Roger N. Hughes' contribution to Bryozoology

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1. Introduction

"From an early age Roger Hughes (Figure 1) was interested in ponds, streams and woods" wrote his friend Steve Ward in an obituary for *The Guardian*, published on 4 October 2015. Rephrasing such words we can say "From early age Roger, the scientist, was devoted to molluscs, crustaceans, and fish". Clonal organisms, mainly bryozoans, were a later, but a fertile topic. In the present work we aim to review his contribution to bryozoology using as a tool the citation index of ISI Web of Science (WOS from here onwards) and Google Scholar (GS). Although Citation Indexes as tools are too coarse to assess the relevance of a scientific contribution, we have to agree that such approach gives us at least an approximation of the impact a publication produces in the scientific community. A cited paper has been read, thought through, and made relevant to the reader's own research and scientific findings. In that sense Roger Hughes was relevant and profusely quoted, with more than 4600 and 9300 citations in WOS and GS, respectively (as recorded until 6 January 2016).

Figure 1. (a and b) Roger Hughes at Llyn Idwall with María Cristina Orellana, February 2012 (Photograph by J.M. Cancino).

2. Roger's path through science

Roger N. Hughes (1944–2015) studied Zoology at the University College of North Wales, now Bangor University, and obtained a PhD in Marine Ecology in 1968, under Dennis Crisp's Supervision. In 1969, he was awarded a Killam Post-Doctoral Fellowship at Dalhousie University to study benthic ecology and feeding behaviour of marine gastropods. In 1971 he returned to work at the University in Bangor, at which he remained until his retirement in 2011. However as a Professor Emeritus he stayed on at Bangor University, until his final illness, acting as an editor for prestigious journals dealing with marine biology and marine ecology.

Roger became well established as an invertebrate zoologist during the 1970s with his work on gastropod ecology, leading later to his book *A functional biology of marine gastropods* (Hughes 1986; GS 184 citations). While we here deal with his contribution to bryozoology, it should be realized that, throughout his career, he continued to study the ecology and eco-physiology not only of molluscs (both bivalves and gastropods), but also crustaceans and fish. Among the gastropod taxa he studied were vermetids: sessile, filter-feeding prosobranchs with partially uncoiled shells that form dense aggregations on certain warm water shores (Hughes 1979; GS 32 citations). Such aggregations, the result of larval settlement patterns, are of course not colonies but led Roger to discuss them at the influential Durham symposium on *Biology and systematics of colonial organisms* (Larwood and Rosen 1979).

Roger Hughes wrote 3 books and 207 papers. Over 77% of these publications were written with one or more co-authors, from which is clear that one of Roger's talents was his willingness to work in partnership, giving support, and being open to new ideas. In total he supervised 36 Ph.D. and 27 M.Sc. students and at least 6 postdoctoral fellows.

In his GS site (https://scholar.google.cl/citations?user=hlLlDAMAAAAJ&hl=es), by January 2016 he included 209 publications, with 9300 citations. Since at the time of death part of his work was in press, by 1 October 2016 the number of entries in GS had increased to 230, and the citations to 9,835.

Table 1. Roger Hughes. Number of publications classified by taxa and subjects. (Source of data Google Scholar, 6 January 2016)

	Mollusca	Crustacea	Fish	Clonal organisms and Bryozoa	Other Taxa General topics	Total
Optimal Foraging and Ecological energetics	28	21	18	0	17	**84**
Autecology and distribution patterns	24	8	7	6	11	**56**
Life history and reproductive biology	10	1	0	24	4	**39**
Taxonomy and morphology	3	0	0	3	2	**8**
Genetic bar-coding and genotype-environment interactions	6	0	1	13	0	**20**
Total	**71**	**30**	**26**	**46**	**34**	**207**

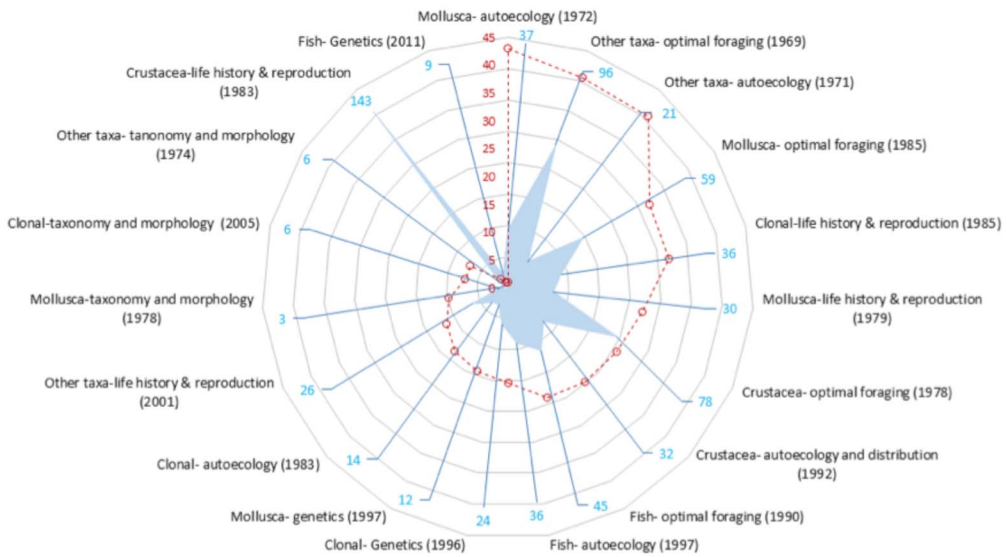

Figure 2. Research topics of R.N. Hughes, with year of first paper published (in brackets). Number of years the topics were pursued are indicated by open circles and dotted line, in a scale from zero at the centre and 45 years in the outer circle. Note that duration decreases clockwise, from year 43 to year 1. Average GS citations of the papers by topic, as classified in Table 1, are indicated by the stared filled area and the numbers at the outer circle.

Using the data base available in January 2016, his publications can be classified as shown in Table 1. Regarding taxa, molluscs and clonal organisms (bryozoans included) were the two principal groups of interest, followed by crustaceans, general topics (multi-taxa, models and books) and fish (Table 1).

The main subjects of interest included optimal foraging and ecological energetics; followed by distribution patterns and autecology; reproductive biology and life history; genetic-barcoding-genotype – environment interactions; and lastly taxonomy and morphology (Table 1).

Molluscan autecology and distribution patterns were pursued by Roger for 43 years (first paper published in 1972, last in 2015), with 17 papers published (Table 1, and an average of 37.1 citations (Figure 2). His first scientific publication (Hughes, 1969; cited 202, and 141 times, according to, GA, and WOS, respectively) deals with the feeding behaviour of *Scrobicularia plana*, an intertidal mud-flat bivalve mollusc. Energetics and distribution patterns, mostly in molluscs, were the subjects of his first 9 years of research, in Wales, Barbados, Canada and Aldabra in the Indian Ocean. With Bob Elner as a first author, Roger published his most cited paper (Elner and Hughes 1978; cited 372 times (WOS) and 482 (GA)), dealing with energetics in the crab *Carcinus maenas*. From there onwards, crustaceans became one of his main topics, without leaving the molluscs, his first group of interest. Later topics included clonal organisms and fish.

Total WOS citations per year increased through time, reaching a maximum of 212 in 2008 (Figure 3). Note that at the time data were obtained, WOS did not include any information of publications before 1977, molluscs therefore, are not seen here as the first group of interest.

Most citations refer to foraging behaviour and energetics (Figure. 3). Reproductive biology, distribution patterns and taxonomy (not shown in Figure 3) were themes that Roger kept active all through his scientific life. From the early 1990s DNA fingerprinting and barcoding was included as a tool of his work, becoming by 2012 the second most cited subject among his publications (Figure 3).

3. From clonal organisms to Bryozoa

Early in his scientific life Roger worked with corals and, as mentioned before, larval settlement patterns of vermetids, the latter leading him to the Durham Symposium on Biology and Systematics of Colonial Organisms (Hughes 1979). By that time he was showing an increasing interest in clonal organisms. In Bangor he was an active member of a multidisciplinary discussion group on this subject, which included botanists and zoologists: John L. Harper, colleagues and students from Plant Biology, plus colleagues and students from Zoology and Applied Zoology, the former Departments of today's School of Biological Sciences.

His interest in genuinely clonal organisms led to his contribution on reef associated organisms to a Darwin anniversary symposium in 1982 (Hughes, 1983), which concentrated mainly on corals. That neo-Darwinian evolutionary theory, based essentially on the life

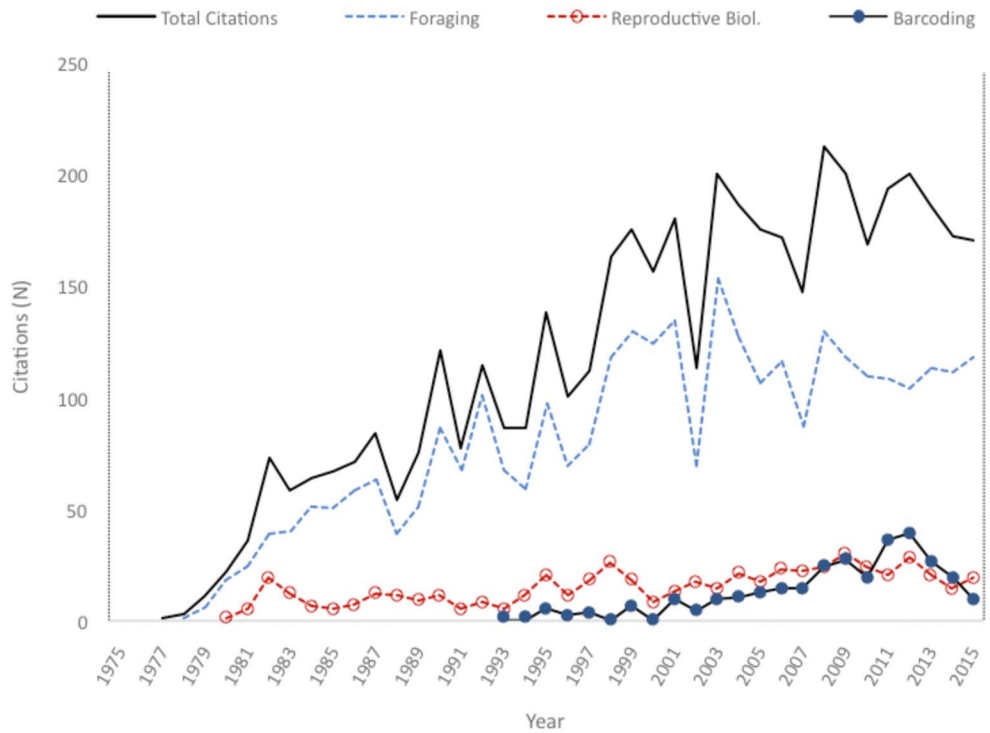

Figure 3. Roger N. Hughes. Total citation per year classified by research topic (source of data WOS, 6 January 2016). Note that database does not include any information of publications before 1977.

histories of unitary (or non-colonial) organisms, had largely ignored clonal (and colonial) organisms, was becoming widely appreciated at around this time (e.g. Harper 1977, Bell 1982). Also in February 1982, at a symposium on clonal organisms, held at Yale University, Roger gave a paper reviewing cloning in the Metazoa, though the resulting volume containing expanded versions of the contributions was published much later (Hughes and Cancino 1985, with more than 100 citations in GS). Undoubtedly, the participants and presentations at these symposia stimulated Roger's interest in Bryozoa and other genuinely colonial invertebrates. His book, the wide-ranging *A functional biology of clonal animals,* followed in 1989, (with over 300 citations, and his fifth most cited contribution in GS). To read the acknowledgements in this book is very instructive, giving an idea of the variety of scientists and specialists that Roger kept in contact with to produce such a far reaching book covering all clonal animals.

4. Bryozoa

In 1979, Juan M. Cancino arrived from Chile, with the idea of working on Optimal

Foraging, but Roger advised him to think of a totally different subject, clonal organisms, and gave him the freedom to choose the taxa and the subject for his Ph.D. thesis. Roger took him to the outflow stream from Llyn Idwal in Snowdonia, as he did with John Ryland in 1984, and with many visitors (Figure 1) to see over-wintering gemmules of the freshwater sponge *Spongilla lacustris*, which, like the sessoblasts of *Fredericella sultana*, and the hibernacula of the diffuse colonies of the freshwater ctenostome *Paludicella articulata,* also present in that lake, are asexually produced, non-dispersive propagules. These organisms were considered as study subjects for Cancino's thesis, as well as marine Bryozoa, common organisms in the Menai Strait and on Anglesey shores easily accessible from Bangor. Information on their occurrence and some aspects of their ecology was readily available from John Ryland's studies at Menai Bridge in the late 1950s. After reading Ryland's papers (1959, 1962), *Celleporella hyalina* (L.) was the species selected (Cancino, 1983, 1986). At that time Gary Carvalho was working, with Roger's supervision, on another cloning organism the crustacean, *Daphnia magna* (Carvalho and Hughes, 1983, 143 GS citations).

The decision to study *Celleporella hyalina* was inspired, as important advantages of the species for experimental work soon became apparent. The non-feeding larvae are easily released and settled rapidly in the laboratory, and colonies were found to grow and reproduce well in small culture vessels, both in the field and in the laboratory (Cancino 1983). Initial topics were naturally in the realm of eco-physiology (e.g. Hughes and Hughes 1986) and life-histories (Cancino 1983, Cancino and Hughes 1987, 1988), as had characterized his work on gastropods. Studies with Juan Cancino (Cancino and Hughes 1987, 1988, Cancino *et al*. 1991, 1994) and David Hughes (Hughes and Hughes 1986a, D.J. Hughes 1987, 1992) provided valuable understanding of the species and its requirements and initiated consideration of the effects of genotype on environmental responses.

Although bryozoans had been maintained in the laboratory before, especially by Jebram (e.g., 1975), the development of reliable mass culture methods for suitable phytoflagellate food was a landmark achievement that paved the way for ground-breaking studies on the growth and reproduction of *Celleporella hyalina*. Using protocols developed with Ewan Hunter (Hunter and Hughes 1993a, b) and perfected with Patricio Manríquez (1999) well-grown colonies could then be reared and physically divided to produce a set of independent clonal (sub-) colonies. This allowed variation between genotypes to be assessed experimentally, with each genotype represented in each experimental treatment. Colonies in laboratory culture could be kept in reproductive isolation from other genotypes until contact was deliberately instigated by moving genotypes into the same container, giving the opportunity for mating (Figure 4). The presence, unusual in a bryozoan, of three morphologically distinct zooids – feeding, female and male – in *C. hyalina* enabled the assessment of *in vivo* reproductive investment and relative allocation to the two genders from simple counts of the three zooid morphs. Brooded embryos were visible and easy to count (Cancino and Hughes 1987, 1988). *C. hyalina* also proved amenable to molecular approaches, starting with the development of a suite of microsatellite markers with Kathryn Hoare in the late 1990s (Hoare *et al*. 1998).

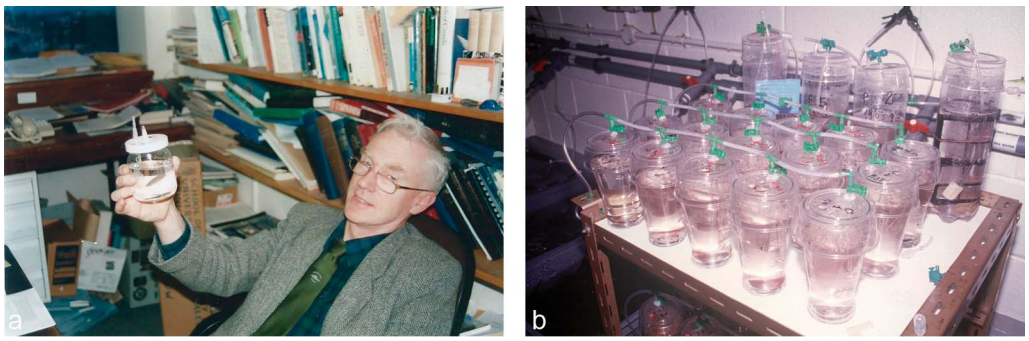

Figure 4. (a) Roger handling an experimental jar for growing isolated colonies of Celleporella hyalina*; (b) experimental setting as designed by P.H. Manríquez (Photographs by P.H. Manríquez and J.M. Cancino respectively 1998).*

Exploiting these advantages, Roger and his co-workers used *C. hyalina* to explore several basic questions in bryozoan biology concerning life-history strategy and the factors influencing reproductive investment, as well as characterizing the mating system and the physical means of mating in this sessile hermaphrodite. Studies based on cultured stocks originating from wild populations in North Wales, augmented by molecular paternity analysis where appropriate, established that reproductively isolated colonies brooded at a much-reduced rate, if at all, and selfing resulted in marked inbreeding depression (Hunter and Hughes 1993b; Hoare *et al*. 1998). The production of female zooids was low in reproductive isolation but was increased by even brief exposure to allosperm, particularly from an unrelated clone (Bishop *et al*. 2000, Hughes *et al*. 2002) – an example of restrained investment in female function in the absence of an opportunity to outcross. Hughes *et al*. (2002) also documented the uptake and storage of sperm by very small, immature colonies and the transfer of sperm from feeding zooids to female zooids budded after the period of allosperm availability; the mechanism of this transfer remains to be elucidated. Sperm released into in the water were shown to be relatively long-lived despite their dilution (Manríquez *et al*. 2001), and recipient colonies could take up and use sperm from relatively very dilute suspension (Pemberton *et al*. 2003). These results suggested that limitation of zygotic output by insufficient sperm availability ('sperm limitation') was unlikely in natural settings, but rather that sperm competition (with the added potential for female choice to influence paternity), was likely to predominate during the remote mating process. This mechanism was likely to be shared by many bryozoans and several other sessile aquatic groups which release sperm but retain eggs for fertilization and generally brood the resulting embryos. Broadly similar conclusions from a different evidence base were reached by Hughes *et al*. (2009) from a study of self-compatible genets of *C. hyalina s.l.* from other parts of the geographical range (see below).

Molecular analysis was also used to investigate the population-genetic consequences of the species' mating system and of developmental mode in natural populations, in comparison with the cyphonautes-producing species *Electra pilosa* (Goldson *et al*. 2001;

see also Seed and Hughes 1992 for comparisons including these two species). In parallel, molecular analysis of samples from widely geographically spaced locations was also applied to document cryptic speciation in *C. hyalina* and its relatives, and to detect multiple distinct lineages within *C. hyalina* in the NE Atlantic (Hoare *et al*. 2001, Gomez *et al*. 2007a, b, Hughes *et al*. 2008, Waeschenbach *et al*. 2012). This molecular phylogeography was paralleled by laboratory-based testing of reproduction by the sampled genotypes in reproductive isolation and when paired with colonies from the same and from different localities, to assess between-population reproductive compatibility. In addition to elucidating species boundaries, this work resulted in the discovery of lineages that routinely selfed, in contrast to the original cultures obtained from natural populations in North Wales and Devon. This provided the opportunity to compare routinely selfing and non-selfing lineages in laboratory culture, to test theoretical predictions concerning the relative strength of inbreeding depression, and the allocation to female function in the absence of a source of allosperm (i.e. in reproductive isolation) (Hughes *et al*. 2009); this work involved molecular paternity analysis. The basic approach of manipulative experiments on cultured and cloned colonies of *Celleporella hyalina,* discussed above, was also used to demonstrate the influence of relatedness on fusion of colonies (Hughes *et al*. 2004a), and to demonstrate an effect of temperature, but not food supply, on zooid size (Hunter and Hughes 1994), this effect being confirmed while investigating the influence of temperature and oxygen supply on the number and size of structures from cellular to colony level (Atkinson *et al*. 2006).

Another important topic investigated was the role of light in initiating the release of *Celleporella* larvae and their subsequent behaviour (Cancino *et al*. 1991, 1993, 1994, see Figure 5). Most bryozoans release their larvae as a direct response to increasing irradiance levels in early morning, the effect declining during the day. Roger and co-authors carefully controlled and quantified results also showed how the response was affected by the tidal cycle: high tide, especially in turbid waters, substantially reducing the amount of light

Figure 5. (a) with the larval collecting machine and collaborators in Chile, January 1990 (clockwise, Roger, P.H. Manríquez, M.H. Muñoz, and J.M. Cancino); (b) collecting fronds of Laminaria saccharina *with* Celleporella hyalina, *to study larval liberation pattern, with Claudio Ramírez in Wales August 1990 (Photographs by J.M. Cancino).*

reaching the attached algae on which the bryozoans live. They also related the patterns of release to the behaviour of larvae during their free-swimming period, comparing these in the species pair *Alcyonidium hirsutum* and *A. gelatinosum*, which cohabit *Fucus serratus* in the Menai Strait. In the former, light is the trigger for larval release, and the larvae initially display positive phototaxis; in the latter, larval release is largely at night and the larvae do not respond to directional illumination. The question on how long the non-feeding lecithotrophic larva are able to swim for, without losing the ability to settle and metamorphose was also addressed, and for the first time in bryozoan consequences of larval behaviour on the future performance of the colonies they generate were demonstrated (Orellana and Cancino 1991, Orellana *et al*. 1996, Hunter and Fusetani 1996, Cancino and Gallardo 2004).

A different strand of Roger's work on bryozoans investigated the occurrence of polyembryony (the production of multiple clonal progeny from a single sexually-produced zygote) throughout the bryozoan order Cyclostomata. This reproductive mode is widespread thoughout the living world but relatively uncommon, and is regarded as an evolutionary puzzle, involving paying the cost of sexual reproduction while apparently forsaking the perceived benefits, and thus has broad interest as potentially offering insight into a major evolutionary enigma, the persistence of sex. The occurrence of prolific polyembryony throughout an entire order (or almost so) of Metazoa is unique to the Bryozoa and requires explanation, but this topic had received relatively little attention for some decades and was ripe for the exploitation of new technologies. Roger's work with various collaborators confirmed the basic occurrence of polyembryony in cyclostomes by molecular means (Hughes *et al*. 2004b). The distribution of genetic diversity in natural populations was investigated in one species (Pemberton *et al*. 2007), and the results suggested that one of the published hypotheses for the adaptive value of polyembryony in the group could be discounted. Helen Jenkins' recent Ph.D. study, a collaboration between the University of Bangor, The Natural History Museum in London, and the Marine Biological Association of the UK, brought two species of cyclostome into culture for experiments with cloned colonies, and developed molecular markers for paternity analysis and the recognition of clonal genotypes. The data published so far (Jenkins *et al*. 2015) extend the evidence of restrained female investment in reproductive isolation, shown previously for routinely outcrossing *Celleporella hyalina*, to the two species of cyclostome (one outcrossing, but the other self-fertilizing to an appreciable degree in reproductive isolation). As with the cheilostome *C. hyalina*, production of female zooids in the cyclostomes is promoted by exposure to allosperm, but differences of detail between the bryozoan species studied so far suggest that the mechanism by which this effect operates might have a complex evolutionary history within the phylum.

Roger provided elegant reviews of the biology of modular animal colonies in Hughes, (2005, GS 35 citations), and in the final chapter of the 1989 book on clonality in animals (Hughes 1989). Here, as previously in Hughes and Cancino (1985), he repeatedly emphasized the parallels, as sessile modular entities, between these colonies and land plants. Consequences of colonial encrusting body form on metabolic rate was also

explored as a general topic of interest (Hughes and Hughes 1986b). However, dealing with clonal organisms the most ambitious endeavor he achieved was his 1989 book, nicely reviewed by Richard K. Grosberg (1989) and in which Roger set to explain "how clonal reproduction arises, whether it is responsive to natural selection, why many clones also reproduce sexually, and whether clonal reproduction has new implications for life history theory" (Hughes 1987).

In total 53 of Roger's publications dealt with clonal organisms (listed in chronological order below), 42 of them with bryozoans, which led Roger, in his most recent CV to describe his current research as: "*Gametic recognition and mate choice in marine colonial invertebrates. Use of clonal animals to partition genetic and environmental control of resource allocation in the investigation of life-history evolution. Molecular phylogenetics and phylogeography of hippothoid bryozoans*".

5. Roger N. Hughes' service to science and to the scientific community around the world.

Roger obtained all his degrees from the University of Wales (B.Sc. Hons Zoology class I in 1965; Ph.D. Marine Ecology 1968; D.Sc. 1982) and all his academic life was linked to the same University, starting as a Lecturer in Zoology in 1971; Senior Lecturer 1984, Reader 1984, Personal Chair 1988, The Lloyd Roberts Chair of Zoology 2000, to his final nomination as a Professor Emeritus in 2012. However from early in his scientific life he had the world on mind. In April–July 1968 he was a Member of the Royal Society Expedition to Aldabra Atoll, in the Indian Ocean. The following year he was awarded a Killam Post-Doctoral Fellowship that allowed him to move to Dalhousie University, Halifax, Nova Scotia, Canada, for two years 1969–1970.

Financed by the Royal Society Travel Grants for Marine Biological Research he visited: Jeddah**,** Saudi Arabia 1973; Cape Town 1975; Barbados 1980; Panama 1982; Hong Kong 1983; Trinidad 1984; Cape Town 1985; Panama 1988; Japan 1990; Perth Australia 1991; Italy 1992; USA 1993; Chile, 1995 and 2004.

He was a Visiting Lecturer at University of Cape Town July-December 1975, and July-December 1985; visiting Scientist under British Council Links Scheme at Universidad Católica de Chile, Santiago November-December 1986, and January 1989. Universidad Católica de la Santísima Concepción, Concepción in 1993, and 1995, and financed by CONICYT in April–July 2014 (his very last international trip).

As a good international ambassador he received at Bangor many visiting fellows, in his last CV, he mentions: Dr A.J. Underwood 1982 (Biology, University of Sydney); Dr C.L. Griffiths 1986-87 (Zoology, University of Cape Town); Dr R.L. Vadas 1989 (Botany and Plant Pathology, University of Maine, Orono); Dr J.M. Cancino 1990 (Ecologia, Pontificia Universidad Católica de Chile, Santiago); Dr M.D. Subosky 1991 (Psychology, Queen's University, Kingston, Ontario); Professor C.D. McQuaid 1991–1992 (Zoology, Rhodes University, S. Africa); Dr K. Warburton 1992 and 1995 (Zoology, University of Queensland, Brisbane); Dr J. Blay 1994–95 (Zoology, University of Cape Coast, Ghana); Dr J.-G. J.

Godin 1994 (Biology, Mount Allison University, Canada); Professor H.U. Riisgård 1996–7 (Biology, Odense University, Denmark); Dr C. Nielsen, 1997 (Zoology Museum, University of Copenhagen); Dr M.H. Son, 1997–8 (University of South Korea, KRF scholarship); Dr S. Craig, 1998-9 (University of California, NATO / NSF scholarship). It is most likely there were many more not in the list (including bryozoologists such as Dr Andrey N. Ostrovsky, for example, in 2002).

He served science with a prolific editorial output being a member of the Editorial board of the *Journal of Animal Ecology*, 1991–1996; Contributing Editor, *Marine Ecology Progress Series* 1984–2015; Managing Editor, *Journal of Experimental Marine Biology and Ecology* 2005–2015; Managing Editor *Oceanography and Marine Biology: an Annual Review* 2010–2015. Volume 53 of the *Annual Review* was published in 2015 with Roger as the chief Editor for the final time (Hughes *et al*. 2015).

He acted as a Referee for 65 journals: *Advances in Marine Biology, Acta Ecologica, African Journal of Ecology, American Naturalist, Animal Behaviour, Animal Cognition, Aquatic Sciences, Archiv für Hydrobiologie, Asian Marine Biology, Australian Journal of Marine and Freshwater Research, Basic and Applied Ecology, Behaviour, Behavioural Ecology, Behavioural Ecology and Sociobiology, Biodiversity and Conservation, Bollettino Malacologico, Canadian Journal of Zoology, Current Biology, Ecology, Ecology Letters, Ecological Monographs, Ecological Applications, Ecosphere, Estuaries, Ethology, Ecology and Evolution, Evolution, Experientia, Functional Ecology, Hydrobiologia, Human Reproduction, Israel Journal of Zoology, Journal of African Zoology, Journal of Animal Ecology, Journal of Comparative Psychology, Journal of Crustacean Biology, Journal of Estuarine and Coastal Research, Journal of Experimental Marine Biology and Ecology, Journal of Fish Biology, Journal of the Marine Biological Association, U.K., Journal of Molecular Evolution, Journal of Molluscan Studies, Journal of Natural History, Journal of Shellfish Research, Journal of Theoretical Biology, Malacologia, Marine Behaviour and Physiology, Marine Biology, Marine Ecology, Molecular Ecology, Molecular Phylogenetics and Evolution, Nature, Oikos, Philosophical Transactions of the Royal Society, London, Physiological and Biochemical Zoology, Polar Biology, Proceedings of the National Academy of Sciences, USA, Proceedings of the Royal Irish Academy, Proceedings of the Royal Society, London, Revista Chilena de Historia Natural, Scientia Marina, South African Journal of Marine Ecology, South African Journal of Marine Science, South African Journal of Zoology, Trends in Ecology and Evolution* and *Vie et Milieu*.

He also acted as a referee for research councils such as NERC, BBSRC, NSF, Italian Ministry for University and Research, UGC Hong Kong, New Zealand, Israel, South Africa, Netherlands Organisation for Scientific Research (NWO, the Dutch Research Council).

He obtained 18 Grants from the Natural Environmental Research Council, 1 from Leverhulme; and 6 from the European Union, jointly with scientists from the UK and overseas including G. Carvalho, (Swansea, and Bangor); B. Bayne, (Plymouth Marine Laboratory); R. Seed (Menai Bridge); S.J Hawkins; T.A. Norton, and D. Atkinson

(Liverpool), M. Burrows and R. Batty (Dunstaffnage); J.D.D. Bishop, (MBA Plymouth); A.R. Cossins and C.V. Howard (Liverpool), B. Howell (Conwy); S.F. Craig, (Bangor); D.H. Lunt (Hull); J.M. Cancino and H.I. Moyano (Concepción, Chile); G. Chelazzi, (project coordinator, Florence), M. Valero, Lille); K. Johannesson, (project coordinator, Gothenburg). Most likely many others are missing, since among bryozoologists, for example, A. Waeschenbach, from the Natural History Museum, London and J.S. Porter, from Edinburgh, coauthored Roger's papers.

Many of the 36 Ph.D. students he supervised kept in contact with him for life, and as he mentions in his last CV "*many secured posts in biological research, notably at the University of Aberdeen, University of Wales, Bangor, University of York and the Catholic University of Chile, Santiago, Catholic University in Concepción, Chile; and research posts at The Water Research Laboratory, Marlow; the State University of New York at Stony Brook; The Institute of Fisheries and Oceans, Canada; The Smithsonian Tropical Research Institute, Panama; Dunstaffnage Marine Laboratory, Scotland; Ministry of Agriculture, Fisheries and Food, Conwy*". Post-doctoral Fellows included: Isabelle Colson, Peter Wright, Simon Morley, Mike Burrows, Kei Kawai, Kathryn Hoare.

He also acted as an External Examiner for 51 Ph.D. and 7 M.Sc. theses in the UK, Italy, Spain, Australia, South Africa, India, Canada, and the USA.

Several of his former students, colleagues and friends from different Universities assembled in Bangor to honor Roger at his retirement (Figure 6) and left to posterity the special issue of *Marine Ecology Progress Series* entitled "Evolution and ecology of marine biodiversity: mechanisms and dynamics" edited by Michel J. Kaiser, Michael T. Burrows, and Helen Hughes (*MEPS* **430**, 98–288, 2011).

Figure 7. (a) with Juan Carlos Castilla at Bangor University on 14 July 2008 (photograph by Elena Rho); (b) with Helen, beside the Andean mountains, near Santiago, in Roger's second trip to Chile, January 1990 (photograph by J.M. Cancino); (c) with P.H. Manríquez (front), Helen and friends near La Serena, Chile, May 2014 (photograph by P.H. Manríquez).

6. Roger and Chile

The disposition to work with others is clear from above and from the long list of coauthors in Roger's scientific publications. However another and most appreciated feature of Roger (and Helen as well), was the talent for establishing long lasting friendly relations. One example we know well is that of Roger's relationship with people in Chile, which dates back to 1967–1968. In those years, he and Juan Carlos Castilla as Ph.D. students at the University of Wales shared the same supervisor, Professor Dennis J. Crisp. Since then Roger, Juan Carlos and their respective wives Helen and Elena became good friends (Figure 7a). Years later, in 1979 Juan M. Cancino, a former student of Castilla, followed a similar route and as described above, became Roger's Ph.D. student. His friendship with Juan Carlos and Juan paved the way for 6 visits to Chile; the first in 1986 and the last one in 2014 (Figures 7b, c). During his visits to Chile Roger conducted short studies using local bryozoans as biological models and he taught short courses on topics as optimal foraging, reproductive biology (Figure 8a) and biology of clonal organisms from which many Chilean marine and terrestrial biologists benefited across the country.

Figure 6 opposite. Former students, colleagues and friends that attended the Symposium to honor Roger at his retirement, beside the Menai Strait, on 20 March 2010. Three of the authors of the present paper are in the picture (Helen Hughes, Ryland and Bishop). Juan C. Castilla also attended from Chile (second from the right, front line). J.M. Cancino, being the President (Rector) of his university, could not attend due to the 8.8 Chilean earthquake, on 27 February. (Photograph distributed by the organizers of the Symposium, photographer unknown).

Figure 8. (a) in a field trip near Concepción with a class attending a Marine invertebrate reproduction course given by Roger, on the left, and colleagues from Bangor University (Raymond Seed, standing beside Roger, and Chris Richardson, far right) on January 1998, at Universidad Católica de la Santísima Concepción (UCSC). Staff member from the latter on the picture: Ricardo Otaíza, on the back behind R. Seed, and J.M. Cancino, beside C. Richardson, photograph by J.M. Cancino); (b) at Pan de Azúcar, National Park, northern Chile, January 2004 (photograph by J.M. Cancino); (c) in Antofagasta with John Ryland, waiting to see Chilean bryozoans, as part of the Pre-conference Trip, January, 2004 (photograph by Hans Arne Nakrem); (d) bryozoologists attending the IBA Post-conference trip at Punta Arenas Main Square, beside Magellan and the Magellan strait native people sculpture, January 2004 (photograph by Hans Arne Nakrem)

*Figure 9 opposite. (a) a conference on Clonal Organisms to UCSC Science faculty members and students, 14 April 2014 (photograph UCSC); (b) after a conference on penguins to students of 3 English High Schools in Concepción, 18 May 2014 (photograph USCS); (c and d) the last trip to the Andes, (c) with Helen and a millenarian monkey puzzle tree (*Araucaria araucana*); (d) with Helen, M.C. Orellana, and the Lonquimay Volcano on the background (19 April 2014, photographs by J.M. Cancino).*


a


UCSC
b


c


d

In two of those courses a former student of Juan M. Cancino and Juan Carlos Castilla's research assistant, Patricio Manríquez, met Roger. Few years later, in 1996 Patricio with the strong support of Roger started his Ph.D. with him as supervisor, using *C. hyalina* to investigate different aspects of reproductive ecology.

In 2004 Roger and Helen attended the 13th IBA Conference held in Concepción, and as part of the Pre- and Post-Conference field trips had the opportunity to travel from the desert in the far North to the Magellan Strait (Figures 8b-d)

During 2014, Roger and Helen visited Chile for the last time. As usual he managed to visit his Chilean friends; Juan M. Cancino, Maria Cristina Orellana and Antonio Brante in Concepción, Juan Carlos Castilla and Elena in Las Cruces, and Patricio Manríquez in Coquimbo. During this long-term scientific-human connection with Chile Roger always showed the most generous attitude, sacrificing invaluable family time, to cooperate with us. Roger's support included both improving the edition of our manuscripts as well as inspiring, encouraging and stimulating improvements of some un-tackled aspects of our own research. To prove our gratitude his name was commonly present in the acknowledgement section of many of our manuscripts, and for this he will surely stay forever in our minds.

Roger also received at Bangor undergraduate students of UCSC (a new University created in 1991 from a former Campus of the Pontificia Universidad Católica de Chile), including Dr Antonio Brante, (Head of the Ecology Department at UCSC at the time this paper is written). Brante and Hughes, (2001) resulted from trusting in an unknown undergraduate student from a faraway, small University, (recommended by Roger's former student: Juan Cancino, Dean of Science). After retirement Roger accepted Antonio's invitation to visit UCSC for 2 months under a financial scheme of the Chilean CONICYT, supported as well by UCSC (Figures 9a-d). Solas *et al*. (2015) is the result of this last stay at UCSC. Illness struck Roger soon after his return from Chile. This was his 6th and final trip to Chile and perhaps his most clear tribute to friendship across 4 Chilean academic-generations (from Castilla, to Cancino to Manríquez and Brante to Maribel Solas, Antonio's student). The photos included in this publication are here for us to remember him by.

Another version of this same history, written by Juan Carlos Castilla and Roger, while in Chile in 2014, can be read following link (Chilean News at page 23):

https://www.bangor.ac.uk/oceansciences/alumni_newsletters/the_bridge_2014.pdf

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