My Life and Work: an unstructured affair[1]

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https://sites.google.com/view/mackiefamily/home

The career of a scientist can be an unstructured affair. To counter this, recruiting expert Deb Koen has come up with a check list of ten hot strategies to develop your career. In at number six, ***build your brand****. This involves developing and managing your reputation through your results and your relationships. Even the greeting on your voice mail can help reinforce your brand, she says. (Nature 447, 7147, p. xi)*

Looking at my work in retrospect I clearly failed to adopt some of Ms Koen's hottest strategies, for example *Strategy No. 5. Target a Trend*. I tended to avoid mainstream topics and usually found myself working on obscure and neglected ones. If in retrospect a structure can be discerned, it was much less the result of advance planning than something that emerged gradually as the years went by, in the same way that a plant seeking the light finds its way up through a thicket, instinctively avoiding obstacles, and taking advantage of unexpected openings.

Building my brand

Even in my early twenties, after completing my military service, I still had little idea of what I wanted to do in life. The way things worked, decisions were made for me by adults - not in itself a bad thing (indeed that's what adults are for) - but it left me lacking in a sense of being responsible for my own fate. I had gone first to prep school in England, then in 1940, as a war evacuee, to another school in Canada run by my uncles, then back to public school (Blundell's) in England in 1944 and then at 18 into the army for 2 years as a national serviceman - "a creature that moves in predestinate grooves".

My brother Richard was exceptionally gifted intellectually but not much interested in doing things with his hands whereas I was only averagely bright but had a more practical bent. We were characterized in these terms in the family and I grew up thinking of myself as the practical one. My mother said I was a good all-rounder. It didn't bother me that Richard was brilliant as I knew I was handier. If he was *Homo sapiens*, I was *Homo habilis*. When I was evacuated to Canada during World War 2, I got lots of largely unsupervised carpentry experience in the workshop of my uncles' school and helped with all sorts of chores around the place. I have written an account of these years in Mackie Men and the Empire (2006). Later in the 1940s my mother and I lived in a run-down former farm at Mark, in Somerset. As a teenager there I developed rudimentary practical skills with

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machinery, carpentry, raising pigs and poultry and gardening. I was interested in all these things and, lacking instruction, inventive in the way I did them. My father died when I was 14 and, though a distinguished medical administrator and specialist in tropical diseases, he was not a handyman in the domestic sense. Anyway, there was no one to tell me the 'right' way of doing things so I learned by trial and error, and still do to a large extent. If my father had lived, he might not have allowed me such a free rein around the farm as my mother did, so I wouldn't have developed the same practical know-how and confidence. On the other hand, he might have seen where my abilities lay and arranged for me to receive proper instruction.

After leaving the army, I wondered about going to Wye Agricultural College (I liked looking after our pigs, geese and poultry at home in Somerset) or become a forester (like my friend John Brasnett's father, a don at Cambridge) – something practical and outdoorsy. I also thought about dentistry, as I like working with my hands. The one thing I was clear about was that I wouldn't go into medicine, the reason being that my father and both brothers were doctors. I had just enough gumption or hubris to want to strike out on my own. This was the nearest I came to adolescent self-assertion. In retrospect, this was foolish, and medicine might have been a good choice, as it would have given me the opportunity to do something directly beneficial to other people as well as giving me scope to develop practical skills. I would probably have become a surgeon or medical researcher or gone into some clinical field where I could work hands-on. I often feel my work as a zoologist, apart from the teaching aspect, is self-indulgent and contributes little or nothing to improving the lot of suffering humanity. I tried to make up for this by working as a hospice volunteer for 7 or 8 years in the 1990s and later as a volunteer medical driver. Perhaps for similar idealistic reasons my friend Quentin Bone became a magistrate.

The decision to go to Oxford was mostly due to my mother and my brother Lawrence. My mother must have thought I was setting my sights too low in talking about going to an agricultural college. Besides, I knew nothing about real farming and might very well have been bored by it. Anyway, going to Oxford seemed like just another step in the ongoing process whereby adults steered one through life. It turned out when I eventually made a trip to Oxford to decide on a course of studies that it pretty well had to be science of some kind, given the subjects I had studied for my higher school certificate. St Johns College was prepared to have me (my brother Lawrence had been there and was now in general practice in Warwickshire) and I had even managed to pass my Chemistry prelims on the third attempt, after going to a crammer. With good marks in Physics, which was well taught at Blundells by "Slug" Chanter, I could still have got into medicine but had set my mind against this. The senior tutor at St Johns, W.C. Costin suggested a walk around the garden. He must have been used to helping clueless young men decide what degree they were going to read for. It is a big garden and the walk took 20 minutes. By the time we got back to the Canterbury Quadrangle, where Costin had his rooms, it had been decided that I would read zoology with William Holmes, a Fellow of the college, as my tutor.

Once again, the benign world of grownups had made a decision for me, and it's not one I can really complain about. Zoology is a very broad field, broad enough to accommodate people

with many different sorts of mentality including those of us with little flair for mathematics or abstract thinking. It may seem paradoxical for a would-be zoologists but I was not much interested in Nature *per se*, and had little urge to know the names of plants and animals, or to collect specimens, but I was curious about how things (including animals) are put together, how they 'work', and I had an experimental bent. At home on the farm, I had discovered I could hypnotize geese by arranging them upside down with their necks in a certain configuration. They would remain in this posture for minutes on end. I made a kind of kayak out of bent willow poles covered in a cowhide and paddled it on the rine that flowed by our place (the village of Mark is bang in the middle of the Somerset Levels, flat peatlands traversed by deep drainage ditches called 'rines', from the Dutch rijn).


1947. My boat on the rine.

My life as a zoologist has been satisfying in giving me a chance to develop and practice the skills needed to do experiments on how animals work. I twice started to write a book but each time gave it up as I got bored reading and synthesizing other people's work - I just wanted to do research and the demands of teaching and administration left with me little enough time for my own work as it was. Nevertheless, later in life, I did write reviews covering the main fields I have worked in. With various collaborators I reviewed tunicate nervous systems in 1982 (No 69 on my publication list) and again in 2005 (148), siphonophore biology in 1987 (92), the *Aglantha* work in 2004 (143) and the biology of hexactinellid sponges 2007 (153). The siphonophore and sponge reviews were long enough to have been books themselves if we had gone that route. When writing these reviews, I was in effect drawing a line underneath a bunch of my own work and trying to put it into context in the broader fields of which it was part so that I could move on to other things. I like to tidy things away and not leave them in a mess for others to sort out. I also wanted my own part of the story to be 'got right' for posterity to the extent this is ever possible. I suppose this marks me out as someone who takes himself and his research findings too seriously, but academics like us have nothing else to show for all our years of hard work - just their research findings and perhaps some lingering influence on the thinking of former students.

Research for me is very much like the sort of aimless tinkering one does when young. Very often I have only a vague idea of where I'm trying to go, but just follow my nose. One set of tests may suggest something interesting, which in turn suggests further experiments. I don't much mind where this takes me, though it may be into a blank wall. The process is quite different from that practiced by some scientists, typically leaders of big groups, who have to have clear, consistent strategies and objectives and to approach their solution like a military campaign with careful planning and deployment of forces. This works, and produces big results, but may not be so much fun for members of the team if they feel they are just minor cogs in someone's else's machine. For some reason, it comes more naturally to me to play around with a topic than to approach it in an

organized way. Perhaps I have a lingering attachment to the snobbish notion of amateurism which was fashionable at Oxford when I was young. The idea was to convey an impression of effortless ease of accomplishment, to be brilliant and successful without ever appearing to work very hard. Whatever its roots, this attitude is not one I would recommend to an aspiring scientist. Its downside is that I never made the effort to master certain basic skills like those involved in biochemistry techniques, molecular biology and biometrics which should be part of every experimental biologist's tool kit. I don't know how I ever had the nerve to accept the editorship of an important zoological journal (The Canadian Journal of Zoology) and run it for 10 years without being competent in statistics.

My undergraduate career, though not distinguished (I was expected to get a 1st but got a 2nd) apparently showed enough promise that I was allowed to embark on a graduate programme, supported by a grant of £325 per annum from the Department of Scientific and Industrial Research.

Libby Hyman , Friday Harbor, 1920

I picked siphonophores as a group to work on for my doctoral thesis. I needed a project on a marine topic in order to apply for the Oxford Naples Scholarship and I had been struck by a statement by Libbie Hyman in vol.1 of her *Invertebrates* that she had seen *Halistemma* "dart about vigorously, often executing loop-the-loop curves." I put this forward as my proposal for Naples. How could a colony of dozens of different 'persons' swim in a coordinated manner? When I went to Naples, I was entranced with the complexity and weird beauty of these extraordinary animals, something I was completely unprepared for after seeing them only as textbook drawings and pickled specimens. Later, in the library of the Stazione Zoologica, I came across the marvellous illustrations in older reports by Chun, Haeckel, Vogt, P.E. Müller and others. These workers had been there before me and felt the same thrill. Learning enough German to read these old monographs now became (almost) a pleasure! Nowadays, videos from ROVs and manned submersibles bring this world vividly to life for television viewers.

Whether I was aware of it then or not, I think I must have been influenced a great deal as a student by my contacts with A.C. Hardy. Hardy, who had invented the continuous plankton recorder, was fascinated by the problem of vertical migration and other mysterious processes in the sea, as vividly described in his book The Open Sea: The World of Plankton (Collins, 1956). If ever a book was a labour of love, that was it. He had an infectious enthusiasm for marine invertebrates and an artist's delight in their diverse shapes and colours. Though much occupied as Linacre Professor with administering the department he followed my development with genuine interest and guided me at several critical junctures. Another important influence at Oxford was J.R. Baker, who gave us a strong grounding in optical microscopy. I am not sure however that he always kept

up with recent developments. I remember his impassioned lectures on the Golgi controversy- are Golgi bodies real cell organelles or merely artefacts of the special methods used to show them? He argued that they were artefacts. This was at a time when the whole debate was virtually a dead issue - electron microscopy in the USA was showing that the Golgi component was universally present in animal and plant cells. There were no electron microscopes in Oxford as far as I know and the word 'ultrastructure' was not part of our vocabulary. The department was even more backward in neurophysiology; it was ineffectually taught and there was little equipment, none of it up to date. On a trip to Cambridge I was amazed to see real physiology going on, with rows of cathode ray oscilloscopes set out in the labs for the students to use for recording neuromuscular activity.

My supervisor William Holmes, in his effete and laid-back way, trained me and his other students in the habit of critical thinking and gave me much-needed confidence in my own abilities. He told me, and I came to accept, that being the practical type was not incompatible with having serious intellectual goals[2] - something which I suppose I knew in my heart of hearts but for some reason (romantic affectation? melodrama?) chose not to admit. I used to tell people "my brother Richard hogged all the brains in the family". When the philosopher J.H.Woodger visited the college, I told him I belonged to a 'lost generation'. I had no idea what I meant by this, it was pure tragic-romantic affectation, as he quickly ascertained.

William had been a brilliant young man who in his middle years lost much of his research momentum. As a bachelor with rooms in college he could enjoy to the full the rather sybaritic life made possible by a college Fellowship, the comfortable quarters, his own key to a side door into the North Quad through which special friends were ushered, discreet scout service, the St John's wine cellar, and an income that allowed him to indulge his taste for long-drawn-out meals with his cronies, mostly young men. He would order in smoked eels and other delicacies from Schmidt's of Hamburg, have a selection of wines brought up from the cellars, and happily spend whole afternoons at the table elegantly laid out with college silver on fresh linen, and Sibelius in the background. He never made sexual advances to me and the subject was never discussed between us, though in other areas we were close.


William Holmes

William had a complete set of first editions of the seven volumes of Scott-Moncrieff's translation of Proust. Somehow I managed to lose one. This was one of the few times he was seriously upset with me, though I never once saw him lose his temper. Contrariwise, one of the few times I fully engaged his interest was when I told him something he apparently did not know, that

[2] "Anyone who combines strong common sense with an ordinary degree of imaginativeness can become a creative scientist" (P.B. Medawar, New York Review of Books, 28 March 1968)

the title Remembrance of Things Past came from a Shakespeare sonnet and I was able to quote a few lines. I read the Proust books with great pleasure and have since reread them, chiefly for their psychological insight. William also introduced me to the C.P. Snow novels. I recently re-read them all and found them still good reading, as well as being penetrating commentaries on the class structure and social life in England in the 40s and 50s, and sardonic portrayals of the academic world in particular.

William's love of music, especially Sibelius, also led me to think more seriously about music and listen to it carefully instead of just letting it wash over me as pleasant background sounds (although that has its place too when one is trying to work). Years later when I was 50 I took up the cello and for once made a real effort to learn to play an instrument properly (I hadn't got very far with previous attempts on piano, recorder and viola da gamba because I couldn't be bothered to practice). I now play regularly with a string quartet and other chamber music ensembles. Though I am no whiz, I can get along in much of the music of the baroque and classical periods. Things start getting dicey with Brahms, and as for Debussy and Ravel- forget it! However, Ravel's directions on how to play one of his movements - *assez vif, bien rythmé* – could serve as my motto. Lively and well-balanced is how I would like to live my life.

As my mother noted, I am an all-rounder, and have always been interested in plenty of things that have nothing to do with science. As a youth in Somerset I listened avidly to BBC Third Programme broadcasts regardless of whether I knew or understood anything about the topic. I enjoyed the wit and articulateness of C.E.M. Joad, Bertrand Russell, Phillip Hope-Wallace, Pamela Hansford Johnson and other radio pundits. Only one of them, Ralph Whiteman, spoke with a regional accent -thank goodness that has all changed now. Funnily enough, now in my retirement, I have gone back to being a big fan of BBC Radio 3 which you can get on the internet. They save all their broadcasts for a week so if you miss Tuesday's Composer of the Week, say, you can still go and find it. I am patriotic as only we expats can be, and I rejoice in everything the Beeb stands for, apart from its sometimes-snotty attitude to American pop culture. As one who forsook his mother country, and however much I love my life in Canada and have tried to Canadianize myself, I am always there, egging Britain on from the sidelines, hungering for news of health in the economy. Such news was in desperately short supply until the 1990s when things began to pick up, following the draconian Thatcherite reforms. As Nicolas Sarkozy, the new French President, said recently "The most dramatic case is that of Great Britain, which at the end of the 1970s seemed to be a country completely out of its depth with GDP 25 percent below that of France. The British GDP is now 10 percent higher than that of France and the standard of living of the British is higher than that of the French" – this sort of thing was all music to my ears. I took comfort in our scientific breakthroughs, successes in the arts, drama and literature and signs that the country still stands for something special in the post-imperial world. Now in the last year of Tony Blair's prime ministership, I hope the UK will again find someone with strong principles and a strong voice in world affairs.

By listening to highbrow radio programmes I acquired a spurious gloss of sophistication that I tried to impress my friends with. Lacking self assurance, I wanted to *be* someone. I dare say everyone saw through this. I was, and remain, a dilettante. Nevertheless, I did genuinely hunger for intellectual stimulation. At home in the Somerset marshes as a teenager I read books left by my father - Kroeber's Totemism and Exogamy, Wegener's The Origins of Continents and Oceans, various medical tomes, travel books by Alan Moorhead, Wilfred Thesiger, Aurel Stein and Lucas Bridges as well as the Manchester Guardian (my mother was a stalwart of the Liberal Party) and large amounts of whatever works of biography and fiction came to hand. Robert Graves' Claudius novels and his Goodbye to All That made as deep an impression on me as anything I read as a teenager, and I also admired his wonderfully lyrical early poems and his simple, telling prose style. To this day I have little interest in literary artifice or complex, obscure poetry, especially if it fails to appeal to the ear in the way music does. Graves's poems had everything I wanted and when I have tried to write poetry myself (rarely successfully) it has been in a Gravesian style.

The Oxford system provided opportunities for informal meetings with senior members of the college and of the Zoology Department, often in pubs. I got to know several of them quite well. W. Costin and John Mabbott, both fellows of St Johns, took my friend Basil Harley and me on a grand tour of Europe in Costin's car visiting among others a prewar Rhodes scholar at St John's, now General von Senger und Etterlin (and his beautiful daughter) in Bavaria. Von Senger had commanded the XIV Panzer Corps in Italy during the war and was a German war hero. Brainwashed by wartime propaganda, it was astonishing for me to meet this civilized and kindly man. Then we went on to Venice and Ravenna and back through France, Costin lecturing us non-stop on the history of the places we passed through. I also got to know George Richardson, Peter Brunet and Alistair Hardy fairly well. Hardy (now Sir Alistair) and his wife Sylvia came to visit us later when I was working at Villefranche, and again in Edmonton. E.B. Ford even asked me round for a meal one evening. I asked him about the Drosophila team, (Morgan, Bridges, Sturtevant and Muller) and how they had each contributed to the Nobel prizewinning work. With my romantic, literary bent, I was more interested in the drama of the stories surrounding the people behind the science than the science itself, genetics being one of the abstract, numerical subjects which I shirked.

W.C. Costin and J.D. Mabbott, Dinkelsbühl, 1951

I am grateful that the senior people at Oxford were somehow able to see past the callowness and brashness and to discern that I had the desire and potential for research work, despite my lack of self assurance and lacklustre performance in Finals.

Looking back on my early efforts at research at the Stazione Zoologica in Naples, I realize I worked on the scattergun principle, not really knowing why I was doing things half the time, trying things out for fun. I had bought the 11th edition of The Microtomists Vade Mecum, a recipe book full of ancient lore, and I wasted many a long day trying out obscure fixative and staining procedures. I suppose I learned some useful things in the process. Hope sprang eternal in my breast. I was inventive and indefatigable, much as I had been around the farm in Somerset. I did not seek guidance from people who could have guided me and I would probably not have gone along with their advice anyway. I wanted to do it all myself. I was finally, in a chaotic sort of way, in charge of my life.

My friends at Naples included Pierre and Ruth Tardent, Bob Allen (Robert Day Allen), Jane Westfall, David Arnold, Martin and Joyce Wells and Mike Bernhard. I tried to learn enough Italian to have normal conversations with Italians but ended up mostly hanging out with a circle of anglophones. Before Martin was joined by his wife Joyce, he and Mike and Jane and David and I would eat together in the evening, sometimes at Umberto's Pizzeria, sometimes in the lab where we cooked the octopuses left over from Martin's experiments on tactile sensitivity and learning. When Joyce arrived, she made it clear that these bachelor evenings had to cease, a shame really as I for one looked forward to them all day. I could not grasp that a recently married young couple would want to have their evening meals by themselves.

With Carlo Cognetti and Mike Bernhard, Naples, 1954

Mike Bernhard was five or six years older than me and had been in the Wehrmacht during the war despite being part-Jewish. He had that typically German cynicism and worldly-wise manner - he had seen it all and done it all and couldn't help being a bit patronizing with innocents like me

with our cloistered backgrounds who knew nothing of the real world. But he was generous and kind and helped me get started in photography, even giving me an old 35 mm single lens reflex camera, (a Praktiflex) which could be clamped on top of a microscope and he introduced me to the process of developing film and printing out the pictures. I greatly enjoyed the exercise of these simple skills and the (sometimes) beautiful images that resulted, so my career as a microscopist owes almost as much to Mike as to John Baker. It is still, in this era of confocal microscopy, my métier.

Marriage and move to Canada.

In my final undergraduate year at Oxford Gillian Faulkner and I became pals and (both somewhat distracted by the blossoming relationship) we sat our finals at the same time. Gilli was my first real girl friend. Visiting her at Somerville, I met her friends in that hothouse of femininity, Susan Brown, Susan Sharpe, Deborah Bosanquet, Xanthe Wakefield and others and a whole alluring new world of young women suddenly seemed to open up. How different from the world of men I had known at school and in the army. I wasn't sure what to make of it all.

When I went to Naples Gillian went to Yugoslavia to work on flatworm chromosomes and speciation in Lake Ohrid. She managed one visit to Naples while I was there and we went sightseeing to Pompeii and Paestum. She set the table in my lab for meals. We still have a tablecloth she brought me from Belgrade. The idea of eating on none-too-clean bare wood did not appeal to her then and does not now. Not long after returning to Oxford in 1954, we got married and lived happily ever after. We weren't very efficient at birth control and she got pregnant and never found the time to finish her D.Phil. (later however she got a doctorate in Art History). Alexander was born in August 1955 and Christina in August 1956, on the very day I defended my doctoral thesis.

As my thesis neared completion, we started thinking about jobs. There were positions advertized in various commonwealth countries and I applied for one in Nigeria. At the interview one of the examiners, Graham Cannon, asked me if I had tried a dye called chlorazol black. I had indeed tried it out along with almost everything else in Bolles Lee's handbook. I also happened to know Cannon was responsible for introducing it into microtechnique. When he asked me what I thought of it, I was honest and said it wasn't as good as Heidenhain's. He glowered but said nothing. Someone then asked me how I felt about teaching at a redbrick university. I had never heard this expression and said so to loud guffaws along the table. I went red in the face and stammered that I was not in the least prejudiced about provincial centres of learning. I must have come across as a complete stuck-up Oxonian prick. Nevertheless I was offered a position in Ibadan junior to the one I had applied for. In the meantime however I had heard about two openings in Canada.

The Fontaines in 1958

We were good friends with Arthur and Marion Fontaine, Canadians from McGill who were fellow graduate students in Zoology at Oxford, Marion doing copepods and Arthur ophiuroids. Arthur had feelers out for jobs in Canada and generously passed the information along to me. Arthur landed one in Victoria. I applied for jobs in Fredericton and Edmonton. The University of Alberta one came through. When I told Prof Hardy about this he was a bit taken aback - apparently he had something lined up for me at Plymouth. When I mentioned the word Alberta people either had blank faces or if they knew anything about it, they knew it as the place where the economic theories of C.H. Douglas were first put into practice. Implementation of "social credit" monetary theory included issuing "prosperity certificates" to Alberta residents. Known as "funny money" these now fetch high prices among collectors of curiosa. More guffaws, politely stifled, issued from my seniors when I told them I was going to Alberta.

Nevertheless, a job is a job, Alberta was the next-door province to British Columbia where my Vernon relatives lived (a mere two days drive by the route that follows the Big Bend of the Columbia river) and the pay sounded good ($3900 annually plus cost-of living bonus) so we decided to accept. Our family of four left Liverpool in the Saxonia in September 1955. On arriving in Montreal we got a tiny bedroom on the train to Edmonton and set off across the endless Canadian Shield and prairies, cheerless and bleak in wintry weather. Any apprehensions we may have had about life in Edmonton were soon dispelled by the warm welcome we got from our neighbours in the duplex housing reserved for new faculty members. Fran and Ian Sowton, friends from those days, are still close.

Ian and Fran Sowton

I will not say much here about our family life, as this is meant to be about my work as a zoologist. Suffice it to say we were blessed (and I mean blessed) with three more children, Richard (1957), Rachel (1959) and Quentin (1962). Though it didn't always seem like this at the time I had lucked out in coming to a job in a city which was just beginning to enter a period of phenomenal expansion. As our department grew, with the accumulation of more and more new teaching staff in junior positions, I found myself pushed up as if by the force of gravity to increasingly senior rank, becoming a full professor when I was 35 - the same year (1965) my Canadian citizenship came through.

In 1968, thanks again to the support of Arthur Fontaine, I got a job in Victoria, a beautiful city with an English type of climate, and we have lived here ever since.

'Leverage your strong points'

Play to your strengths. Being true to yourself is the only solid foundation on which to build a career. When you consider career development, avoid the tendency to focus only on weaknesses to the exclusion of your strengths. Instead, concentrate your efforts on work that gives you personal satisfaction while leveraging your strong points.

This is one of Deb Koen's strategies which I heartily endorse and have faithfully followed. She might have added that it is also the best way to make your professional life enjoyable. All jobs involve a certain amount of drudgery and things one would rather get out of but if a major part of it is enjoyable, you've got it made, and academic salaries, though paltry by some standards, are perfectly adequate for most normal people.

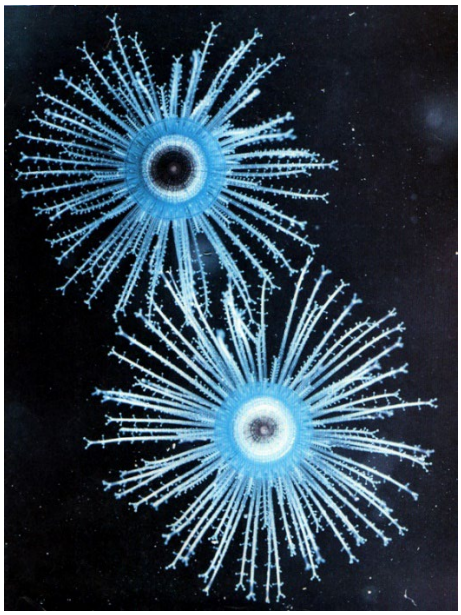
The work I did on siphonophores for my thesis continued to keep me busy off and on for years to come. My friends think of me as a jellyfish scientist, but my interests spread to encompass other groups, chief of which were ascidians, pelagic tunicates, ctenophores and finally hexactinellid sponges. Once I had become seriously involved with a group of animals I tended to keep coming back to it, even after lengthy periods working on other things. I was a serial polygamist who loves them all and I had casual dalliances with echiuroids, squid, echinoderm larvae and gastropod veligers. My friend Quentin Bone is another such person. His job at Plymouth, technically a civil service position, seems to have allowed him complete freedom to work on any of the wide range of animals and problems he is interested in and, like me, he has been able to retain lab space and to keep on working in his retirement years. This must be a luxury few people in government labs can enjoy.

Initially, from my Oxford days under the influence of William Holmes and John Baker, my work was almost entirely histological and I looked at animals and their behaviour from the viewpoint of a microscopist. This led me naturally into electron microscopy in the 1960's, but I was pulled increasingly in the direction of functional morphology. I wanted to understand how animals 'worked' in the sense of how their activities were produced by their nerves and muscles. While a strong grounding in histology was to prove a major asset in all my later work, often giving pointers about what to look for in the functional domain, electrophysiology was the key to analysing the underlying processes. Following my introduction to electrical recording techniques while working with Bob Josephson and Mac Passano during my first sabbatical leave in1963/4 and encouraged by the heady success in demonstrating epithelial conduction, I set about getting funding for neurophysiological equipment and learning how to use it. No one in our department in Edmonton did neurophysiology at the time and I didn't know enough electronics to make the special equipment I needed. The nearest I ever got to doing this was in 1963 on a visit to the Gatty Marine Lab in St Andrews where Adrian Horridge was Director. Adrian always knew exactly what other people should do, and he told me to start by making a radio. I got the bits and pieces and a little instruction book and made one. In fact, however, by the mid sixties neurophysiologists could buy most of the equipment they needed 'off the shelf' so knowing about circuitry except in the most superficial way wasn't as essential as it had been in previous decades. By 1968 I started

publishing independently in this area and the pattern of much of my future work was established as a mixture of histology, ultrastructure, electrophysiology and behavioural observations. After 1970 I stopped doing the tedious preparation work for electron microscopy myself, and worked collaboratively with others in this area, principally my former Ph.D student Chaman Singla who ran the EM lab, but I continued to work on many other things, keeping my hand in by working at the bench myself even through periods when I had heavy administrative duties. This meant that I was able to go on with primary research long after my official retirement in 1995, when I was back working on my own again. I was never a specialist per se of any one technique, nor of any one group of animals. I still think of myself as an invertebrate zoologist more than as a neurobiologist. In the following sections I will talk about the main things I have been interested in, and how my work fitted in with that of other people.

Syncytial nervous systems

An early product of my thesis work was my proposal that a subset of nerves in the chondrophores *Porpita* and *Velella* were interconnected in the form of a syncytium, that is, the nerves flowed into one another continuously without being separated by membrane barriers. This was based on what one of the two nerve nets looked like in silver impregnations using a technique developed by my supervisor, William Holmes. This came at a time when the 'contact versus continuity' debate, dating back 50 years to the famous controversy between Golgi and Cajal (who had attacked one another in their Nobel acceptance speeches) appeared to have been settled finally in favour of contact, with nerves making chemical synapses with one another but retaining their independence as separate cells. The picture for *Velella* was at odds with this paradigm and challenged the conclusions of C.F.A. Pantin whose work since 1935, culminating in his Croonian Lecture to the Royal Society in 1962 appeared to lay to rest all notions of syncytial connections in coelenterates, at any rate in sea anemones.



Porpita came floating by at Lanzarote

After emigrating to Canada, I got more specimens of *Velella* and *Porpita* sent to me and did some more preps. I sent in a paper (3) to the Quarterly Journal of Microscopical Science. The Editor, John Baker, wrote back to tell me I should insert a footnote saying that "ink had been added to the pictures", i.e. that I had retouched them to enhance the contrast! Instead of taking this as the roundabout compliment it was, I was outraged and hurt and promptly sent him my best slide to show him how wrong he was. I was hungry for recognition and for me the *Velella* work was my widow's mite, priced above rubies. Back in Oxford, Baker was impressed by the slide but then

instead of returning it he put it up on a shelf and forgot about it and was petulant and irritated at my repeated efforts to get him to look for it, but he eventually found it and sent it back. I may just add that Baker was fussy and irascible, but he took an interest in all of us and spotted me as a microscopist before I knew it myself.

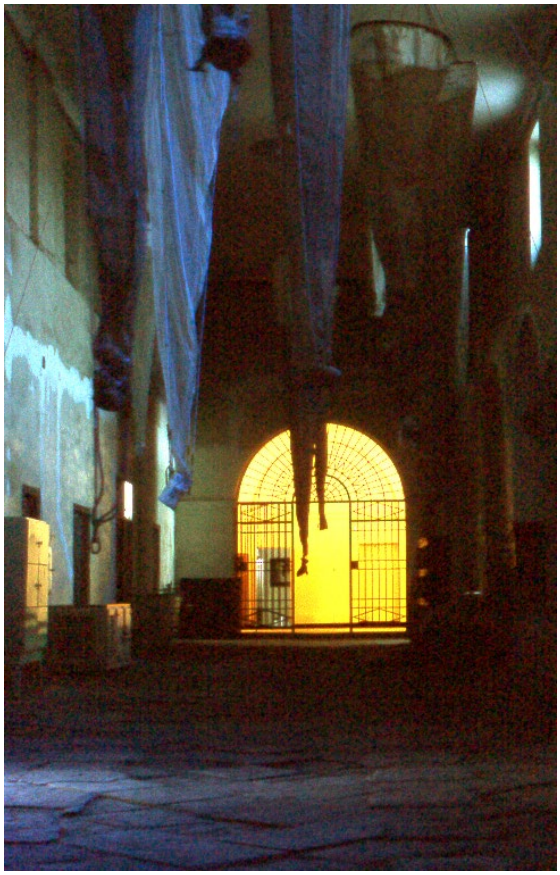
It subsequently turned out that there are a number of cases in both siphonophores and hydrozoan medusae where dyes injected into one neuron spread to others, either through the tiny aqueous channels of gap junctions or through open cytoplasmic bridges, showing that such systems are either syncytia or their functional equivalents. The picture for *Velella* itself is still slightly murky as the continuity may be due to gap junctions rather than open cytoplasmic bridges as I had supposed (gap junctions were unknown when I wrote that paper) but the continuity principle has since been validated in several other hydrozoan species. Systems where the neurons are dye-coupled and electrically-coupled act very much as if they were single, large syncytial cells. It seems very likely that multinucleate giant neurons found in *Aglantha* and elsewhere arose from such coupled groups of neurons, the final step being the complete breakdown of the intervening membranes. Giant neurons in *Aglantha* conduct at velocities up to 3m per second, many times faster than normal neurons, and they play a key role in escape behaviour (106), as discussed further below.

While hydrozoans are peculiar in having nerve nets in which the units are either fused into a syncytium or electrically coupled by gap junctions (which comes to much the same thing), they also have conventional, synaptically-interconnected systems, an arrangement that is the norm in sea anemones, as Pantin and his colleagues had shown. Thus, as far as coelenterates are concerned, the contact versus continuity issue was more or less laid to rest: both conditions existed in different groups.

Epithelial conduction

Ever since my doctoral work in Naples, I had suspected that siphonophores have a conduction pathway distinct from nerves but working in conjunction with them to transmit behavioural responses. Simple experiments of the sort carried out by G.J. Romanes in the previous century, convinced me that the exumbrellar epithelia covering the swimming bells of certain siphonophores must be capable of nerve-like conduction. My knowledge of the histology was crucial and gave me the confidence to believe what the experiments were telling me. I knew that nerves were absent because I could see them perfectly well where they were present, and I knew from simple behavioural tests that the layer conducted. Therefore, the epithelium had to be excitable. Later (1953) in the Canary Islands I worked on the Portuguese Man-of-War with A.K. Totton of the Natural History Museum. Here too there were places where it looked as if epithelia or epithelio-muscular sheets devoid of nerves were capable of conducting impulses. Similarly, in the siphonophore *Nanomia* which I started studying at Friday Harbor in 1961, it was impossible to explain the behavioural evidence without assuming that excitable epithelia were involved. But none of this was proof. Satisfactory proof of epithelial conduction called for electrophysiological evidence.

Entrance to the Station Zoologique, 1963 Capt.A.K.Totton and my wife Gillian.

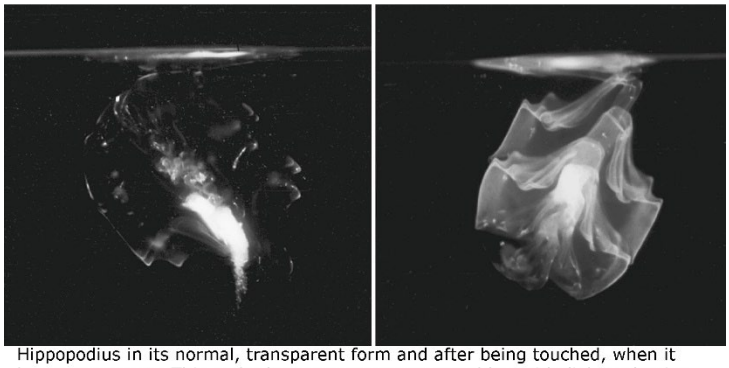


The great hall at the S.Z., with plankton nets hanging from the ceiling.

Grave of Octave Dubosq, prof at Montpellier, in the garden of the S.Z.. His student G. Tregouboff was the last Russian director of the station.

S.Z. 1975, my salad garden outside Stalle 41 where Quentin and I worked on *Pyrosoma.* Photo by my friend Yvette, femme de ménage.

In 1963/4 I went on sabbatical leave to the Station Zoologique, Villefranche-sur-Mer. A friend from Yale University, Mac Passano, was there at the same time and showed me how to carry out electrophysiological recordings using suction electrodes. Mac was primarily interested in the signals he was picking up from the nerve rings in hydromedusae and I worked along beside him but, when he had to go back to the States for a week to see about a job in Madison, he generously let me have the use of his equipment. This was organized around a large copper-lined, lidded box that served as a Faraday cage, whilst doubling as a packing case for transporting his amplifiers and manipulators. Using this rig and the suction electrodes we had made for recording from the nerve rings, I managed to get some crude recordings from several calycophoran siphonophores that proved that impulses did indeed propagate across the exumbrella (15). Ladd Prosser, who chaired the session of the meeting of the American Society of Zoologists where I presented this work, described the new work as 'revolutionary' though in fact there was a long history of speculation about "neuroid conduction" dating back to G.H. Parker and before. Siphonophores like *Hippopodius* continued for years to be the animals of choice for me, for exploring the multifarious behavioural roles of excitable epithelia and also the mechanisms underlying epithelial conduction. A highlight of this work came on my second sabbatical leave in 1974/5 when I was able to demonstrate gap junctions and electrical coupling between excitable epithelial cells and make a preliminary analysis of the ionic basis of the propagated electrical events (45). The ionic analysis was prompted by discussions with a Cambridge physiologist Robert Meech, who was at Villefranche at the same time, working on *Beroe*. He knew about channels and ion fluxes, and how to demonstrate calcium currents by blocking them with other divalent cations. Meeting Bob Meech was the best thing that ever happened in my working life – we were still working together when I finally quit work in 2008.



Hippopodius in its normal, transparent form and after being touched, when it becomes opaque. This and other responses are spread by epithelial conduction

The Station Zoologique was undoubtedly the most beautiful and interesting lab I have ever visited so I have put in a page of snapshots of it. The Eastern part of Provence had been part of the Duchy of Savoy since 1388 but this area, the County of Nice, was hotly disputed between the Holy Roman Empire to which Savoy was allied and the French. In the late 17th century, the area fell to the French but was returned to Savoy after the Peace of Utrecht (1713) and at the same time the Duke of Savoy regained his original possessions and received the Kingdom and the title of King of Sardinia.

The building itself was built in 1769 as a prison for the Sardinian Navy's galley slaves. In the main hall, where plankton nets were hung up to dry when we there in 1963/4, there are still iron rings in the floor to which the slaves were shackled. Quentin Bone tells me that the slaves were one of the sights of the grand tour. If not tipped enough they would shake a cloth with lice over the

visitor! In 1793, the French once again occupied Villefranche and the County of Nice became part of the Napoleonic Empire until 1814 when it was returned to the Kingdom of Sardinia by the Congress of Vienna. Finally, in 1860, it was given to France by treaty following a plebiscite. In the late 19th century the Russian Navy negotiated an agreement whereby Villefranche became its Mediterranean base and coaling station.

The remarkable richness of the plankton in the bay had fascinated zoologists since early in the nineteenth century. The mouth of the bay falls off rapidly into deep water (there is no continental shelf) and under certain wind and current conditions deep water plankton is brought to the surface. Péron, Fol, and Vogt all worked on this treasure trove and in 1850 Vogt suggested establishing a permanent marine lab there. It was not until 1884 however that Korotneff, Professor at the University of Kiev, established a marine laboratory in the old Sardinian prison building. Korotneff is one of my heroes for his pioneering work on siphonophores and his picture still hung in the entrance of the Station Zoologique when I was last there in the late 70s. Following the Russian revolution, the station ran into severe financial difficulties and in 1931 it was taken over by the University of Paris. The last Russian director Tregouboff, continued on until 1956, when Paul Bougis took over. I have a letter from Trebouboff in his elegant spidery handwriting about the best time to come for siphonophores, a link with the Russian past.

Aleksei Alekseevich Korotnev

Not only did the finding of excitable epithelia in siphonophores help to explain a great deal that had been mysterious about the behaviour of these animals, but it raised the question of whether non-nervous conduction was a factor in other groups of animals. Mac and I decided to team up and work together on jellyfish at Friday Harbor. We soon found that hydromedusae such as *Sarsia* also have excitable epithelia. Mac was primarily interested in the nervous organization of these animals, while I was keen on extending our understanding of excitable epithelia, but it all came together when we collaborated, as both conducting systems play their part in the production of behaviour. At almost the same time as my paper from the ASZ meeting came out, Alan Roberts in Bristol, working independently, validated an old idea put forward by Wintrebert that amphibian tadpoles have excitable skins at a stage before the innervation is established. I later found excitable epithelia in salps and doliolids and a good many other examples eventually came to light (P.A.V.Anderson 1980. Progr. Neurobiol. 15, 161-203). Quentin Bone, my partner in the work on pelagic tunicates, went on to find skin excitability in lungfish larvae, the only known example from fishes. These studies provided the groundwork for understanding the roles played by excitable epithelia in animal behaviour.

Epithelial, or non-nervous conduction is very important in the behaviour of some animal groups, but few new cases have come to light in recent years. For me, the most interesting of these is that of hexactinellid sponges. Nerves are absent in sponges, but transmission of electrical signals in non-nervous tissues through a trabecular network gives this group of sponges the ability to respond rapidly to external stimuli almost as if they had nerves. I will cover this later in a separate section, as it came to fruition much later in my working career.

Mac Passano, my partner in this early work at Villefranche, was a close friend and collaborator for several years in the '60s. We had first met at a conference in Miami in 1961 and hit it off right away. As we were saying goodbye, Mac said "George, this isn't the end, it's just the beginning". We teamed up during my sabbatical leave in 64/5 and later at Friday Harbor for several summers. During our work at Friday Harbor, Mac would sit absorbed watching the electrical signals marching across the oscilloscope screen and chart recorder while I handled the preparation, positioning the stimulating and recording electrodes and observing behavioural responses. I think this suited us both in some strange way. In the evenings we would meet with our wives and children in one of our cottages and more often than not I would haul out my guitar and we would sing folk songs. Mac had served in the US Army during the war as a forward spotter, identifying targets for artillery bombardment, and providing feedback by field telephone to the gunners to correct their aim- dangerous and distasteful work. Like most ex-servicemen who had seen combat, he rarely spoke of his war experiences. One of his favourite songs was Down by the Riverside which contains the line 'Ain't goin' to study war no more' (see final section below). These were very happy and productive years, memorable for all of us, halcyon days for our children who had friends among the visitors to the lab (some of whom came back every year, as we did). Taking the kids out of school in Canada meant that they had to go to school at Friday Harbor for a few weeks, where they made friends with children in the local community.

Mac and Kari Passano at Villefranche, 1964

Despite his name, Mac Passano is not a Chicago mafioso, but a New Englander from a distinguished Long Island family with a clipper Captain and whaling skippers in his ancestry. He himself has sailed a lot in the Caribbean and crossed the Atlantic in a small sailboat. With his interesting family history and his years at Harvard and Yale, he seemed when I first met him somehow a bit like one of us Oxbridge types. Before I knew him, I hadn't realized that there were such people in the USA and tended to look on Americans as a species apart, with sides to them that both fascinated and repelled. Now of course, having lived and worked a lot in the USA I can see how taken in I was by superficialities, and I was still hung up on English notions of class. At the same time I came to realize more and more that Canadians are different again, not just a sort of American who happen to live in Canada. It is easy for some of us British expats to feel at home

here in British Columbia in a way we would find difficult in the States, even in such havens as Friday Harbor, not so much because of the politics but because of deeper, hard to define, cultural differences. I have had job offers at one or two really good institutions in the USA but, largely for this reason, never quite managed to take the plunge. Gillian was probably more open-minded in this respect, she takes people as they come wherever she meets them and makes friends wherever she goes.

From aggregates to integrates: the problem of coloniality

The question which had initially intrigued me about siphonophores – how a colony of many different members can act like a single, well-coordinated individual - continued to interest me. After discovering the marine station at Friday Harbor, which I first visited in 1960 as a guest of Joe and Margaret Connell I spent more and more of my time working there, establishing a pattern of spring visits that lasted on and off for more than 40 years. This was where Libbie Hyman had seen 'Halistemma' (actually *Nanomia*) "dart about vigorously, often executing loop-the-loop curves" - my project for the Oxford Naples Scholarship when I was a graduate student. I had made little progress with it back then, but now at Friday Harbor things went better. I found that siphonophores such as *Nanomia* can swim both forwards and backwards in a coordinated manner. They do so by synchronously altering the direction of the water jets emitted from the mouths of their swimming bells (locomotory individuals). In some activities, the members of the colony turned out to be interconnected by nerves, but excitable epithelia provided conduction pathways for electrical signals controlling other activities (92)

I first described the *Nanomia* work in a general article about coloniality in which I struggled to make sense of the concept of individuality, the varieties of coloniality, and its adaptive advantages (9). In the case of highly polymorphic colonies like *Nanomia*, where different individuals are specialized for different functions, I argued that coloniality provided a way of escaping from the limitations of diploblastic tissue organization, allowing the colony to become a sort of superorganism in which the original individuals were converted into the equivalent of organs. Reading this stuff now, it seems rather naive. I am not much good at theorizing about biological principles, probably because I don't read enough of what other people have written. However, it got my foot in the door of what later emerged as an important debate centering around the ecological roles of clones and colonies, and their genetic significance as life history strategies.

In 1963 I worked with Bob Josephson at Woods Hole on coordination of Tubularia, a colonial hydroid, which opened my eyes to what one can learn from relatively simple electrophysiological techniques and also made me realize what an amateur, slapdash worker I was compared to Bob, who had been properly trained and grounded in the rigorous academic disciplines considered necessary in the USA for effective research. Nothing daunted and remembering what I had learned from Josephson and Passano, I plunged into electrophysiology on my own back in Alberta and eventually became quite adept at the basic techniques, and perhaps even more important, learned

how to interpret the recordings in terms of what was really going on in the animal. My now ingrained understanding of hydrozoan histology helped enormously and sometimes let me grasp the truth about what was going on more or less intuitively. Josephson used to say the animal is trying to tell you something, your job is to keep your ears open and listen to what it is trying to tell you. I think he got this adage from his supervisor Ted Bullock, the leading American comparative neurobiologist of his era. Anyway, I looked at a number of other colonial hydroids, bryozoans and tunicates. Tunicates were the most fascinating, as they include many colonial groups, - salps, doliolids, pyrosomes - and some ascidian species. In no case are the zooids (members of the colony) interconnected directly by nerves, but instead they have evolved novel and sometimes bizarre ways of coordinating their behaviour. A symposium on Modularity held at the Royal Society in 1985 allowed me to bring all this work together in one place and I tried to relate it to the work of the ecologists, though our approaches were poles apart (88).

With Bob and Ginnie Josephson, 1978

Ciliary control in invertebrates

One of the best things about the Friday Harbor Labs is the opportunities it provides to meet other visitors, young and old, typically in meals in the dining hall and at the popcorn socials, who work in other fields. It was in this way that I came to work with Richard Strathmann, then a University of Washington graduate student, after he told me that echinoderm larvae can arrest their cilia and stop swimming when touched. With Andrew Spencer, who was doing his Ph.D with me, we attached recording electrodes to echinopluteus larvae and were able to record electrical signals correlated with the ciliary arrests. When the animal was swimming normally there was no electrical activity (25). This was in 1969 and must have been one of the first times electrophysiology was done on an invertebrate larva. The pluteus larvae were only about a millimetre long but we got quite respectable patterns of potentials. Dick Strathmann later became a faculty member at the University of Washington and at the time of writing is Associate Director of the labs. His wife Megumi, also a biologist, plays the piano and for many years now we have met at their waterfront home on San Juan Island for musical evenings, usually with other players such as Claudia Mills(flute), Christiane Biermann (violin) and Alison Longley (oboe). Dick joins us for wine and snacks after we have played and we have interesting discussions about what's going on at the labs and in marine biology.

A year or two later something similar happened when Charles Galt, another UW grad student, told me about the ability of a pelagic tunicate *Oikopleura* to control its ciliary beating. In this case,

the cilia don't arrest but reverse their direction of beating. Again, we recorded patterns of electrical signals associated with changes in beat direction (29). An incidental observation made during these experiments was that the skin of *Oikopleura* appeared to be excitable producing 'skin impulses' when touched. Later, with Quentin Bone, I returned to this question and found excitable epithelia not only in *Oikopleura* but in ascidian larvae, salps and doliolids.

Chuck Galt and his wife and family were very much into the sixties things: weaving, bread-making, playing banjos, dulcimers and recorders etc. I eagerly embraced the music part and Gillian the baking and weaving. The Galts lent me a tenor recorder and this is how I got back into music, playing renaissance and Jacobean consort music. Later I got a viola da gamba which helped at the bass end. Transcriptions of polyphonic choral works by Palestrina, Victoria, Tallis and others are among the most satisfying additions to the recorder/viol repertory. Palestrina is still one of my favourite composers.

Once introduced to tunicates, I wanted to do more work on them. This was partly because they are not a mainstream group for neurobiologists and my tendency has always been to shun bandwagon animals and to explore dusty corners. Also, sea squirts like *Corella* could be collected off docks and floats all year round in Victoria, where we had moved in 1968. Jellyfish on the other hand are highly seasonal.

It turned out that *Corella* and other ascidians can control their ciliary beating. This was not a new finding- it had been reported several times, but we found we could monitor the arrests electrically with great ease and precision. Exploring the ciliary control pathways with Michael Sleigh and others resulted in a lengthy paper (38) based mainly on extracellular recordings but also including the first intracellular recordings of ciliary arrest potentials in any invertebrate, made by Dorothy Paul. Daphne Williams, another member of our team, was a very beautiful girl who looked just like the young Vivien Leigh but unfortunately she quit biology, became a lawyer and is now Deputy Minister of Agriculture in the BC government.

With Miles and Dorothy Paul and Gillian at the Hopkins Marine Lab, 1978

Dorothy Paul and Nancy Sherwood were two exceptional women and close associates who greatly affected the course of my scientific work. Both came to UVic as faculty wives, I found spaces for them in my lab, and both eventually got regular teaching positions in the department. Dorothy got us organized as a neurobiology group and we all

met with our students and others for 'neurolunch' once a week, and someone gave a talk on a current research topic of interest. Dorothy is a natural teacher and virtually single handed made me read a mass of literature I should have known about for years, so that eventually I could teach neurobiology myself. Nancy, an endocrinologist, got into molecular work sequencing neuropeptides and made a big name for herself in that field. I used some of the antibodies she and her students made and was able to elucidate aspects of tunicate sensory- and neurobiology as a result.

The upshot of our work on control of the branchial cilia in ascidians and gastropod larvae etc was to show that ciliary arrests in invertebrates work much the same as in ciliate protozoa, that arrest is the 'active' state resulting from an influx of calcium ions, that it is triggered by nervous input, and that during normal metachronal beating, the ciliated cells are not depolarized and show no transmembrane potential changes (contrary to an earlier report by Horridge). Later work with Stuart Arkett dealt with the innervation of the branchial cilia and central control pathways in *Corella* (100) and with ciliary control in gastropod larvae (43, 95).

All in all, I had as much fun with this useful but not particularly earthshaking research as with anything else I did.

Bioluminescence and 'special effects'

Many marine animals have evolved ways of changing what they look like by changing colour, emitting light etc. (Squids and octopuses are not the only ones that can change colour, though they do it much faster than most). Working at Friday Harbor in 1961 I noticed that the siphonophore *Nanomia* can expand and contract its pigment spots. These spots figured in all the 19th century literature and their distribution was often included in taxonomic descriptions, but it had never been understood that the spots are mobile and that the animals can change the way they look. When contracted the spots are barely visible, but expanded they break up the colony's outline and make it look like a cloud of separate scarlet points ("disruptive coloration") that might be mistaken for a swarm of microscopic crustaceans. Perhaps small fishes in search of food are lured into the siphonophore's reach by this device. At the time, this was the first case reported of colour change involving mobile chromatophores in a cnidarian (8). Interestingly, when I looked at the animals in a dark room at night, I saw flashes of light being emitted when the colony was a swimming. The pattern of coloured spots seen by day was rather like the pattern of tiny lights seen at night, though different organs were responsible for two effects. I called this 'self-mimicry'.

At Villefranche in 1964 Gillian and I studied another siphonophore *Hippopodius*. I was already familiar with this animal from Naples days. Prof Hardy had visited me there and was struck by the animal's ability to change from being transparent to opaque ("blanching"). At Villefranche we found that this opacification is due to the sudden appearance of light-scattering granules in the jelly layer just beneath the external epithelium (21). The granules appear out of nowhere, then fade away

again slowly. Blanching is set off by contact with other objects. We proposed that, by making the animal loom up suddenly as a large white object where previously it was virtually invisible, blanching served to dazzle or dismay interlopers that might otherwise come crashing in and damage the delicate surface layers. It would still be interesting to know how the granules appear and disappear. It seems likely the protein involved undergoes a configurational change. Knowing nothing about protein chemistry, I hadn't a clue how to follow this up and nor has anyone else looked at the process.

As with self-mimicry in *Nanomia*, the blanching seen by day is matched by bright waves of light at night, which doubtless serve the same purpose as a deterrent. There are parallels in certain squids. Those living in the photic zone produce a cloud of ink to retreat behind when scared while some living in deep, dark water produce a cloud of luminescent particles. In both cases, attackers are distracted, blinded, confused, while the squid escapes.

Fascinating though it was to look at these phenomena, the real payoff came when I was able to show that both blanching and bioluminescent responses in *Hippopodius* were set off by propagated waves of electrical impulses that spread across the animal's surface. It is the covering epithelium itself that conducts the impulses. This was the first clear case of an excitable epithelium in any member of the animal kingdom (15) and led to a lot of other work as described above (p.15).

When in Villefranche in 1975 I made frequent forays out into the bay in a tiny rowboat I had bought, which had to be registered with the port authorities and given a name. I named it the Maurice Bedot after a hydrozoan specialist who had worked at Villefranche. For some reason my French friends found this name hilarious but my French is not good enough for me to know why it seemed so funny. Equipped with a British Seagull ("The Best Outboard Motor in the World") the Bedot enabled me to collect plankton in the bay at times when the lab's fishermen were unavailable. By watching where the sea birds were clustered over the water you could often get a good idea where to go to look for deep water animals brought to the surface by local upwelling.

In my plankton hauls I sometimes found peculiar little box-like aggregates which turned out to be tetrazooid larvae of *Pyrosoma*. Adult pyrosomes are colonies of dozens of small zooids, all of which are capable of producing light, so when they all go off together the effect is dazzling. Colin Nicol says that they can be seen from on board a ship 100 metres away. The tetrazooids also light up and behave just like miniature adults but have the great advantage of small size, which means that their inside workings can be seen in great detail under the microscope. I attached recording electrodes to them and picked up ciliary arrests when they were touched- just like ascidians. When I did this in conjunction with a photocell to record light emission it turned out that the two responses always happened at the same time, in response to the same stimuli. This had never been seen before, because if you turn the lights off to observe the bioluminescence you can't see the cilia arrest, and if you look at them in the light you can see the arrests but not the light emission. The ciliary arrest response in ascidians (and presumably here too) is defensive, preventing the animal from ingesting unsuitable food particles or contaminated water. Presumably the light emission was also somehow defensive, but how?

Quentin Bone and I teamed up again in 1977 and went over it all again and got the same results. We suggested the following explanation. Each zooid in the colony has an eye, so can presumably

Teatime at Plymstock, 1980. Quentin and Susan Bone

see the light flashes given off by its neighbours. Indeed, we could show that zooids respond to an artificial flash by turning off their own cilia. The idea then is that anything which causes a defensive ciliary arrest in any part of the colony results also in light emission which is picked up by the other zooids successively, causing them to arrest their own cilia whilst simultaneously emitting light themselves, so a wave of light emission travels rapidly along the colony accompanied by a wave of ciliary arrest. In other words, these colonies, lacking direct nervous or excitable epithelial connections between the zooids, use a photic signal to set off a communal defensive response.

Back in Plymouth, Quentin cut sections of the light organ and found that the cells are full of luminescent bacteria. This is a unique case of symbiosis where the photogenic bacteria actually live inside the hosts cells- usually they lie outside. The superiority of the arrangement in *Pyrosoma* is that instead of emitting light all the time, the bacteria are under the animal's control and only emit light when suitably stimulated (54). We seem to be seeing here the beginnings of a process reminiscent of the way mitochondria and chloroplasts evolved from symbiotic associations with prokaryotes.

Midwater plankton work with Pisces IV submersible.

Anyone who works on marine planktonic animals in the lab must wonder constantly about the relevance of the behavioral patterns they observe to the life of the animals in the sea but not many of us have the chance to go down and look at deep sea animals in their natural environment. Such a chance came along for me the early '80s. A young Canadian postdoc, Verena Tunnicliffe, had recently arrived at the Institute of Ocean Sciences fresh from doing her Ph.D at Yale. Verena was looking for somewhere to live and she rented our guest cottage so we got to know her well and heard about her work. The I.O.S. was home at the time to the submersible Pisces IV. It had been used a bit by biologists but was mostly used for marine geological surveys, checking cables, retrieving oceanographic gear that had fallen overboard etc. Verena quickly realized that it held tremendous possibilities for studying the benthic and epilithic fauna of the deep-water fjords up the BC coast and embarked on a series of trailblazing studies that led later to work on hydrothermal vents and their extraordinary fauna. I joined her in one or two dives up the coast in Jervis and Bute inlets. As we went down I was astonished to see the stratification of the zooplankton- it was almost like a layer cake, each layer characterized by a different set of jellyfish, ctenophores, pteropods, crustaceans etc.

Lowering Pisces into the water for a dive to 700m in Jervis Inlet

After a while I discovered that I too (though not part of the I.O.S.) could get time on Pisces and her tender vessel, Pandora. There was no charge (though it cost the institute $12,000 a day) but the sub was underused and I suppose they needed to have it used in order to justify keeping it at Pat Bay. At any rate, Verena's many publications and a couple by me and Claudia Mills must have proved that it was being put to good use, because we continued to get free Pisces time for several years before it was finally moved to the East coast.

Verena Tunnicliffe, Brenda Burd and Max de Ceccatty in Knight Inlet

Claudia Mills

With Claudia, my other students and postdocs I organized a series of dives and simultaneous plankton net hauls aimed at answering questions about the reliability of observations made from submersibles- how closely did the counts made by different observers on the same dives agree? How accurately could we estimate numbers and densities? How closely did counts from visual observations agree with data from net hauls? Which species changed their vertical distribution over the 24 hour cycle? (71). Later, after many more dives in fjords up the BC coast and around Vancouver Island (35 in all) I had a pretty good overall idea of how some 20 readily identifiable members of the macroplankton community were distributed in relation to depth and light penetration (85).

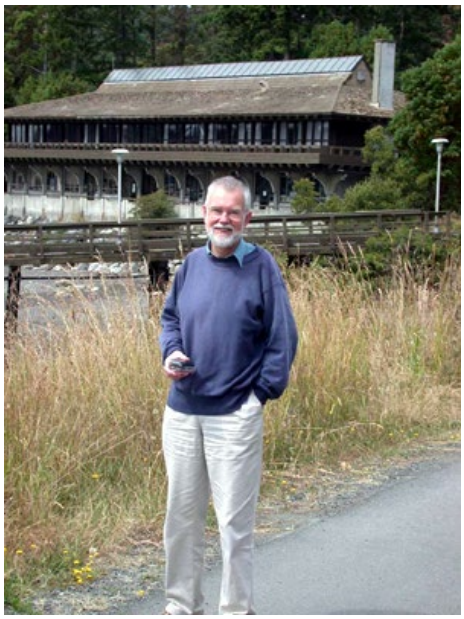
Giant axons

Following J.Z. Young's discovery (or rediscovery) of giant axons in squid, electrophysiologists realized that these enormous nerve cells make it possible to analyze the electrical and ionic events underlying the nerve impulse, hence the Hodgkin-Huxley model for the action potential. In 1972 I rediscovered the giant axons described by 19th century workers (and subsequently forgotten) that run in the stems of physonectid siphonophores and managed with some difficulty to get stable recordings from them with intracellular microelectrodes. I found that the axons conducted conventional, overshooting action potentials (34). These were the first intracellular recordings from nerves in a coelenterate. I went on to look at other siphonophores and found even larger giant axons conducting at up to 4m per second in Forskalia. Even some ctenophores proved to have giant axons (115). Like giant axons in other animals these huge cells invariably mediate escape behaviour. They consume a lot of space and must be metabolically expensive to maintain, but by reducing response time by even a few milliseconds they evidently proved worth their keep in the highly competitive world of the plankton.

A major breakthrough for us came in 1978 with the discovery of giant axons in the jellyfish *Aglantha* digitale. This came about by accident. I had asked Chaman Singla to cut some sections of this animal because it has very heavily ciliated tentacles (unusual in hydromedusae) and I wondered if it might be a ciliary-mucus feeder, creating water currents with the cilia and trapping food particles in mucus streams that were conveyed to the mouth in ciliated tracts on the conveyor-belt principle. This turned out not to be the case- no such tracts were present. Singla did however find structures running up the subumbrella that looked like giant axons. I investigated with microelectrodes and found that they conducted nerve impulses.

It happened that Alan Roberts from Bristol had a leave coming up and was planning a visit to our part of the world in 1978/9. I told him about the giant axons and we agreed to work on them.

Alan was an accomplished neurophysiologist and working with him was an eye-opener. I am good at finding interesting phenomena to work on but tend to be impatient and slapdash in following through. Working on *Aglantha* with Alan taught me to be more systematic and precise and not to jump to conclusions. We found that *Aglantha* has a rapid escape response superimposed on its normal 'slow' swimming pattern, and mediated by the giant axons. I enjoyed working with Alan not just because of the way his mind worked but because he had taken up baroque violin at the same time as I was learning the viola da gamba. Together with various friends we explored the world of early music.



Bob Meech at Friday Harbor Labs

The discovery of these remarkable axons obviously needed following up, and the ability to get electrodes into them meant we should be able to determine the cable constants and find out about the ionic currents responsible for propagated impulses, as well as recording intracellularly from both sides of neuromuscular junctions. Alan suggested I team up with someone who knew about ion channels and current analysis and suggested I contact Robert Meech, who had recently taken up a post at Bristol University. This was the best piece of advice I ever had. Bob Meech and I had already met at Villefranche and liked each other, and he agreed to come and work with our group on the giant axons, starting a collaboration that has lasted to the present day.

My student Patrick Kerfoot had noticed something odd when recording from the *Aglantha* giant axons while injecting them with markers to trace their connectivity patterns. He found that in addition to the rapidly propagating action potentials accompanying escape swimming, there was a second type of electrical potential resembling a large synaptic potential but seemingly able to spread along the axon from its presumed origin at the margin, being recordable further along than it "should" have been, given that such potentials are supposed to be non-propagative, decrementally spreading events. I investigated it further and found that it seemed to be associated with contractions of the swimming muscles and to "spread" all the way along the axon as far as the axon went. The potentials didn't look like any action potential I had ever come across and it never crossed my mind that these were action potentials. We already knew what the action potentials looked like, and they were quite different. I tried to explain the potentials in terms of a semi-regenerative process like putting booster stations along an oil pipe line.

When Bob Meech joined me at Friday Harbor in 1984, we were able to show that the small potentials in question depended on a calcium influx, whereas the fast action potential was based on sodium, and that the potentials conducted without decrement all the way along the axon. It was Bob who drew the logical (if seemingly impossible) conceptual conclusion. I still remember him

saying “George, I think they are calcium spikes”. This was an astonishing idea. All the conventional wisdom at the time said that nerves conduct only one kind of action potential and it is always sodium-based. Once we realized that we were dealing with two different action potentials conducted by the same nerve and using different ions, a lot of other things fell into place, most particularly the puzzling fact that the swimming muscles could apparently be excited in two different ways, enabling the animal to swim at two different speeds. The sodium spikes set off fast swimming and the calcium ones the slow (81). Bob’s name should have gone first on this paper but he wouldn’t let me put it there, and gave some spurious explanation about preferring an alphabetical arrangement.

From then on Bob took the lead in exploration of the ionic currents and channel analysis using voltage and patch clamp procedures, while I set about trying to unravel the central circuitry underlying the two sorts of swimming. Both tasks occupied us for a long and wonderful succession of summer collaborations at Friday Harbor, as the picture gradually built up to quite impressive proportions (143).

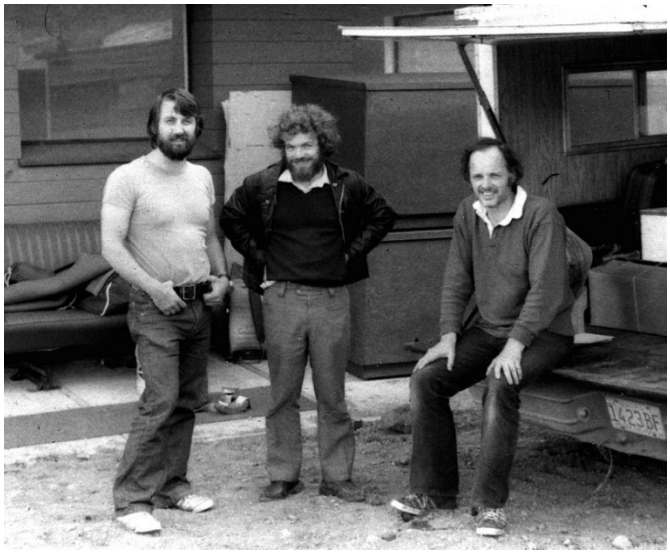
Bob Meech is a meticulous worker and, as with Alan Roberts and Bob Josephson, I learned much from him about being more careful, more cautious, less impatient, in a word more disciplined in the way I worked. For Gillian and me, he is one of our very best friends and we have many happy memories of visits with him and his wife Bonnie and their children. Bob and I have collaborated on sponges too, with trips to Bamfield to work there with Sally Leys, and we are still, as I write this on my 77th birthday, finalizing a chapter for a book to be published by Cold Spring Harbor Laboratory Press.

Impulse conduction in sponges

My interest in sponges goes back to my undergraduate days (1951) when I had to choose a topic for my essay for the Casberd Scholarship. I wrote about the question of whether sponges have a nervous system. William Holmes probably put me up to this. This meant boning up on the papers by a group of French workers, led by Max Pavans de Ceccatty. Max had done his doctoral work with Odette Tuzet and I believe that the idea that sponges have a nervous system originated with her, and Max pretty well had to go along with it. These workers explained the slow contractile responses of sponges like *Tethya* by pointing to *cellules du type nerveux* which they identified in histological preparations. I can’t remember what I said in my essay but it was evaluated and supported for the award by an outside reader, Peter Medawar, the most distinguished Oxford zoologist of his generation, who had recently moved to the University of London. In his appraisal, Medawar mentioned that I showed a tendency to “high class journalism”. I have tried to fight this tendency, though I still find it hard to write in the correct deadpan style. Getting the Casberd Schol was an intoxicating event, the first scholarship of any sort I had ever won, and it entitled me to wear the long scholar’s gown rather than the commoner’s bum-freezer. The long gown streamed grandly out behind when riding a bike but tended to get caught up in the chain and spokes.

The idea that sponges have a nervous system was pretty well demolished by W.C. Jones in 1962 (Biol. Rev. 37, 1-50) and faded from the scene, at any rate in the English-speaking world. I met Clifford Jones, an otherwise low-profile sponge biologist, in Bangor in 1995. He was pleasantly surprised when I, a complete stranger from across the Atlantic, arrived out of the blue and said he remembered the impact of his paper of 33 years previously. I caught a glimpse of his wife looking at him with blank eyed astonishment when I said that Clifford had 'blown the whole thing wide open'. I don't think it had ever struck her that her mild, soft-spoken husband had changed the way invertebrate workers all around the world think about an important topic.

In 1975-76 my colleague Arthur Fontaine went on sabbatical to Fiji and asked me to act as deputy-supervisor for his graduate student Gary Silver. Silver was a SCUBA diver and his project was to set up monitoring devices in the proximity of sponges to investigate their activities in the natural habitat in Barkley Sound, as others had done in the Caribbean. When I met with Silver to go over his results, he showed me a record of changes in water movement through a hexactinellid sponge. The sponge appeared to stop pumping periodically and then start again. He noticed that this was more likely to happen when a diver was in the region and could happen suddenly, the whole sponge turning off its feeding currents in less than a minute. Could the sponges somehow detect the presence of the diver? Such quick and complete responses looked most unspongelike, more like what you would expect from an animal with a nervous system. We decided to investigate this in the lab at Bamfield. Ian Lawn was there working on sea anemones and he had an electrophysiological setup in his room. Ian was officially my postdoc but was free to work on whatever he wished and he agreed to place his setup at our disposal and to join with us in looking at the sponge.



Bamfield Marine Station 1979, with Gary Silver and Ian Lawn

Luckily, the sponges were in a cooperative mood (they are not always, as we later found). We could induce pumping arrest by single electrical shocks. A shock at one end of the sponge caused cessation of pumping that spread rapidly through the animal and pumping stopped everywhere within a few seconds. Clearly, these sponges had a conduction system that worked on the all-or-nothing principle, and we could measure the conduction velocity and show that it had many of the characteristics associated with impulse propagation in nerve nets and excitable epithelia (66). This called for a thorough investigation of the structure of the sponge for which I enlisted Max Pavans de Ceccatty and Chaman Singla as collaborators. It turned out (as Ijima in 1901 had claimed) that hexactinellid

sponges are indeed unique in having a branching, ramifying tissue running through their bodies that is essentially a single cell with thousands of nuclei - a syncytium in fact. As there are no membrane barriers to be crossed, electrical impulses could in theory propagate freely in all directions throughout this reticulum as they do in giant axons. It seemed we had found our substitute nervous net but we could not yet record the impulses.

Following up on this initial discovery kept us busy for several years and I finally wrote it up while on sabbatical at the Hopkins Marine Station (72,73). One thing was still needed to complete the picture and to prove that the propagated events were really electrical impulses - we needed to get electrophysiological recordings. This proved frustratingly difficult, and many attempts with different sorts of electrode configurations came to naught. Finally, years later after we had almost given up, Sally Leys and I found a way to do it. I can't help thinking of this as the crowning achievement of my career, if only because I was two years into retirement when it was published.

With Sally Leys and Bob Meech, Bamfield, 1996

Sally was doing her doctoral work on aggregation of dissociated hexactinellid sponge tissues and she found that the dissociated tissues formed themselves into a more or less spherical ball which, seen under the electron microscope, was clearly a syncytium like the reticular tissue of the sponge it came from. We hit on the idea of getting these balls to reattach to the original sponge as grafts. It worked, and produced substantial patches of tissue on the sponge surface which were solid enough and big enough to allow attachment of recording electrodes and yet were part of the sponge in the functional sense, being syncytially connected to it. Big, beautiful, slow action potentials crossed the oscilloscope screen before our fascinated gaze when the sponge was turning off its feeding currents. Now at last we could record the impulses directly and everything fell into place (128). To get more information on the ionic basis of the impulses, Bob Meech joined us at Bamfield and we did the experiments that showed it to be a calcium-based event. (133).

This work was among the most satisfying I ever did, partly because I did it with people who were close personal friends, and partly because it was a completely new area we opened up, and one which attracted quite a lot of attention, influencing the way the whole field developed. Science and Nature published the two breakthrough papers, and specific aspects of the work came out in other notable journals, like the *Comptes Rendus* of the French Academy of Sciences, and the Philosophical Transactions of the Royal Society. As I write, a long review on hexactinellid sponge biology is in press with Advances in Marine Biology. Sally Leys, now a faculty member at the

University of Alberta, is first author. It's particularly satisfying for me that our work together helped launch her on what promises to be a terrific career.

Recognition

I was elected to the Royal Society of Canada in 1984 and to the Royal Society of London in 1991. The two Societies are quite separate institutions but both, as national academies for their respective countries, are highly prestigious. Getting elected to the RSC meant a great deal to me as it represented the collective judgement of some of the best biologists in Canada regarding the significance of my research work. What have we biologists got to show for our time on earth? A bunch of research publications and a few former students we have helped on their way. It doesn't sound like much but some of the students go on to do great things and the research papers go out into the world and are read by complete strangers in far off countries. After slogging away for years, one's work gets known and may start to influence the ideas and experiments of others. This is rewarding enough in itself and is the best kind of recognition. However, if fortune smiles on them, a few get elected to fellowships in our national academies. I know that luck enters into the election process from having served for three years on a selection committee of the RSC. The system efficiently filters out the weaker nominees but a lot of excellent ones remain and for the tiny percentage who get elected in any given year there is an equal number just as good who don't.

Gillian at Gairloch, 1963, mother of five.

All through the years of my research, from Naples to the present time I have had the good luck of having a loving and supportive wife and family. The fact that I have barely mentioned Gillian in this account doesn't mean her friendship, love and support were not critical to my getting so much done. In fact we helped each other career-wise as having a stable home base and ample resources meant she could study for her doctorate once the children had grown up and have a successful career as a scholar of late antique and early Christian iconography.

Television interviewers are fond of asking their subjects "how did you feel when…" hoping to get an emotional response out of them to liven up the interview. Trying this on myself, how did I feel when I heard from London that I had been elected a FRS? I felt an immense, simple satisfaction beyond all words. I felt simultaneously humbled, reassured and vindicated. I thought "my cup runneth over". I felt that although I had left England and made my career in Canada, abandoning my roots, my roots had not abandoned me. The umbilical cord was still intact. Added to this was the awesome prospect of belonging to an institution of such fame and grandeur, founded in 1660 and part of the pageant of English history, with its enormous prestige in the UK and beyond. I knew too that my work must have been subjected to careful, objective scrutiny by a succession of committees involved in the selection of new Fellows, proof that I really must have produced some first-rate stuff.

Gillian and I went to London, got rooms at the Society's premises at 6 Carlton House Terrace where, after a brief ceremony I was invited by the President to sign my name in the same old ledger that bears the signatures of Newton, Darwin, Leibniz, Franklin, Freud, Einstein, Watson and Crick. Wow!

In Canada there were heart-warming letters of congratulation from friends and from people who knew my work including some whose own achievements I most admired. Reporters phoned up to get something they could tell their readers about my work. A reporter for the Vancouver Sun asked me what drove me to do research. I told him "My work is my hobby. They pay me to do it. I would do it anyway." As soon as I said that, he thanked me and hung up – he had got his punch line.

Predestinate grooves and the songs we used to sing.

Adopt a healthful practice. Healthy habits are easily crushed under mounting workplace pressures. With sedentary roles and stressful environments, it's unlikely that your need for exercise, nutrition, spiritual renewal and relaxation will be met without conscious effort. Through meditation, a yoga class or a buddy system, embracing a healthful practice is essential to your overall development. (Deb Koen, hot strategy #7)

At the start of this essay, I quoted a line from the limerick:

There was a young man who said "Damn!
I perceive with regret that I am
But a creature that moves
In predestinate grooves
Not a bus, not a bus, but a tram."

While it can be argued that free will is an illusion, it is clear that as individual animals we are programmed to behave as if we have free will, and as social animals we have to take credit or blame for what we do in our lives.[3] Thus, we regret the lost opportunities, the myriad experiences passed by, and wonder what sort of people we would have become if, if, and if..., for we are only one of

[3] *The bells which toll for mankind are like the bells of Alpine cattle; they are attached to our own necks.* (P.B. Medawar in The Future of Man, 1959)

the many people we might have become, had things been only a tiny bit different. One can console oneself with the thought that it might have gone a lot worse, but still...

Coming to North America was an eye opener because it made me realize how trapped I was in the attitudes and prejudices of a young Englishman of my class. The classlessness and freedom here couldn't have been more different from what I was used to in the 'tight little island' I came from. No one here gave a damn about my accent so long as they could understand what I said. Just getting in the car and driving with the children to a gas station coffee shop for a pancake breakfast was a liberating experience. The coffee shops were warm and snug and there was a juke box terminal at each formica-topped table where for 25 cents you could punch in a pop song of your choice. The Beatles were in their heyday. I began to shed my snobbish aversion to popular music.

In early May every year while we were in Alberta I used to take a group of honours students in their final year on a field trip to the coast (about 1000 miles), to introduce them to marine life. Though very self-conscious, I am not inherently standoffish indeed, given half a chance, I am interested in other people's lives, and it was interesting getting to know the students as people rather than just as the objects I was required to teach. We weren't that far apart in age. The trip was an eye-opener for them too, and not just because of the marine life - many of them had never been out of Alberta. We would camp in snow at Fort MacLeod in southern Alberta one night and the next night after crossing the Crows Nest Pass we were into apple blossom country - Pend Oreille, Coeur d'Alene, in northern Idaho. The long drive across from Spokane to Anacortes brought home forcibly the vastness, complexity and diversity of this continent, and the relative insignificance of the little worlds we came from.

Some like my friend and Oxford contemporary Andrew Packard had adventurous lives with jobs in New Zealand, Edinburgh and Naples, expeditions to Antarctica, mountain climbing, running the mile in the same race with Roger Bannister, fluent in Italian and French with homes in both countries, and so on, and I have often wondered about all the alternate lives I missed by being channeled so precisely along one particular groove. Realization comes only after it is too late to do much about it. One is stuck with the person one has become, the job, the responsibilities, the family loyalties, and it is virtually impossible to throw it all over and go off and become someone else. The only way out is to experience these other worlds vicariously through books, poetry and music. This brings me to the songs we used to sing, which for me at any rate were a way of entering, however briefly, into the feelings and experiences of people in these other worlds and imagining myself as being a part of those worlds.

As I mentioned earlier, at Friday Harbor in the 1960s Mac Passano and I used to sing old American folk songs in the evening after the children were in bed, sometimes with other friends, and with a gallon of Guild Tavola and Olympia beer close at hand. Mac had a fine singing voice and I sang along with him in the choruses and played the guitar accompaniment. The women usually chatted in another room behind closed doors – I can't really blame them! I already knew many of these songs because of the folk song revival then in full swing with singers like Pete Seeger, Joan Baez and Jean Ritchie. Many of these singers were politically active and sang protest

songs about Vietnam as well as the traditional stuff, but I wasn't much interested in these. Politics and music don't really mix and Vietnam wasn't my problem. I just longed to escape into lost worlds of heroism, beauty, tragedy and despair, to live the lives of simple, poor people, people who despite their lack of education knew the full range of human emotion and somehow managed to express it with a force and pungency denied to the more sophisticated. Folk songs are where it all began – all music and all poetry. Nothing could be a better antidote to Oxonian exclusivity and snobbery.

Some of the best songs were Appalachian mountain songs. One from Arkansas was about *Old Blue*, the brave hunting dog who treed possums but grew old and died:

The doctor come and he come on the run
He says 'Old Blue, your huntin' is done'
Come on Blue, you good dog you.
Old Blue died and he died so hard
He dug up the ground all over the yard
Come on Blue, you good dog you.
Lowered him down with links of chain
Every link I did call his name
Come on Blue, you good dog you.

Then there was *Wake up, darlin' Corey*, about moonshine whisky and women:

Go 'way from me, darlin' Corey
Quit hangin' round my bed,
Pretty womens' run me distracted,
Corn liquor's killed me stone dead

The *Old Grey Goose* was another sad one:

Go tell Aunt Rhody (3 times)
The old grey goose is dead
The goslin's are cryin'
Because their mammy's dead

Then there was this lullaby from the Ozarks:

Hush, little baby, don't say a word,
Mama's gonna buy you a mockin' bird
And if that mockin' bird don't sing
Mama's gonna buy you a diamond ring… and so on. It ends up:
If that horse and cart fall down,
You'll still be the sweetest little baby in town.

I have the feeling that many of these old songs were written by lonely men in far off places:

I asked your mother for you
She told me you were too young
I wish to the Lord I'd never seen your face
I'm sorry you ever was born
Irene good night, good night Irene
I'll see you in my dreams.

(When it was just Mac and me I usually transposed the accompaniment to a key that suited male voices in our range. There are still scribbled notes in the songbook saying which keys worked best.)

Frog went a-courtin an' he did ride,
Um-hum
Sword and pistol by his side….
He took Miss Mousie on his knee
An' says 'Miss Mouse will you marry me?'
"Without my uncle Rat's consent
I wouldn't marry the Pres-i-dent."

With Mac Passano and Susan Schill, our baby sitter, at Sugar Lake, 1965.

Mac particularly liked some of the old songs from the mines and cotton fields, such as *Down by the Riverside* and *John Henry*. This was about a champion steel driver who hammered in the long steel bits on railway lines by the strength of his arm, but in the 1870s a mechanical steam drill was introduced. John Henry took on the steam drill, like chess-champion Kasparov and the IBM computer Deep Blue.

John Henry told his captain
'A man ain't nothin' but a man,
'Fo I let your steam drill beat me down
I'll die with this hammer in my hand, Lord, Lord
I'll die with this hammer in my hand."

By a stupendous feat of strength and endurance John Henry beat the steam drill, but it cost him his life. Kasparov won against Deep Blue and lived on but lost against its successor.

Cowboy songs from the old west were a rich source of folk melodies and often had a lilt to them that suggests jogging along in the saddle. *I'm a-ridin'Old Paint* is such a one

I'm a-ridin' old Paint, a-leadin' old Fan
I'm off to Montana for to throw the hoolihan…

Aaron Copland turned this song into something he called "Saturday Night Waltz" but nothing can destroy the beauty of the simple old folk melody.

Another western song we liked was *Black Jack Davy*. Black Jack won the heart of another man's wife and rode off with her. The husband came after them, but the woman had made her choice:

"Yes, I'll forsake my house and home,
Yes, I'll forsake my baby
And I'll do it all for the one I love,
To roam with the Black Jack Davy."

Some of our favourites dated from relatively recent times, though they often used older tunes, including many stemming from the British Isles. *Careless Love* is about abandonment. I can still hear that transitional chord leading down into the rueful conclusion: "You see what careless love will do".

Mac really let himself go in *St James Infirmary*:

I went down to the St James Infirm'ry
My baby, there she lay,
Laid out on a cold marble table
Well, I looked and I turned away.
'What is my baby's chances?'
I ask'd old Doctor Sharp,
'Boy, by six o'clock this evenin'
She'll be playin' her golden harp.'

Chorus - (here I too could let myself go):

Let her go, let her go, God bless her
Wherever she may be
She can hunt this wide world over,
But she'll never find a man like me.

The House of the Rising Sun is tear-jerker in a minor key

There is a house in New Orleans
They call the Rising Sun
It's been the ruin of many a poor girl
And me, O God, for one.

We really needed a woman to sing that one.

Nothing could be more different from the insipid Victorian ditties I had grown up with (*Drink to me only with thine eyes* etc) than these powerful, raw earthy songs from the mountains, cotton fields and urban ghettoes of America. I never threw the houlihan, I never rode off with anyone's wife, and I will not die with a hammer in my hand, but I can sense something of what those people were talking about as I have entered their worlds through the magic of their poetry and music.