collections, Sir Charles Maurice Yonge Collection, Great Barrier Reef Expedition Photo Album 2, Creators: Frederick Stratten Russell and Gweneth Kate Moy Russell (1928). Reproduced with kind permission of the James Cook University Library, Australia).

by Hopley (1982). This Holocene model of reef development proposed initial vertical reef growth upward from antecedent reef platforms in juvenile stages, transitioning to horizontal, lateral outward growth once the upper reef surface had reached sea level in later stages. This was followed by sediment infill and the development of reef-top sedimentary landforms. This arrangement of reefs into a temporal sequence of morphological evolution therefore placed a longer-term geomorphic perspective of reef development at the centre of Great Barrier Reef Marine Park management.

Not all the intended technical innovations were successful. Debenham and Hinks' 'armchair plans'[46] of mapping from stereo pairs of photographs obtained by photo-theodolite failed at the first attempt, at Orpheus Island in August 1928. Here, Spender and Steers were unable to establish sight lines in thick vegetation, found moving the heavy instrumentation across steep terrain difficult and 'sand and ants prevail everywhere'.[47] In retrospect, the methodology was never going to work on a low relief, sea level reef system, unlike the spectacular success that Spender was subsequently to have with the technique in the extensive mapping of the mountainous terrain of the southeast coast of Greenland in 1932–1933 (Norlund & Spender 1935) and on the north face of Mt. Everest in 1935 (Spender 1936).

Fourth, the Expedition incorporated strong collaboration between Australian and English scientists with some Australians spending a full 12½ months at Low Isles while others visited for periods between four and six weeks. The Expedition was also noteworthy for the participation of a number of female scientists – Mrs. M. Yonge, Mrs. G Russell and Mrs. A Stephenson were wives of the Expedition leader, his deputy and leader of the shore party, respectively, but all had active parts to play in research activities with Anne Stephenson working on the ecology and zonation of reefs, growth and asexual reproduction in corals and breeding patterns of other reef invertebrates and, towards the end of the Expedition, assisted with ground survey measurements (Figure 8). Mattie Yonge assisted in both laboratory assays and environmental measurements. Other women scientists, such as Miss S. M. Marshall, Miss S. M. Manton and Miss E. A. Fraser had specific zoological roles. Sheina Marshall specialized in phytoplankton production but also studied the breeding of reef corals and the effects of sediments on corals. Sidnie Manton participated in the ecological and quantitative surveys of coral reefs and detailed study of *Pocillopora* growth, while Elizabeth Fraser specialized in the life-history of hydroids on the reef. While not without precedent – as Caroline (Cara) David (née Mallett)[48] (Cantrell 1993) had accompanied T.W. Edgeworth David on the second drilling expedition to Funafuti in 1897 – the inclusion of women in the research party, widely commented upon in newspaper and other popularist accounts at the time (McCalman 2014), served as a catalyst for greater involvement of women in Australian science.

It is also worth pointing out that none of the British biologists had ever visited a coral reef before but many were classically trained zoologists equipped with powerful observational skills and a sound understanding of invertebrate structure and function. Similarly, almost half a century later, Steers reflected 'when Spender and I began work on the reefs we had no definite idea of what there was to do, and how we were to do it! Discussions with geographers were optimistic rather than helpful, because no one interested in geomorphology had visited the Barrier . . . We had to find our problems as we sailed along the coast' (Steers 1978, 161–162). Taking his cue from Debenham, Steers was always a strong advocate of the primacy of field measurements; in later life, he wrote 'I am convinced that physiographers should travel, and observe intelligently, as much as possible' (Steers 1960, 9) and that 'wide reading, field excursions, personal field work are all vital in the training of a physiographer' (Steers 1960, 13).[49] There is no doubt that he brought these observational skills into play on the Great Barrier Reef, not least in setting the studies at Low Isles into the broader regional context, initially visiting the Capricorn and Bunker Group (23°S) and then establishing, through the cruise of the *Tivoli*, the variability in both reef and mainland shoreline types between the Whitsunday Islands (20°S) and Cape Melville (14°S), a distance of almost 1500 km. Steers was the first scientist to extensively study the reef islands of the Great Barrier Reef, separating out the often highly dissected high or rocky continental islands with their fringing reefs, distinguishing

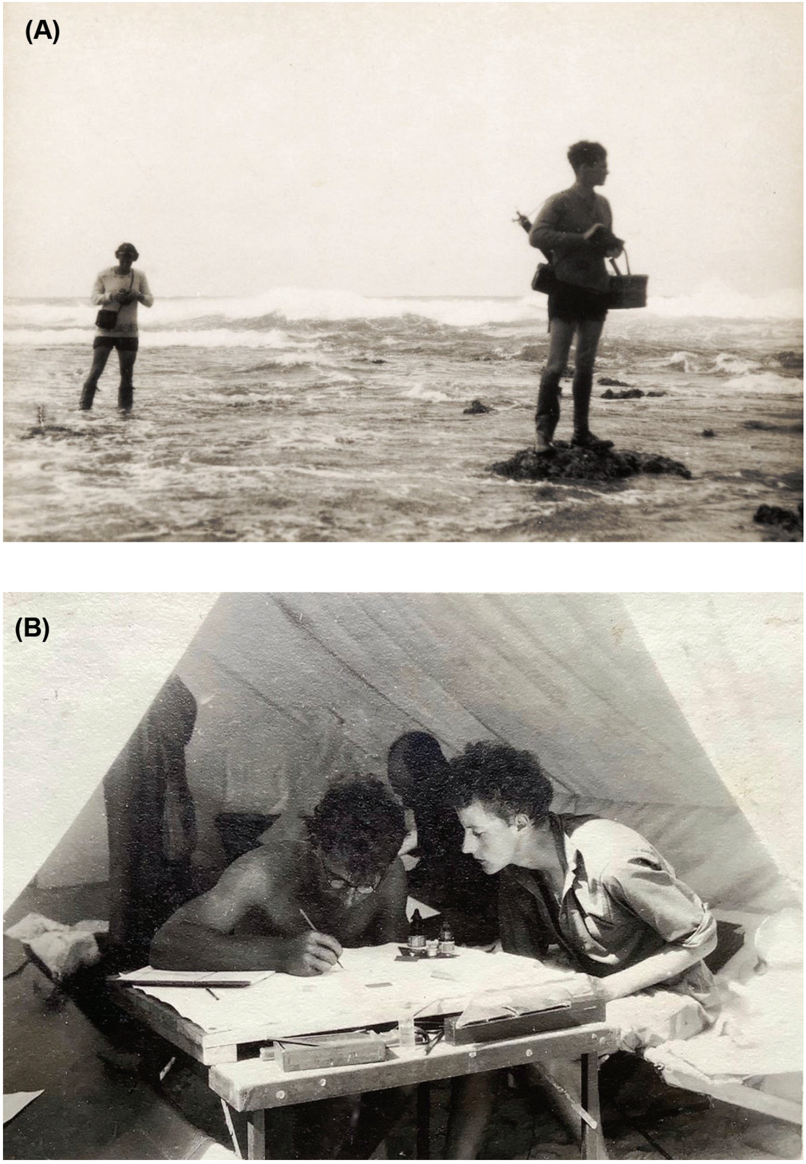

Figure 8 (A) Sidnie Manton (left) and Anne Stephenson mapping on the outer barrier reef. Stephenson carries 'pail, hammer, chisel, "chicken run" and numerous things tied about for mapping' (Clifford & Clifford 2020, 100) (reproduced by kind permission of the Royal Geographical Society); (B) drawing up from field mapping, (from left to right: Michael Spender, Alan Stephenson, Anne Stephenson) (photo credit: S. Manton, with kind permission from the family's archives). These images relate to the Expedition's excursion to Lizard Island and the reefs of the neighbouring outer barrier, 31 May to 13 June 1929.

between sand cays and shingle cays and providing the descriptive term 'low wooded island' for the complex reef systems of the inner shelf north of 16°S. The other main member of the Geographical Section, Michael Spender, was a supremely talented surveyor who, at Low Isles and Three Isles, took reef surface mapping to a completely new level, as recognized by Yonge when writing to Steers in April 1929; 'Spender is making a beautiful job of the map and when it is finished you will have the finest survey of this type of island ever accomplished'.[50]

Significance of the scientific findings from the Expedition

Five areas of particular significance to coral reef biology and geology/geomorphology are identified below. We do not review the collection and preservation of marine specimens which was an important remit for the Expedition; ultimately, three of the six volumes of Scientific Reports were devoted to descriptions and identifications of marine invertebrates and fish, culminating in 29 papers by various taxonomic experts. The coral collection, of 174 species divided among 54 genera, was eventually described by Cyril Crossland (1952) where Veron & Pichon (1976, 1) were of the view that 'this study is of particular value because of the care with which the collections were made at Low Isles, and also because Crossland had had extensive experience of coral reefs. His approach to coral taxonomy is therefore quite different from that of Vaughan, basically a geologist and palaeontologist'. Nor do we review the Expedition's activities in the field of 'economic zoology', led by Frank Moorhouse, studying bêche de mer and sponges and the cultivation of pearl oysters and trochus in specially constructed reef flat pens (Moorhouse 1932).

Yonge's work on coral physiology

C. M. Yonge's research remit on the Expedition relied strongly on his PhD and postdoctoral investigations of the comparative physiology of digestion in marine invertebrates, particularly the bivalve molluscs (Yonge 1928). Specifically, he agreed to make a thorough study of feeding mechanisms in corals by investigating their food, mode of digestion and assimilation as well as assessing the function and significance of their symbiotic algae.

The background literature available to Yonge was very limited, but even in 1928, there was considerable controversy over the role of zooxanthellae in the nutrition of corals. Gardiner (1931), Gravier (1908) and Boschma (1926) all considered that zooxanthellae contributed to at least part of the coral's diet while Murray (1889), Duerden (1906), Carpenter (1910), Vaughan (1912) and Mayor (1918) believed that corals fed exclusively on zooplankton. The most significant findings arising from the Expedition's experimental work were that corals were carnivores with highly specialized feeding mechanisms (Yonge 1930b) and that they could live perfectly well without zooxanthellae (Yonge & Nicholls 1931a). However, Yonge (1930b) admitted that the artificial nature of the experimental setup used at Low Isles would favour a greater carnivorous tendency than that observed in a natural setting. The conclusion that zooxanthellae did not contribute to the diet of corals resulted from experiments in outdoor aquaria near the laboratory base (Yonge & Nicholls 1931b) and also from experiments in a large light-tight box on the reef flat (Figure 9) (Yonge & Nicholls 1931a) where massive corals survived highly shaded conditions for 152 days although practically all their zooxanthellae were killed or ejected. Yonge & Nicholls (1931a) found no evidence for digestion of zooxanthellae by corals but noted disintegration of algae within host tissues, a common finding in cnidarians subsequently studied by other workers (Muscatine 1973, Trench et al. 1981, Suharsono et al. 1993, Brown et al. 1995, Titlyanov et al. 1998, Dunn et al. 2004, Ainsworth & Hoegh-Guldberg 2008). Yonge & Nicholls (1931b) also concluded that there was no evidence for transference of material from the zooxanthellae to the host, a fact that was later refuted by the elegant experiments of Muscatine & Hand (1958) using novel radio-autographic ^{14}C techniques and the anemone *Anthopleura elegantissima*.

Yonge et al. (1932) also ran an extensive set of experiments on conditions affecting the production of oxygen by coral zooxanthellae as a result of photosynthesis and the consumption of oxygen by coral respiration. These experiments were carried out both 'in nature' using light and dark crates on the reef and also in outdoor aquaria. The relevance of these studies today is reflected in a recent comprehensive review on the significance of oxygen in the functioning of coral reefs (Nelson & Altieri 2019) where the work of the Great Barrier Reef Expedition is highly cited. These modern-day authors recognize the work of Yonge et al. (1932) as the first to quantify oxygen consumption

Figure 9 Aubrey Nicholls (left) and Maurice Yonge demonstrate the 'coffin-shaped box' used to test the effects of darkness on selected corals and their zooxanthellae (by kind permission of the Royal Geographical Society).

over a range of oxygen partial pressures and the Expedition's resulting conclusion that 'reef building corals are exceptionally well fitted for survival in water of very variable oxygen content' (Yonge et al. 1932, 244) is one that is repeated throughout the studies that followed over 50 years later.

Results of other experiments with zooxanthellate corals and the azooxanthellate coral *Dendrophyllia nigra* in dark and light conditions also provided important findings on the role of zooxanthellae in excretion of waste products (Yonge & Nicholls 1931b). While *Dendrophyllia* excreted large amounts of phosphorus, the zooxanthellate corals did not. In contrast, they frequently removed phosphate from the surrounding water, even when this had been greatly increased by the addition of phosphate. Yonge (1931b, 309) noted that 'zooxanthellae are thus capable of utilising much more phosphorus than is normally produced by the catabolic processes of the corals in which they live. The same is probably true of nitrogen and possibly sulphur'. The role of zooxanthellae in removal of waste products of the animal host was seen by Yonge (1931b) as a critical element of the symbiotic association and an important factor in the overall success of reef corals.

One aspect of the Expedition's work that is seldom referred to in the now extensive modern literature is that concerning coral bleaching. Interestingly, the expedition scientists published the first account of thermally induced whitening or 'bleaching' in the field in 1929 (Yonge & Nicholls 1931a) although Mayer (1914) had described corals being 'injured' by high seawater temperature in the Caribbean as early as 1911. On 29 February 1929, the Expedition scientists noticed widespread coral bleaching on the reef flats surrounding Low Isles, with seawater temperatures of 35.1°C in coral pools during a particularly calm spell of weather. Yonge & Nicholls (1931a) report that many corals were killed during this period. These authors made little of their observations in the field (Figure 10) and included no photographs of the bleached reefs in their extensively illustrated reports although they followed up these observations with temperature experiments, histological descriptions of possible bleaching mechanisms and notes on the coral recovery which occurred three months later.

Figure 10 Mattie Yonge sitting on the aerially exposed reef flat at Low Isles during February 1929 at the time of a very low tide and surrounded by corals bleached white by unusually high seawater temperatures (with kind permission from Maurice Yonge Collection, the Natural History Museum, London.© The Natural History Museum, London).

It is clear that Yonge considered the 1929 bleaching as a natural event that might regularly occur during the warmer summer months (Yonge & Nicholls 1931a). Indeed, attempts were made by the Expedition scientists to quantitatively measure zooxanthellae densities of corals in the field on a monthly basis throughout their 13-month stay on Low Isles, but these were abandoned because of the difficulty of obtaining adequate numerical accuracy.[51] Had they succeeded they would have predated by 67 years the observation of a natural seasonal pattern of coral bleaching noted first by Stimson (1997) and soon after by others from reefs all around the world (Brown et al. 1999, Fagoonee et al. 1999, Fitt et al. 2000).

Adult and juvenile coral growth, coral reproduction and effects of sedimentation on reef corals

(Thomas) Alan Stephenson, leader of the Expedition shore party, was responsible for much of the work on the growth and reproduction of corals, working alongside Sheina Marshall and Sidnie Manton and ably assisted by his wife, Anne Stephenson. Again, results from this research significantly expanded earlier work by Vaughan (1923) and Mayor (1924) and provided a foundation for future studies, which in the case of coral reproduction did not develop until the 1980s (Harrison & Wallace 1990, Guest et al. 2005). Like Yonge, Stephenson made full use of the 'aquarium-like' surroundings of Low Isles. He devised ingenious schemes to maintain corals – at all life stages – in the natural environment to monitor reproduction, settlement and growth, with the minimum of human interference. To this end, he used the diving helmet (Figure 6B) to collect and observe marked corals underwater at depths of 4 to almost 9 m. In another example, he created 'clock-towers' for the rearing of planulae in the wild – these structures were solid concrete blocks with four hollow faces, each inset with four finger bowls that could be easily removed (Stephenson 1931). Planulae collected from corals in the laboratory aquaria were settled in these bowls and placed out on the reef to grow, the whole 'clock-tower' structure being set upon iron legs that were planted into the reef. The finger bowls were kept in place by four wooden laths attached to the outside of the block and which could be swivelled to one side for retrieval of the finger bowls (Figure 6C). This methodology proved highly successful and resulted in rapid growth of the settled planulae under natural conditions. His innovative approach for measuring growth in adult corals is best summed up in his own words in the Expedition report of 14 November 1928 (and see Figures 6D and 11):

'The work which has occupied most of my time during the last three months has been the setting up of and experiment on the growth rate of corals. One hundred square blocks of concrete have been made, and upon each one of these has been affixed one or more living corals, belonging to a varied selection of genera. The blocks have been placed in the sea in two specifically constructed pens and fastened down with iron spikes. One of the pens is situated in a shallow lagoon, the other in more open water in the anchorage. Each block with its attached corals has been photographed by the aid of an apparatus which ensures that the same block can be photographed subsequently from exactly the same angle and distance. By the inclusion of an accurate scale in each photograph, measurements can be made from the negatives. Ten further blocks have been provided with the halves of divided colonies, the two halves of each colony being planted out in different habitats so that any differences in mode of growth due to environment may be noted'.[51]

Stephenson (1931) and Stephenson & Stephenson (1933)'s work on coral growth was wide-ranging and included experiments on the development and formation of colonies of *Pocillopora bulbosa* (now *Pocillopora damicornis*) and *Porites haddoni* (now *Porites stephensoni*) following settlement; measurement of growth in 169 corals of various species over a six-month period;

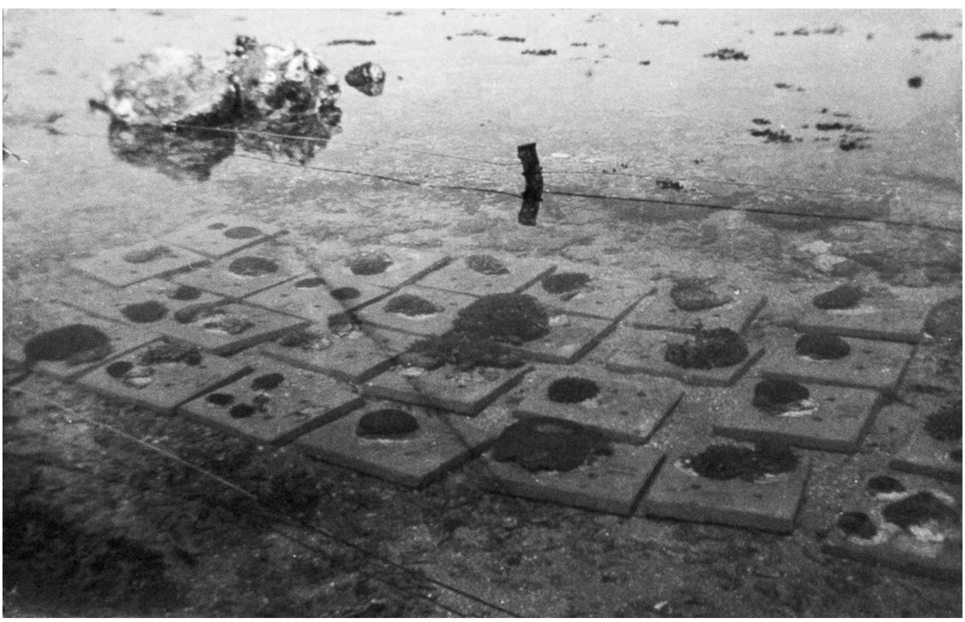

Figure 11 Translocated coral colonies on cement blocks used for measurements of skeletal growth between September 1928 and May 1929 by Alan Stephenson (source: James Cook University Library Special Collections, Sir Charles Maurice Yonge Collection, Great Barrier Reef Expedition Photo Album 3, Creators: Frederick Stratten Russell and Gweneth Kate Moy Russell (1928). Reproduced with kind permission of the James Cook University Library, Australia).

observations of intra-tentacular and extra-tentacular budding patterns in *Favia* and *Lobophyllia*; and descriptions of regeneration in broken branches of *Acropora* and notes on the effect of habitat on colony form in a number of species. Apart from quantitative accounts of growth rate differences between massive and branching corals, the authors highlight the marked within and between variations in growth rate of colonies of the same species. They also note the extreme intraspecific variation in growth forms between colonies living in different environments, a feature that was subsequently described as 'ecomorph' variation by later authors (Veron & Pichon 1976).

The bulk of the work on reproduction of corals was carried out by Sheina Marshall and Alan Stephenson (Marshall & Stephenson 1933) although other members of the Expedition were credited for their collaboration in collections and Sidnie Manton for her examination of fresh gonads. A key aim of this aspect of the Expedition was to evaluate whether sexual reproduction in corals took place all year round or whether the majority of corals reproduced at a particular time of year – a theme that has since been extensively developed for locations worldwide (see reviews by Harrison & Wallace 1990, Harrison 2011). Marshall & Stephenson (1933) attempted to examine 10 species of corals on a monthly basis for over 13 months. Three genera, namely *Favia* (now *Dipsastraea*), *Symphyllia* and *Lobophyllia*, were subject to gonad analysis (using fresh material and histological analysis of preserved samples) while others *Montipora ramosa* (now *Montipora digitata*), *Acropora hebes* (now *Acropora aspera*), *Psammocora gonagra* (now *Psammocora contigua*), *Goniastrea pectinata*, *Porites stephensoni* and *Pocillopora damicornis* were examined for planula production. At the time of the Expedition it was believed that the majority of corals were viviparous and brooders of planulae larvae. However, it should be noted that the authors admit that they only witnessed planulae production in two of their selected species – *Pocillopora damicornis* and *Porites stephensoni*. It is now recognized, since work in the early 1980s, that at least 157 coral species broadcast spawn gametes, 50 species brood planulae and another 10 species display both modes of development (Harrison & Wallace 1990, Harrison 2011).

Nevertheless, Marshall & Stephenson (1933) were the first to note the lunar periodicity of planula production in *Pocillopora damicornis* – this species planulating on the new moon between December–April and with the full moon during July and August – a finding that has since been supported by Harriott (1983) for the same species at Lizard Island on the Great Barrier Reef. Explaining this transition, Marshall & Stephenson (1933) noted a coincidence with tidal pattern, but it has since been shown that lunar periodicity of *Pocillopora damicornis* planula release is a geographically variable phenomenon (Harriott 1983). The drivers are still unclear but with factors such as dynamic light processes, sea temperature, tidal cycles and other biological effects, such as endogenous rhythms and hormones, all potentially playing a role in lunar periodicity of mass spawning species (Boch et al. 2011).

In the preface to their paper, Marshall & Stephenson (1933) recognized the shortcomings of their work, emphasizing that theirs was very much a preliminary study. The small sample sizes and sometimes irregular sampling limited their conclusions, and they stated that after their studies, 'The next workers to take the matter up, however should now be in a position to carry it rapidly to a more advanced stage' (Marshall & Stephenson 1933, 219). It was, however, not until ~55 years later that major advances were made into our understanding of coral reproduction through the comprehensive study of mass spawning on the Great Barrier Reef (Babcock et al. 1986).

As well as investigating important aspects of coral physiology, the 1928–1929 Expedition also monitored sediment production and its effects upon corals at Low Isles. This work was carried out by Sheina Marshall and her colleague A.P. Orr and involved comprehensive deployment of sediment traps across the reef (Figures 12 and 13A) over a seven-month period, with sediments being collected weekly and subsequently, dried, weighed and graded according to particle size. This work showed the role of hydrodynamic processes (waves and tides) in sorting different sediment size populations on the reef flat, pre-figuring the development of environmental sedimentology in the 1950s and 1960s (e.g. Folk and Robles 1964); shallow coring of reef flat surfaces (Figures 12 and 13A) and

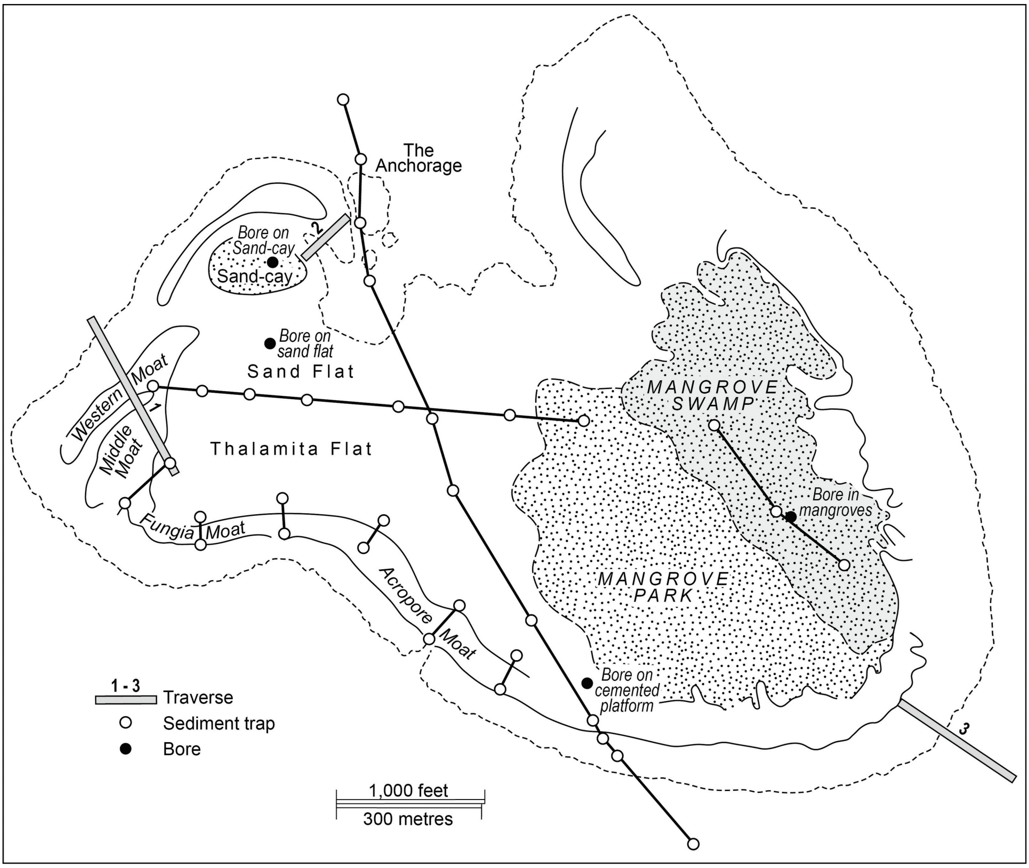

Figure 12 Location of sediment trap transects and shallow bores on Spender's basemap (re-drawn from Marshall & Orr 1931) and positions of three surveyed traverses (taken from Manton & Stephenson 1935).

the sand cay (to 5 m); chemical analysis of sediments; and experiments on sediment shedding by corals (Marshall & Orr 1931). As a result of this work, these authors very quickly realized that the common perception that corals grow well in only clear, sediment free waters was quite false. They comment that 'corals can and do live in slightly turbid waters and for a limited period can withstand large quantities of sediment falling from above. Water movements and ciliary action of the corals themselves are the effective agents of removing sediments' (Marshall & Orr 1931, 131).

Interestingly, even as late as 2012, authors still discussed whether turbid environments should be considered sub-optimal for 'healthy' coral reef growth (Browne et al. 2012). As the 1928–1929 Expedition discovered, turbid reef environments can support a healthy and diverse assemblage of corals, a finding echoed elsewhere on the inner Great Barrier Reef (Browne et al. 2012; Perry et al. 2013), in the Kimberley region of western Australia (Richards et al. 2015); the Andaman Sea (Brown 2007b), Singapore (Guest et al. 2016) and Java (Tomascik et al. 1997).

Marshall & Orr (1931) were the first to experimentally measure the sediment shedding ability of a variety of corals although Wood-Jones (1912) had already observed the efficient removal of sediment by *Fungia*. The Expedition scientists worked with eight coral genera in sediment shedding experiments in the field (*Pocillopora*, *Galaxea*, *Dipsastraea*, *Symphyllia*, *Fungia*, *Psammocora*, *Acropora* and *Porites*) and with four genera in aquaria (*Dipsastraea*, *Porites*, *Fungia* and *Psammocora*). In aquarium-based experiments, they used three types of sediment – muds, fine sand and coarse sand – and concluded that almost all corals were able to readily cleanse themselves of

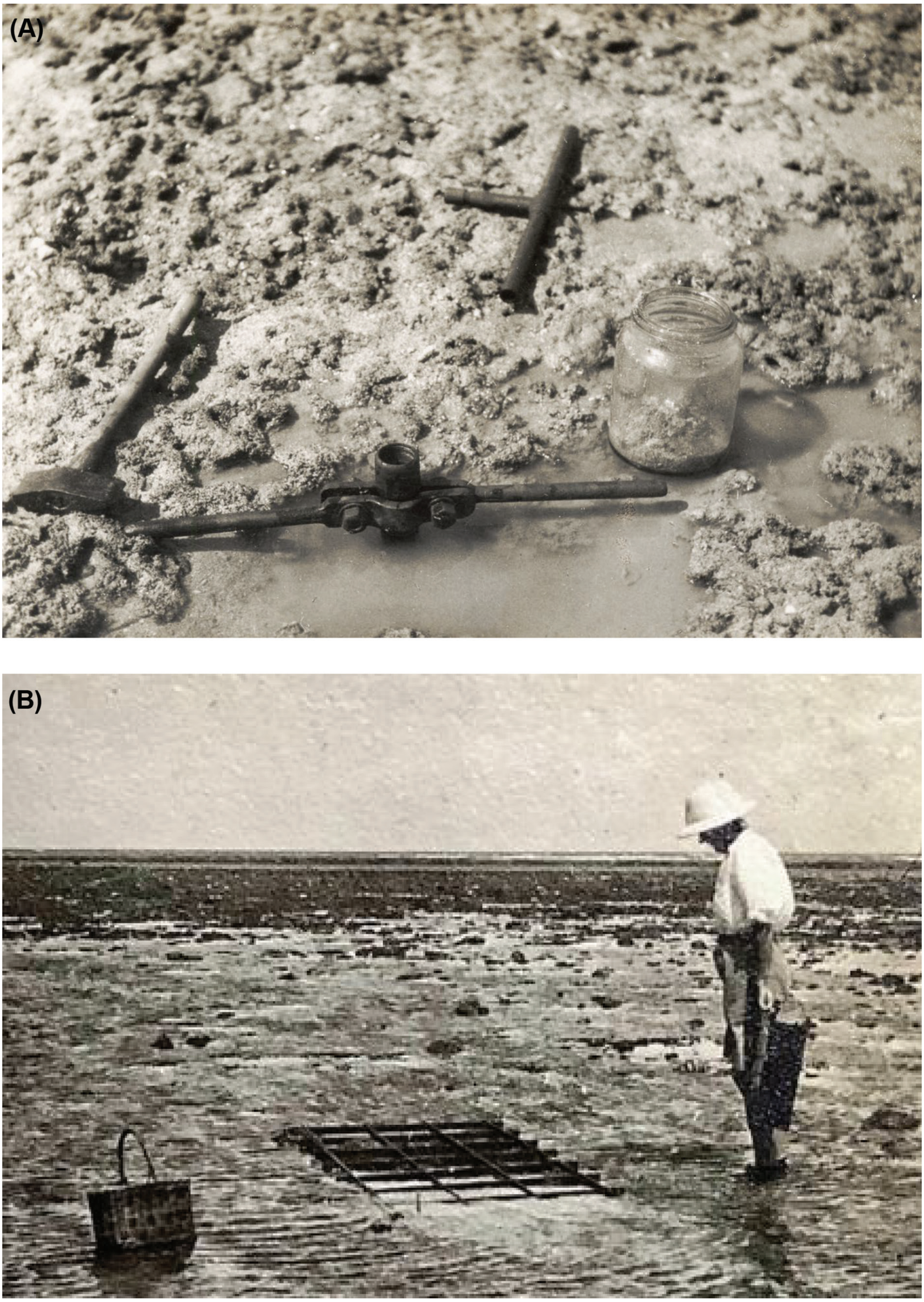

Figure 13 (A) The bore in the cemented platform on the Low Isles reef flat (see Figure 12 for location) and sediment trap sampling jar. Hand boring revealed a surficial layer of cemented 'honeycomb rock' (that required a crowbar, hammer and chisel to penetrate) overlying a soft grey mud with little sand (photo credit: M.A. Spender, by kind permission of the Royal Geographical Society); (B) Mattie Yonge inspects the sampling frame on the Low Isles reef flat (photo credit: S. Manton, with kind permission from the family's archives).

applied sediments with *Porites* being the least efficient. They also noted that sediment removal was most effective in the field where wind-driven currents, tidal water movement and the coral's ciliary currents, described by Yonge when studying coral feeding mechanisms during the Expedition (Yonge 1930b), ridded the sediment load within 24 hours in many species. While the Expedition focussed on sediment shedding, it is now realized that fine sediments may be an important food source of corals living in turbid waters. Such waters contain bacteria, microbial exudates, interstitial invertebrates and adsorbed and detrital organic matter (Houlbreque & Ferrier-Pages 2009) with heterotrophic feeding being potentially significant for corals living on inshore reefs, such as Low Isles (Anthony 2000).

Coral quantification and ecological surveillance

Echoing Mayor (1918, 1924), three traverses (T1, T2 and T3) were established on Low Isles, two on the leeward side of the reef with quantification of corals along their length and a third on the windward edge of the reef where quantification was not possible because of time constraints and lack of suitable weather conditions (Manton & Stephenson 1935). The traverses spanned approximately 100–400 m in length (Figure 12). In the case of T1 and T2, a 0.9 m wide strip of reef alongside the traverse was examined using a rectangular wooden frame measuring 0.9 m × 1.8 m, cross-partitioned into sub-units of 0.09 m^2 (Figure 13B). Describing her first 'marvellous' day diving with the helmet on Traverse 1 in a letter to her family on 24 May 1929, Manton writes 'Yesterday I fixed a rope at low tide to an iron stake 4 ft long 140 yards out on the rich coral rock area, jumped out into space from the coral edge with anchor and rope in hand and swam out with it dropping it in position – I quite forgot that booted and gaitered and carrying the anchor swimming would not be so easy, and I only just kept my nose out! Today we found the place and I went down, bucket and frame in hand and pencils tied about me' (Clifford & Clifford 2020, 91). Counts of coral colonies and dominant algae were made in every sub-unit of the frame along the entire 0.9 m wide strip along traverses T1 and T2. In addition, notes were made of the sizes of coral colonies within the frame by measuring their largest diameters.

Traverse T1 spanned the reef flat, the moat, the boulder tract and the seaward slope to a depth of approximately 5.6 m below chart datum, where datum refers to water level at the lowest low tide. Moving away from the shore traverse T2 comprised beach sand, beach sand-rock, the inshore reef and seaward slope to a depth of approximately 1.5 m below chart datum while traverse T3 covered the outer rampart and windward reef slope where the occurrence of organisms on four successive 30 m long strips was recorded to a depth of approximately 20 m (Figure 12). While the reef slopes of T1 and T2 were accessed by means of the diving helmet, used by Sidnie Manton down to a depth of ~5 m (Figures 5 and 6B), observations on the steeper, windward slope of T3 were made from a boat. Figure 14 shows the reef profile, the distribution of algae and corals and the total number of coral colonies recorded along traverse T1. In addition to these measurements, large-scale maps of small portions of the traverses were made in different habitats so that comparisons could be made of different reef areas (Figure 15). Manton was in no doubt as to the value of this work, writing on 23 June 1929 'The sections are truly handsome- nobody has ever made a section of a reef edge before let alone examine its fauna with anything but a dredge' (Clifford & Clifford 2020, 103).

The interdisciplinary philosophy of the Expedition, referred to earlier in this paper, was probably no better exemplified than in the ecological survey of the reefs around Low Isles. A general description of the reefs and other habitats at Low Isles and a selection of reefs in other locations was provided by Stephenson et al. (1931) with quantification of corals at Low Isles addressed by Manton and Fraser while Tandy monitored abundance of algal cover (Manton & Stephenson 1935). The traverses were accurately mapped and tidal levels established by Spender (1931) while Orr sampled physical and chemical variables (salinity, temperature, pH, turbidity, oxygen saturation

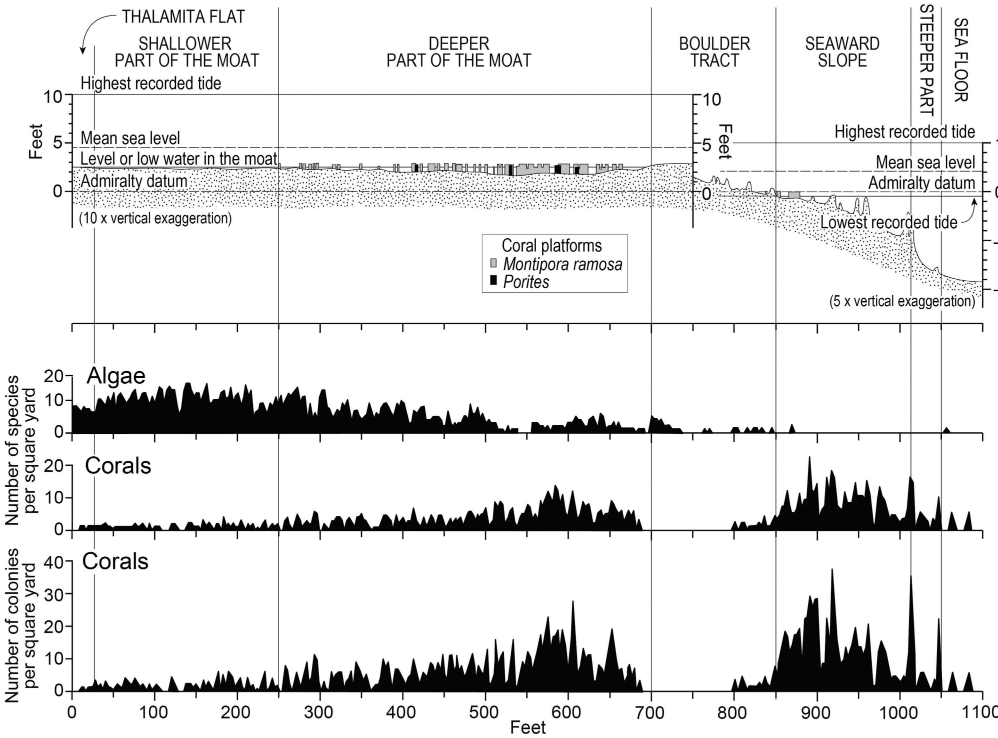

Figure 14 Bathymetry, number of different species of algae and corals and total number of coral colonies, Traverse I (for location see Figure 12). Re-drawn from Manton & Stephenson (1935).

and phosphate concentration) on a diurnal basis at specific points on the traverse (Orr 1933, Orr & Moorhouse 1933). In addition, plankton hauls were carried out over the reef flat and beyond the edge of the reef during the day and night by Russell & Colman (1931) with the aim of determining availability of food for the reef corals (Figure 6A).

The detail of these surveys and importantly their accurate mapping has provided an exceptional baseline for further studies. Subsequent work on the islands was carried out by Moorhouse (1933, 1936), Fairbridge & Teichert (1947, 1948), Stephenson et al. (1958), Stoddart et al. (1978a), Bell & Elmetri (1995), Frank & Jell (2006), Schueth & Frank (2008) and Hamylton et al. (2019). The Australian Institute of Marine Science have been running manta tow (since 1986) and permanent transect surveys (since 1992) on the reef perimeter at Low Isles (AIMS 2015) and the most recent paper (Fine et al. 2019), drawing data from 2004, 2015 and 2019, actually repeated surveys of the traverses described by the 1928–1929 Expedition, highlighting the value of the highly accurate mapping and ecological surveillance contained in this early work. This latest study showed a long-term decline in coral and invertebrate richness at Low Isles since 1928–1929, likely resulting from repeated cyclone and coral bleaching damage and increasing eutrophication, the latter either from regional mainland agricultural activity (Bell & Elmetri 1995) and/or with increased local nutrient inputs from the expansion of the mangrove forest (Frank & Jell 2006) in the intervening years. These findings echoed the observations of Yonge himself: 'When we there in 28/29 the reef flat when exposed at low tide was literally an aquarium. I was briefly there again for some hours in 1965 and over it again in 1975 in a light aeroplane. But I really saw it properly again in 1978 (50 years on) when I was working at AIMS south of Townsville. All that exposed reef was covered with sediments with only holothurians in their element and flourishing. The sediment had come from the mouth of the Daintree River some 10 miles away. This is the result of replacing the rain forest by sugar

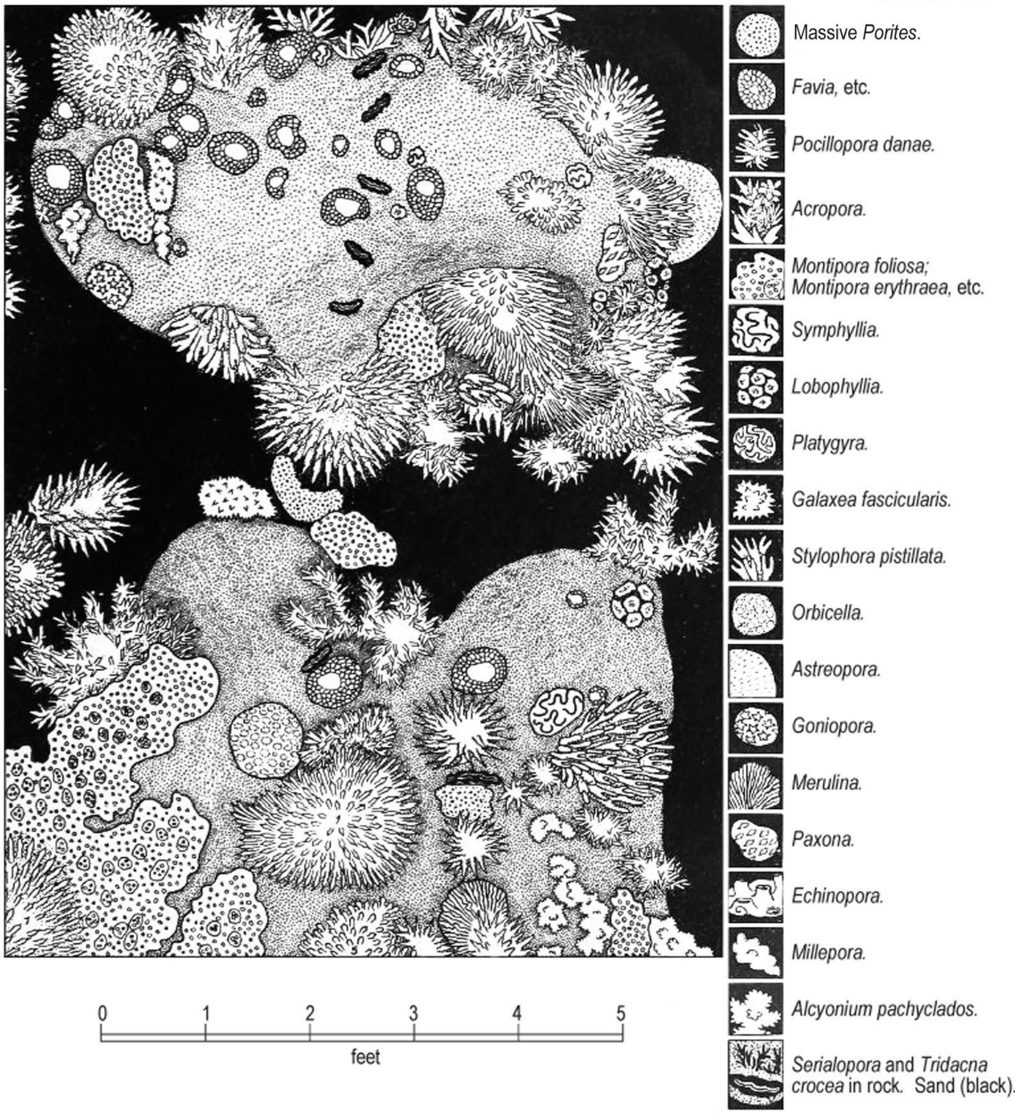

Figure 15 Detail of large-scale map of the area of maximum coral growth on the seaward slope of Traverse I. Rock substrate, in grey, with individual coral colonies (see key to species alongside) and sandy floor in black. Re-drawn from Manton and Stephenson (1935).

cane fields'[52] (and see Morton, 2004). Despite these sombre results (and see Hughes et al. 2011), the value of the ecological surveys carried out by the 1928–1929 Expedition should not be understated, providing as it does the basis for one of the longest (91 years) coral reef surveys published to date.

Regional variability in reef and island types and sea level change along the northern Great Barrier Reef

In establishing the regional variability in both reef and shoreline types between the Whitsunday Islands (20°S) and Cape Melville (14°S) (Figure 1), Steers was the first since Jukes to thoroughly consider the possible evolutionary linkages between offshore reefs and the mainland coast. Furthermore, the 1928 cruise was a precursor to a second expedition to the Great Barrier Reef, in May–August 1936 with FE Kemp of Selwyn College, Cambridge, which ranged even more widely, from Brisbane to Cape Direction (12°50′S) and back to Bundaberg (24°51′S), a track of over 4800 km (Steers & Kemp 1937, Steers 1938). In reviewing the literature on the structural geology of the shelf after the 1928–1929 Expedition, Steers contrasted those who saw the reef as a thin veneer (with some limited submergence) with those who invoked subsidence in the Darwinian sense. Steers found 'himself on the side of those favouring subsidence on a fairly extensive scale, though not necessarily of equal amount in all parts of the Barrier'… 'the subsidence as having been due partly to simple warping and partly to faulting' (Steers 1929, 239, Steers 1933). These ideas ultimately stimulated techniques of reef drilling, seismic surveys and radiometric dating of reefal materials and intellectual debates on eustatic and hydro-isostatic controls on sea level change along and across the continental shelf which were documented in the region during the 1973 northern Great Barrier Reef Expedition (Stoddart 1978, Thom et al. 1978) and later followed up by John Chappell and others (Chappell et al. 1982).

In the 1929 paper (and again in 1938), Steers also pointed out the widespread prevalence of benching on the high islands, particularly at + 30–60 cm above the 'oyster level', which he thought was recent but not contemporary, and a less common level at + 2.4 m, and speculated on the connections between these levels and both the beach rock and conglomerate platforms on the low wooded islands of the inner shelf and the alluvial plains on the mainland coast. The 1973 Expedition also established that northern Queensland experienced a higher sea level at ca. 6000 years BP, peaking in the 4000–3000-year BP period before falling thereafter to its present level. Many recent studies on the Great Barrier Reef have confirmed the generality of this sea level picture using a range of physical and biological indicators (Kench et al. 2012, Lewis et al. 2013), including fossil 'oyster levels' (Lewis et al. 2015). Despite broad agreement on these paleo-sea level trends, two contentious issues remain. One relates to the precise elevation, timing, duration and geographic extent of the mid-late Holocene sea level high stand (Yu & Zhao 2010, Smithers et al. 2018) and the other to whether sea level fell smoothly (Chappell 1983, Beaman et al. 1994, Lambeck et al. 2010) or oscillated during its fall to present position (Baker and Haworth 2000, Lewis et al. 2008, Leonard et al. 2016). It is also evident that reef island development was not only influenced by sea level but also by high wave energy levels and enhanced sediment transport around 5000–4000 years BP (Stoddart et al. 1978b; Kench et al. 2012; Perry et al. 2013).

Reef island mapping and quantitative survey of reef environments

Hamylton (2017) reproduces six maps made of Low Isles, by different methods and to varying degrees of resolution, between 1928 and 2014, to which now can be added Hamylton et al.'s (2019) own drone- and ground-survey-based map of 2017. The earliest map is EC Marchant's plane-table 'physiographical sketch map', reproduced as Figure 5 in Steers (1929).[53] But this was soon superseded by Michael Spender's iconic maps from 1929 (Spender 1930, Plate 1; although not to universal acclaim[54]). Spender's maps were subsequently revised in the Great Barrier Reef Reports by including additions from the 1928 aerial photography (Stephenson et al. 1931), annotated by Moorhouse following the storms of 1931 and 1934 (Moorhouse 1933, 1936) and then substantially revised from repeat aerial photography in January 1945 and a follow-up visit 30 January–4 February 1945 (Fairbridge & Teichert 1947, 1948) (Figure 16). Following the cyclone of 1950, the Great Barrier Reef Committee Expedition of 12–26 August 1954 also noted changes (Stephenson et al. 1958). However, the most detailed re-survey before the application of modern aerial surveys was the detailed compass and measuring tape survey, with complimentary levelling transects, carried out over the period 24–29 August during the 1973 Royal Society and Universities of Queensland Expedition to the northern Great Barrier Reef (Stoddart et al. 1978a).

The Low Isles complex, as described by Spender (1930), includes two laterally extensive, asymmetric shingle ridges on the windward side of a patch reef; a small sand cay with beachrock on

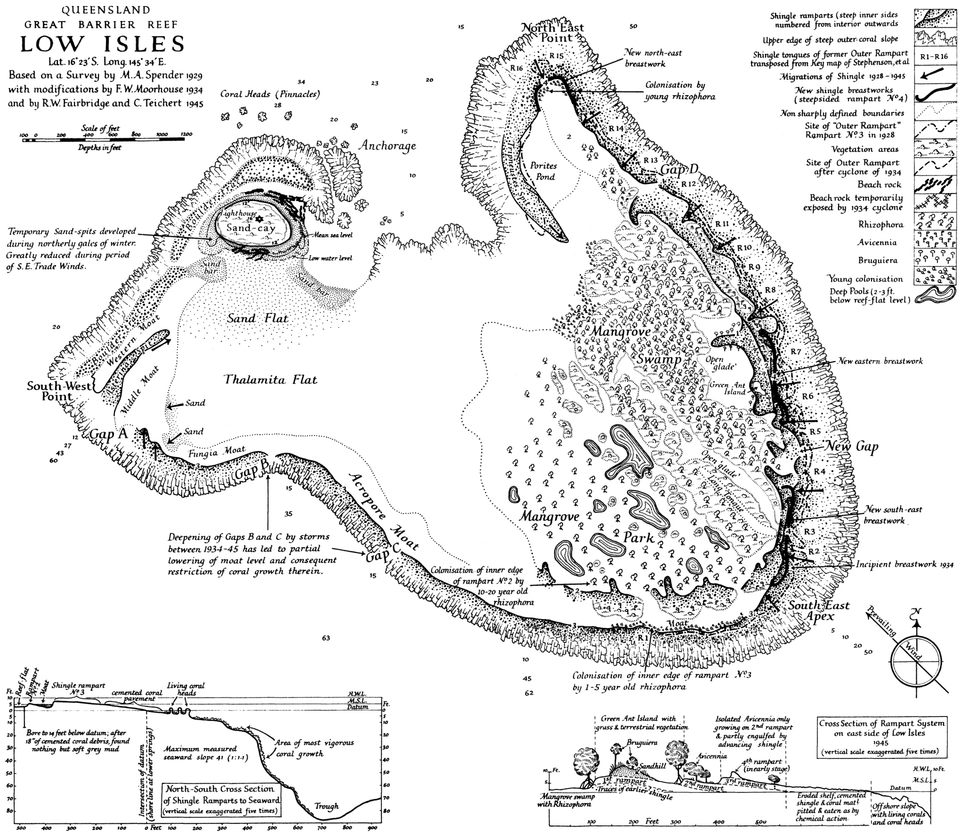

Figure 16 Fairbridge and Teichert's map of Low Isles (1948). The investigation was carried out under the auspices of the Royal Australian Air Force, the object being to improve the accuracy of photo-interpretation of coral reefs during WWII by correlating ground features with their appearance on aerial photographs. Fieldwork on Low Isles in January–February 1945 involved taking the air photographs, Spender's 1929 map and Moorhouse's 1934 post-cyclone map to carefully check every feature on the ground. The detail and commentary on the three panels in this figure illustrate the result of this methodology including changes over the 17 years since the 1928–1929 Expedition (Fairbridge, R.W. & Teichert, C. 1948. The Low Isles of the Great Barrier Reef: A new analysis. *The Geographical Journal* **111**, 67–88 (facing p. 74), by kind permission of the Royal Geographical Society).

the leeward side of the reef, and an extensive reef-top flat, part of which is occupied by mangroves (Figure 2). Stephenson et al. (1931) divided this latter element into two components: a 'mangrove swamp' of *Rhizophora* woodland up to 20 m tall and a 'mangrove park' adjacent to the swamp, formed by outlying *Rhizophora* patches and seedlings in a *Thalassia* seagrass meadow.

In particular, this long record of the changing distribution of reef-top landforms and habitats at Low Isles, and at the other low wooded islands of the Great Barrier Reef, has allowed the evaluation of changes to reef-top landforms including sand cays and mangrove forests (Hamylton et al., 2019). The 90-year evaluation represents a considerable timespan within the global record, exceeded only by the 118-year record provided by the maps of the islands on Funafuti surveyed during the Royal Society of London Expeditions in 1896–1898 (David and Sweet 1904, Kench et al. 2015). Beyond providing an accurate record of the previous location of landforms to provide a baseline against which changes can be estimated, such historic records also allow greater consideration of the fundamental processes determining the nature of such changes. In the case of Low Isles, the 1929 maps reveal insights into two different models of reef responses to environmental forcing. Spender (1930, 290) preferring the term 'island reef' to 'low wooded island', favoured a model of dynamic equilibrium: 'The relics of previous movements seen in the sand-rock, conglomerates, and occasional dead or dying mangroves, the limits of the mangrove-swamp, and also the historical evidence, all suggest that the islands have existed long enough to find an equilibrium of the elements on the reef, about which distribution alternate growth and destruction make small oscillations…. Each [island] has reached for the given form of the reef and weather conditions a comparatively stable and balanced finality'. The alternative model, as expressed by Steers (1937), was an evolutionary one whereby once a reef top has stabilized behind a protective rim, or 'bassett edge', mangrove spreads across the platform surface from the windward margin towards the leeward sand cay, ultimately at the final stage of evolution completely filling the reef-top accommodation space. Matters came to a head in the Discussion that followed Steers paper to the RGS on 7 December 1936. Opening the proceedings, Spender began 'In both of Mr. Steers' papers [published as Steers 1929 and Steers 1937] he describes the cays as "unstable". This is a misleading description. To a scientist "unstable" means that the cay, given a slight displacement, would vanish. Nothing of the sort happens. When the cyclone came to Low Isles in I934, even that enormously displacing factor failed to prevent the cay from being rebuilt as soon as it had passed. A cay is, in fact, a perfect equilibrium structure due to the drift over the reef flat, the wave system of the lee of the reef and the height of the flat. For that reason, cays tell nothing of the past history of the reef but only of the actual momentary level of the reef'. He went on: 'The habit of physiographers to use terms like "less" and "more advanced" stages of development implies an evolutionary idea in this case to which I object. I have already expressed the opinion that the extent to which the mangroves cover the reef is conditioned by the momentary distribution of shingle on the reef. There is no reason to suppose that an island covered with dense mangroves is a "mature" form, because if the platform which protects them is, as Mr. Steers states, being eroded, the sea will eventually eliminate it and strip numbers of mangroves off the reef. As a matter of fact I am prepared to argue that that might have happened at Low Isles and has happened at Three Isles' (Spender in Balfour et al. 1937, 141–142). In reply, Steers only backed down to a degree: 'The use of the word "unstable" need not give rise to any difficulty. I used the word as meaning "apt to change or alter", or "not stationary", and Mr. Spender seems to me to make rather a finical comment' and 'The extent to which mangroves cover a reef is not, I think, fundamental. I have suggested that their spread must depend on many incalculable factors. I would however suggest that the size of the shingle island, or the number and size of the various ridges, does measure a stage in the development of low wooded islands' (Steers in Balfour et al. 1937, 144, 145). And there the matter was left.[55] The 1973 re-survey at Low Isles did not resolve these arguments; rather, it revealed the complex feedback loops between hydrodynamic processes, carbonate sedimentation, mangrove colonization and spread, and the episodic formation and destruction of encircling marginal ramparts under cyclone impacts (Stoddart et al. 1978a). However, following a review of mangrove coverage on 21 reefs on the northern Great Barrier Reef, Stoddart (1980, 282) was able to conclude: 'Depending on the time perspective adopted, one can agree with either Steers's view of an evolutionary progression in low wooded island form, calibrated by development of mangrove, or Spender's of a series of equilibrium states. In the short term, as the comparative surveys of Low Isles and other reefs have shown, mangroves are patterned opportunistically in terms of substrate topography in the manner that Thom (1967) suggested for certain geomorphically active continental coasts. In the longer term, however, there is no doubt that mangrove cover extends to cover the reef-top. The evidence suggests that once mangrove growth is made possible by the protection of the reef-top afforded by construction of shingle ramparts, such extension is variable in rate but can be very rapid. The extent and history of mangrove cover is therefore governed by factors peculiar to individual reefs, and mangrove development per se cannot be used to correlate development sequences between individual reefs'. These arguments, however, sit within the argument for a dynamic environment but one within a recorded range of historical environmental variability. Thus, Hamylton et al. (2019) raise the question as to how these dynamics seen over the last 90 years at Low Isles will be impacted by increased frequencies of coral bleaching consequent upon ocean warming and a rising trend in ocean acidification, pointing out that the short-term impacts of changing water temperature and chemistry on the 'carbonate factory' (Kench et al. 2009) are likely to take time to propagate through geomorphic pathways and thus find expression in changing reef island morphologies.

The legacy – how the Expedition and its results came to be viewed by the rest of the world, its impact on subsequent science and development of international links in reef science

On a broad international scale, the Expedition stimulated such interest in reef processes that, following the Fourth Pan-Pacific Congress in Batavia-Batong in 1930, the International Committee on the Coral Reefs of the Pacific (chaired by Vaughan) suggested building an international institute of marine biological science in the Pacific (Konishi 2004). As a result, Dr. Sinkisi Hatai, from the Tohoku Imperial University, Japan proposed the building of the Palao Tropical Biological Station to the Japanese Society for Promotion of Science and a small laboratory was built in 1935 at Koror Island, Palau (Omori 2012). Yonge (1940) describes the early work of Japanese scientists at the laboratory which followed a programme of research very similar to that carried out by the 1928–1929 Expedition. These early studies were published in the Palao Tropical Biological Station Studies in 1937 (Fautin 2002) and work continued at the laboratory until 1943 when the station was taken over by the Japanese Navy prior to capture by American forces. Research on Pacific coral reefs then resumed after the end of WWII in earnest with projects that included geological (Ladd et al. 1953) and biological work (Goreau & Austin 1947, Odum & Odum 1955) in the Marshall Islands. By 1969, coral reef science came of age with the holding of the First International Coral Reef Symposium at Mandapan Camp, India, with delegates participating from twelve countries. The Proceedings of that meeting boasted 37 papers and included one by Yonge, leader of the 1928–1929 Expedition.

Threaded through these latter developments in reef science were individuals who were influenced either by interactions with members of the 1928–1929 Expedition or by the extension of research themes developed during work on Low Isles and surrounding reefs. Three individuals, in particular, stand out because of their significant contribution to galvanizing reef scientists and influencing reef research in the twentieth century and whose legacy continues to the present.

The first individual whose research was influenced by findings from the 1928–1929 Expedition was Len Muscatine (1932–2007) (Hoegh-Guldberg et al. 2007). Muscatine played a key role himself in development of the science on algal-invertebrate symbioses and his research students (and their research students) and postdoctoral researchers made, and continue to make, outstanding contributions in coral physiology, zooxanthellae diversity, coral bleaching responses and the evolutionary ecology of coral-dinoflagellate associations. Muscatine's PhD supervisor was the invertebrate zoologist Cadet Hand, based at the University of California at Berkeley. Following the work by Odum & Odum (1955) on the trophic structure and productivity of a Pacific reef, Hand (1956) questioned their assumption that corals were herbivores in the light of the most recent evidence from the 1928–1929 Expedition that corals were carnivores (Yonge 1930b). Hand's paper was entitled 'Are corals really herbivores?' (Hand 1956). His collaboration with Muscatine, who suggested the use of radioisotopes to investigate the role of algae in nutrition, provided the first direct experimental evidence of a nutritional role for symbiotic algae in a sea anemone (Muscatine & Hand 1958; and see Muscatine 1967, Muscatine & Cernichiari 1969). Friendly correspondence between Muscatine and Yonge in 1972[56] reveals their shared interest in transfer of photosynthetic products between zooxanthellae and their animal hosts, the exchange of publications and also their admiration[57] of a second individual, Tom F. Goreau (1924–1970), who explored research themes first developed by Yonge on the Expedition.

An assistant oceanographer during the summer of 1947 at Bikini Atoll,[58] Goreau enrolled as a graduate student at Yale under Evelyn Hutchinson, completing a PhD on the biology and histology of corals in 1956. He subsequently established the Discovery Bay Marine Laboratory on the North coast of Jamaica in 1965, in association with the New York Zoological Society's 'Coral Reef Project – Jamaica'.[59] It was here that Yonge joined Goreau to follow up the work on the significance of zooxanthellae to both corals and clams (Goreau et al. 1965, Goreau et al. 1971). Goreau & Goreau (1960) and Muscatine & Cernichiari (1969) demonstrated that ^{14}C could be translocated from the zooxanthellae to coral tissues and in 1971 Yonge, acknowledging the latest research, published with Tom and Nora Goreau (Goreau et al. 1971) a paper entitled ' Reef corals: autotrophs or heterotrophs?' Yonge became a close friend of the Goreau family through his research collaborations and wrote movingly in a tribute to Goreau following his death as follows: 'It remains for the writer to add that six years of scientific collaboration with Tom Goreau starting and ending at Jamaica but ranging from Europe across the Pacific to Australia in the years between, and with continually increasing friendship, were deeply memorable. The difference between our ages seemed to disappear while our interests were entirely complementary. Tom's name will endure indefinitely as amongst the greatest of workers on coral reefs- in all aspects of their wide diversity – and the memory of him will persist throughout the lifetimes of all who knew him as that of a striking personality and a most lovable man' (Yonge 1971a, xxxii–xxxiii).

Today, there is still debate about the relative importance of autotrophy and heterotrophy to reef corals. Scientists have since concluded that corals should be considered as polytrophic, relying on both ingested and translocated carbon (from zooxanthellae) as energy sources, there being considerable variation in their dependence on heterotrophy with species, depth, plankton availability and bleaching status (Houlbreque & Ferrier Pages 2009).

The third person is David Stoddart (1937–2014) whose PhD, on three atolls on the Belize Barrier Reef in the Caribbean, was supervised by Alfred Steers and examined by Maurice Yonge.[60] Both men continued to be an influence on Stoddart who was subsequently based as a young lecturer in Steer's Department of Geography at Cambridge.[61] Stoddart later described his PhD viva as an important factor in reviving the interests of both Steers and Yonge in coral reefs (Stoddart, 1987); Yonge was subsequently a close ally of Stoddart throughout his career, and together, they collaborated in organizing a significant number of international meetings on coral reefs (e.g. Yonge 1971b, Stoddart 1972). Steers visited Brisbane and Townsville in 1967, and later talked to Yonge about further research; on 27 December 1967, they wrote jointly to the Executive Secretary of the Royal Society about the possibility of sending an expedition to the Great Barrier Reef, suggesting possible personnel but noting that the staffing should be 'essentially Australian'.[62] With the full support of the Royal Society and the University of Queensland,[63] planning meetings in Brisbane, Townsville and the UK in 1969, 1971 and 1972, orchestrated by the UK (Steers, Stoddart and Yonge) and Australian (G.R. Orme) principals,[64] ultimately led to a complex, three-phase expedition led by Stoddart from mid-July to mid-November 1973, extending from Cairns to the remote northern Great Barrier Reef (to the latitude of Cape Grafton at 11°30′S) with 24 scientists (the majority Australian), the use of four vessels and collaboration with the Royal Australian Navy (Stoddart 1978). The results were presented at a Discussion Meeting at the Royal Society in London on 28–29 January 1976, the published papers coming to over 350 printed pages (Yonge 1978).

Following the inaugural meeting in 1969, which he had co-convened with Yonge, Stoddart continued to be actively engaged in the organization of regular International Coral Reef Symposia through working with the International Association for Biological Oceanography (IABO). In particular, along with R. Endean, P. Mather and G.R. Orme of the Great Barrier Reef Committee, he organized the Second International Coral Reef Symposium. The meeting immediately preceded the 1973 Expedition, cruising the waters of the Great Barrier Reef between Brisbane and Lizard Island aboard the M.V. Marco Polo. The Symposium was attended by both Yonge and Steers, and there was an opportunity to revisit Low Isles (Figure 17). Furthermore, the Symposium 'provided a chance to let other reef researchers see the Lizard site and discuss a possible research station there. Along with Frank [Talbot], Don McMichael and Pat Hutchings from the Museum, a number of overseas researchers looked at a site on the eastern site of the island. The international group were strongly supportive of the idea… So Lizard Island was chosen...The future of Lizard Island Research Station was set'.[65] Straight after the Symposium (2–10 July 1973), the Coral Reef Working Group of the Scientific Committee on Oceanic Research (SCOR), chaired by Stoddart and with active collaboration from members of the Great Barrier Reef Committee, met at the research station on Heron Island to discuss the standardization of coral reef research techniques,

Figure 17 Alfred Steers (far left), Richard Orme (second left), David Stoddart (back to camera) and other symposium participants discussing the shingle rampart features at Low Isles on a field excursion during the Second International Coral Reef Symposium, 22 June to 2 July 1973 (photo credit: David Hopley, with kind permission of the originator).

to aid comparative studies between different reef areas. This effort represented a revision of the Handbook for Atoll Research, developed by the Pacific Science Board for its coral atoll expeditions of the 1950s (Fosberg & Sachet 1953). In particular, the revision took account of recent advances in the study of functional coral reef ecology, including methods being piloted on the southern Great Barrier Reef (e.g. Kinsey 1972). Draft methodologies were reviewed, with testing of methods both at Heron Island and at the Australian Museum field station on One Tree Island. The ultimate outcome was the publication of the UNESCO Handbook on *Coral Reefs: Research Methods* (Stoddart & Johannes 1978).

Stoddart was the prime founder of the International Society for Reef Studies in 1980 (now renamed the International Coral Reef Society) and key to the establishment of the Society-related journal *Coral Reefs* in 1982. In his first editorial to the latter (Stoddart 1982, 1), he highlighted the changing face of coral reef studies in the twentieth century and the need to improve coordination of reef research and efficient flow of information between scientists:

'For many years, reef studies were carried out during occasional expeditions to remote areas, and their aim was primarily the recording of topographic and biotic diversity. This inventory approach is now largely completed, and the focus of activity has moved from expeditionary work to more detailed and longer-term studies, carried out at research stations, by universities, and on research vessels in the tropical seas. The numbers of research students has increased greatly, especially in the last 15 years, and the doctoral thesis on reef topics –once a rarity– is now an expected means of entry to the field'.

Conclusions

The varied contemporary agenda of the Australian coral reef science community continues to bear the hallmarks of experimental field research that was undertaken during the Expedition, while some of the early observations made, and records established, have paved the way for future comparative work. Key themes that have been carried forward include the work on coral physiology, particularly aspects of coral growth that have informed later reef restoration efforts and, as the influence of environmental change has increasingly been felt on the world's reefs, the causes and implications of coral bleaching on the Great Barrier Reef. In the fullness of time, Frank Debenham's pre-Expedition comments on the value of early, accurate measurement of reef surface features to act as a benchmark against which the movement of coral banks and reef flat sediments could be elucidated would prove to be particularly pertinent. On the 45th and 90th anniversaries of its production, Spender's map of the reef flat has served as a comparative record for studies of landform evolution, which have yielded insights into the dynamic nature of sand cays and mangrove forests on the low wooded islands of the Great Barrier Reef.

As the Expedition was preparing to leave Low Isles (Figure 18), Michael Spender wrote to Arthur Hinks at the Royal Geographical Society to say 'the results of the work will, I am hoping, justify themselves. They cut new ground, so far as I know: but it is difficult and dangerous this navigation among coral reef problems, and the wrecks of many worthy scientists are there as an awful example'.[66]

But surely, Spender was being unduly pessimistic. And it seems apposite to close with an opening. At the First International Coral Reef Symposium at Mandapan Camp, India in 1969, which Stoddart and Yonge co-convened, Stoddart (1972, 17) noted in his opening remarks to the meeting 'The Symposium is timely for three main reasons. First it is being held, in 1969, on the fortieth anniversary of the Great Barrier Reef Expedition of 1928–1929. It implies no reflection on the work of Gardiner and Sewell, Vaughan, Mayor and many others, to suggest that this Expedition set new standards and defined new goals in reef studies. This was true not only of C.M. Yonge's work on coral physiology, but of Stephenson's ecological and Steers'

Figure 18 Getting ready to leave: the end of the Expedition in July 1929 (by kind permission of the Royal Geographical Society).

geomorphological studies too. This co-operative work represented the first major advance on the predominately theoretical and deductive mode of work which had long dominated discussions of the "coral reef problem"'.

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Notes

1. Between 1913 and the publication of *The Coral Reef Problem* in 1928, Davis published 42 academic papers, abstracts and conference proceedings on coral reefs, amounting to over 650 pages of published material; the book itself was 596 pages in length (Chorley et al. 1973).
2. Andrews to Vaughan, 13 May 1922; File FR:IC, Archives, National Academy of Sciences, Washington D.C.
3. Andrews to Vaughan, 26 November 1924; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
4. Richards to Vaughan, 17 November 1924; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
5. Vaughan to Richards, 22 December 1924; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
6. Vaughan to Richards, 8 July 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
7. By way of further explanation of the apparently baffling Michaelmas Reef and Heron Island records: 'As all the fossils in the bores appeared similar to present day forms it was suggested that there was no firm evidence of any sediment older than Recent (deposited within the past 20,000 years). As all the fossils appeared to be shallow-water forms it was concluded that subsidence of perhaps 200 m had occurred. Although the Darwinian hypothesis of reef growth on a subsiding basement received support, the sub-reef material was unconsolidated sand and not volcanics, as required by Darwin's theory. These two findings confused reef researchers for almost 40 years… It was not until the early 1970s that a major breakthrough in the interpretation of the drilling results occurred, when researchers demonstrated that several major solution unconformities or erosion surfaces could be recognized in the drill-cores. These features were identified as zones of calcite, formed by recrystallization of the pre-existing aragonitic skeletal material due to exposure to freshwater during subaerial exposure of the limestone. Subsequent studies of the microfossil content of the bores supported the suggestion of a much older age for the Reef. The time of commencement of reef growth has been established at the Heron Island drill site as being late Pliocene (prior to about 2 million years before present)' (Chivas et al. 1990, 13–15). Interestingly, it was at the Second Coral Reef Symposium, just prior to the 1973 Northern Great Barrier Reef Expedition, that Peter Davies described the solutional unconformities in the Heron Island core and, by comparison with similar horizons identified by Schlanger (1963) at Eniwetok and Bikini Atolls, Central Pacific Ocean, speculated that the Great Barrier Reef cores comprised mainly pre-Holocene sediments (Davies 1974). Subsequently, Searle and Harvey (1982) identified the Holocene/Pre-Holocene boundary at a depth of 8–12 m in the Michaelmas Reef bore (and see also Webster and Davies [2003]).
8. Alfred Goldsborough Mayor was born Alfred Goldsborough Mayer. During WWI, in 1918, he changed his surname to Mayor to dissociate himself from his Germanic ancestry. He is referred to in the text as Mayor throughout, but individual references refer to the surname used in the authorship of the paper.
9. Richards to Nathan, 7 December 1921; University of Queensland archives, S0226/3, quoted in Bowen and Bowen (2002, 233).
10. Nathan to Younghusband, 4 July 1922; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
11. Hinks to Nathan, 4 December 1922; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
12. Harmer to Nathan, 5 February 1923; Zoology Catalogue DF 214/1, British Museum (Natural History) (BMNH), London.
13. Hinks to Nathan, 27 February 1923; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
14. Vaughan to Richards, 8 July 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
15. Gardiner to Richards, 9 January 1925; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
16. Gardiner to Hinks, 17 January 1925; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.

17. Reference contained in the Minutes of the Great Barrier Reef Committee 9 September 1926 (No. 33), filed in Zoology Catalogue DF 214/1, British Museum (Natural History) (BMNH), London.
18. Reference contained in the Minutes of the Great Barrier Reef Committee 23 February 1927 (No. 36), filed in Zoology Catalogue DF 214/1, British Museum (Natural History) (BMNH), London.
19. Gardiner to Yonge, 3 May 1927; Yonge collection of Great Barrier Reef correspondence, reference E48 (3), British Museum (Natural History) (BMNH), London.
20. Gardiner to Vaughan, 28 July 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
21. Richards to Vaughan, 10 August 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
22. Vaughan to Richards, 27 September 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
23. British Association for the Advancement of Science, Report on the Ninety-Fifth Meeting, Leeds-1927, August 31–September 7, Sectional Transactions, 333.
24. Gardiner to Nathan, 24 September 1927, Zoology Catalogue DF 214/6, British Museum (Natural History) (BMNH), London.
25. Minutes of the meeting of the British Great Barrier Reef Committee, 4 October 1927; filed in Zoology Catalogue DF 214/8, British Museum (Natural History) (BMNH), London.
26. Hinks, of course, had already responded to Richards' 'Problems of the Great Barrier Reef', sending a series of notes to Colonel Sir Charles Close, the Director General of the Ordnance Survey (the national mapping agency of the UK) (Hinks to Close, 28 November 1922; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1). In response to Hinks' questions, Close felt that a long tidegauge record would answer the question of subsidence, that mean sea level should certainly be determined but that a 'full geodetic standard may be too much to expect' (Close to Hinks, 10 December 1922; CB9 1921–1930, Great Barrier Reef Expedition, Box 1). A year later, he was still at it: 'what I am of course interested in principally is survey and fixing mean sea level, bench marks etc…' (Hinks to Nathan, 21 December 1923; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1).
27. Gardiner to Hinks, 16 January 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
28. Steers took Part I of the Diploma in Geography at Cambridge in 1917 and was in the first cohort of the BA degree in Geography (Part II of the Geographical Tripos) in 1921, obtaining the highest classification, a starred First. He was appointed to a Departmental Demonstrator in 1922 and a University Demonstrator in 1926, before promotion to a University Lectureship the following year.
29. Debenham to Hinks, 14 February 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
30. Minutes of the meeting of the British Great Barrier Reef Committee, 23 February 1928; filed in Zoology Catalogue DF 214/8, British Museum (Natural History) (BMNH), London.
31. Spender to Hinks, 12 February 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
32. Debenham to Hinks, 15 March 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
33. On Marchant, Spender wrote in mid-expedition (7 January 1929) to Hinks 'I am a little alarmed about men without qualifications since Marchant has been here. I don't mean that he hasn't been exceedingly willing but it is awkward for a young man to have to deal with an older man who knows little of the principles of survey and has not even the mathematics to be able to check one's calculations'. (Royal Geographical Society CB9 1921–30, Great Barrier Reef Expedition, Box 1, file 2).
34. Memorandum on work to be carried out by the R.G.S. members of the Barrier Reef Expedition by F. Debenham, 14 March 1928; filed in Royal Geographical Society CB9 1921–30, Great Barrier Reef Expedition, Box 1, file 2.
35. Gardiner to Hinks, 29 February 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
36. Yonge to Steers, 4 April 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.

37. TA Stephenson to Tandy 18 March 1929; Zoology catalogue DF421/1, British Museum (Natural History) (BMNH), London. The feeling was clearly mutual: ‘I find this a most interesting combination of work and feel sure that you will assent to your geographer’s time being spent in this way’ Spender to Hinks, 7 January 1929; Royal Geographical Society CB9 1921–30, Great Barrier Reef Expedition, Box 1.
38. Spender to Hinks from Low Isles, 8 April 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
39. Statement of Position, 28 May 1929; filed in Zoology Catalogue DF 214/8, British Museum (Natural History) (BMNH), London.
40. Spender to Hinks from Low Isles, 15 June 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
41. Gardiner to Hinks, 19 May 1938; Royal Geographical Society CB10 1931–1940, Gardiner file.
42. Gardiner to Hinks, 19 November 1938; in discussing problems associated with publishing the Expedition’s reports: ‘on Yonge I fear he may have failed altogether in visualising the great geographical problems of these and all reefs’. On 20 November, Hinks replied to say ‘If Yonge failed to visualise the geographical problems of the Reef we shall have to fall back on Spender, who has been visualising a great deal’; filed in Royal Geographical Society CB9 1921–1930, Gardiner file.
43. British Association for the Advancement of Science, Report on the Ninety-Sixth Meeting, Glasgow-1928, September 5–12, Reports on the State of Science, 395–396.
44. A9-4 was one of six Seagull Mk. III aircraft ordered by the Australian Government from the Supermarine Aviation works, Southampton, England, in April 1925. On 1 July 1926, RAAF No. 101 (Fleet Cooperation) Flight was formed to work with HMAS PORT MORESBY on the Great Barrier Reef Survey; Low Isles was flown, from a base at St Bees Island near Mackay, in phase 2 of the Survey (May–December 1928). A9-4 continued to operate until 19 March 1930 when it crashed into the sea, with one fatality, off the Tasmanian coast and could not be recovered intact (McGuiness, 2020).
45. with Fairbridge and Teichert taking it in turns to hang out of the aircraft door with the camera (Crick and Stanley 1997)
46. Debenham to Hinks, 23 October 1928; ‘I have also heard from Steers and he has told me that he was endeavouring to explain to you the difficulties they were up against in carrying out our armchair plans’ (Royal Geographical Society CB 1921–1930, Great Barrier Reef Expedition, file 3).
47. Spender to Hinks, from Orpheus Island, 4 September 1928; Royal Geographical Society Great Barrier Reef CB 1921–1930, file 2.
48. Cara Mallett chronicled her three months on Funafuti in a book of over 300 pages, providing ‘an unscientific account of a scientific expedition’. Following Victorian sensibilities, she dedicated her book ‘To the Leader of the Expedition’ (her husband) and authored it as Mrs. Edgeworth David (David 1899).
49. Physiography is a rather elusive term, subject to multiple definitions and usages since its appearance in the late eighteenth century (Stoddart, 1975). Steers himself compared the terms ‘geomorphology’ and ‘physiography’: ‘geomorphology does not exclude a consideration of, e.g., the plant cover, but it does not of itself include it, although it is much concerned with its effects on weathering. Physiography seems to me to be the more comprehensive word, and in my own field work I have been constantly aware of the importance of tree and plant growth, of climate, and other factors in the development of land forms, so that the wider term appeals to me far more’ (Steers 1960, 1–2). For the application of the ‘Cambridge physiographic tradition’ to the low islands of the Great Barrier Reef, see the detailed analysis of Woodroffe (2018).
50. Yonge to Steers, 4 April 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
51. Yonge Archives at Natural History Museum UK DF214/7 Expedition Progress Report November 14 1928.
52. Yonge to Brown, 14 September 1983; E75, correspondence files, Maurice Yonge Collection, Natural History Museum UK.
53. An abstracted version of Steers’ paper on ‘The Queensland coast and the Great Barrier reefs’ (Steers, 1929) was read by the author at the Royal Geographical Society on 4 February 1929, and at that stage, Spender’s map had not even begun to take shape. On 1 December 1929, Steers wrote to Hinks ‘I have not yet seen his [i.e. Spender’s] maps, but I gather they are good’ (Royal Geographical Society CP9 1921–1930 Spender file); they were not revealed until the Royal Geographical Society meeting of 16 December 1929.

54. Hinks to Spender, 29 May 1929: 'I confess that I did not anticipate that you would spend so long a time on Low Island making a map on so large a scale as 200 feet to the inch which may no doubt be very useful to ecologists but which is hardly in my mind a geographical scale. You will have to be prepared to defend' (Royal Geographical Society CB 1921–1930, Great Barrier Reef Expedition, file 3).
55. The importance of personal field observations did on occasion bring Steers into conflict with Spender. He was clearly irritated by Spender's discussion, on 7 December 1936, of the formation of reef platforms on the Great Barrier Reef: 'I doubt if there is much significance in Mr. Spender's remarks on Beanley Island, on which I do not think he has ever set foot . . . Much more detailed work is necessary to solve the problem, but I would ask him to visualize the whole problem of benches and platforms on the Queensland coast and reefs before he comes to a definite conclusion' (Steers in Balfour et al. 1937, 145). The day after the discussion of his paper, Steers wrote privately to Hinks, to ask to see Spender's written comments before returning his own, noting that 'Spender does not advance the matters at all by merely putting forward his ideas which do not take in the cumulative facts. Spender weakened some of his arguments by talking of places he had not visited' (Steers to Hinks, 8 December 1936; Royal Geographical Society CB10 1931).
56. There is evidence of correspondence between Muscatine and Yonge (C.M. Yonge correspondence files Natural History Museum 1972 E36) regarding Yonge's work with the then late Goreau and papers relating to the translocation of photosynthetic product from zooxanthellae by the giant clam *Tridacna maxima* (Goreau et al. 1973).
57. Yonge to Muscatine, 11 July 1972; 'I am glad you liked my appreciation of Tom – It came very much from the heart'. E36, correspondence files, Maurice Yonge Collection, Natural History Museum, UK.
58. As a diver and a chemist, Goreau collected radioactive specimens from the Bikini lagoon. It seems highly likely that he received lethal radiation exposure from this work and that this lies behind his early death from cancer at the age of 45.
59. Goreau initially trained in medicine and was appointed lecturer in physiology in what was then the University College of the West Indies in Kingston, Jamaica, in 1951. He continued to teach medical physiology until his appointment as Professor of Marine Science in 1967. The Coral Reef Project was formally started by Goreau in 1956, but the paper by Goreau and Goreau (1973) refers to field observations from 1955 and unpublished field notes from the north coast of Jamaica from 1952 onwards. This paper contains remarkable fish eye photographs of the deep reef front. Perhaps, Tom Goreau developed this interest and skill from his father, Fritz Goro, who was a photographer for *Life* magazine and *Scientific American*, specializing in macrophotography.
60. The PhD viva was the first time that Stoddart met Yonge in person. In the course of the viva, Yonge disputed that there were such things as solitary, rolling corals. Stoddart went back to his office, picked one up, returned to the viva and rolled it back across the table to Yonge (Stoddart, pers. comm. to Spencer, Rarotonga, Cook Islands, February 1983).
61. 'I was in Belize in 1962 when I had a postcard from Alfred [Steers] in a hotel on the Isle of Wight. "My dear David, would you like a job in Cambridge? Yours ever, Alfred". No nonsense about curriculum vitae, referees' reports, appointments committees: simply straightforward patronage. In the Cambridge context of the time, it worked. Unless one did something quite dreadful, it meant a job for life. My response was instantaneous "Dear Professor Steers . . ." (i.e., what a good idea)' (Stoddart 2001, 246).
62. Steers and Yonge to the Executive Secretary, Royal Society, 27 December 1967; Committee minute books of the Royal Society, CMB/179b/8.
63. Sir Fred Schonell, Vice Chancellor, University of Queensland to Steers, 10 May 1968; Committee minute books of the Royal Society, CMB/179b/9.
64. Minutes of the Royal Society's Southern Zone Research Committee: 6th Meeting, 13 August 1968 (Committee minute books of the Royal Society, CMB/174/34); 7th Meeting, 2 July 1969 (Committee minute books of the Royal Society, CMB/174/37); 8th Meeting, 16 June 1970 (Committee minute books of the Royal Society, CMB/174/41); 21 February 1972 (Committee minute books of the Royal Society, CMB/179/1); 18 September 1973 (Committee minute books of the Royal Society, CMB/179/4). For an Australian perspective, see Hill (1985).
65. Letter from former Director of the Australian Museum, Frank Talbot, to the Australian Coral Reef Society (S Hamylton (President) and P Hutchings), 5 November 2019.
66. Spender to Hinks, from Low Isles, 20 July 1929; Royal Geographical Society Great Barrier Reef CB 1921–1930, file 2.

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