Interview with Ernest Naylor

emeritus Professor, School of Ocean Sciences, Bangor University, Wales

by Tobias Kaiser, University of Vienna, Austria (October 2015/January 2016)

Ernest Naylor pioneered the study of circatidal clocks by demonstrating freerunning circatidal rhythms in individuals of the shore crab *Carcinus maenas*. He was born in 1931, did his PhD in Liverpool and held academic positions in Swansea, Port Erin (Liverpool) and Bangor.

Part I: The scientist Ernest Naylor

Tobias Kaiser: The major stages of your scientific career were your B.Sc. in Sheffield, your Ph.D. and D.Sc. in Liverpool, with academic positions in Swansea, Port Erin (Liverpool) and Bangor. I would like to highlight with you the formative landmarks of your scientific career.

In recent years, documenting scientific genealogies in terms of PhD or Postdoc supervisor relationships has become increasingly popular. To start with, who are your scientific parents? And who are your major scientific offspring?

Ernest Naylor: John S. Colman (author of *The Sea and its Mysteries*) lectured to me as an undergraduate at the University of Sheffield and was subsequently my PhD supervisor at the Port Erin Marine Biological Laboratory (University of Liverpool). I entered the field of Chronobiology *de novo,* after completion of my PhD and military service (Commissioned in the RAF Education Branch): I therefore have no Chronobiology antecedents. Among undergraduates that I have taught and PhD students and post-docs that I have supervised the following have published substantially in the Chronobiology literature: R.J.A. Atkinson, S.R.L. Bolt, P.K. Bregazzi, R.D. Hammond, M.H. Hastings, A.R. Hough, E. Hunter, K.S. Last,

E. Morgan, D.G. Reid, C.G. Warman, S.G. Webster, D.C. Wilcockson, Barbara G. Williams, J.A. Williams, and C. Zeng.

TK: When and where was your first contact with biology? At which point in your life did you make the decision to become a scientist?

EN: First contact with biology was in school, stimulated by a very good biology teacher. Conventionally, university fostered my curiosity and led me to consider a career in biological science. Lecture course work and field course work as an undergraduate focussed my aspiration to become a marine biologist, enhanced by a successful application to attend a UK national Marine Biology short course for undergraduates held at the Plymouth Marine Laboratory.

TK: Your dissertation dealt with taxonomy, life cycle and ecology of the isopods of the genus Idotea. Throughout your career you build a monumental body of work on various crustaceans. Was there a special reason for you to choose crustaceans as your objects of study?

EN: Undergraduate field courses on sea shores led to recognition of the diversity of some closely-related groups of crustaceans and the subtlety of differences of habitat that there are between one species and another, a theme which I was eventually able to publish on.

TK: You are known for having shown the endogenous nature of circatidal clocks, as well as many of their principal properties. Your interest in Chronobiology only started after your PhD. How and when did you get into the study of tidal rhythms?

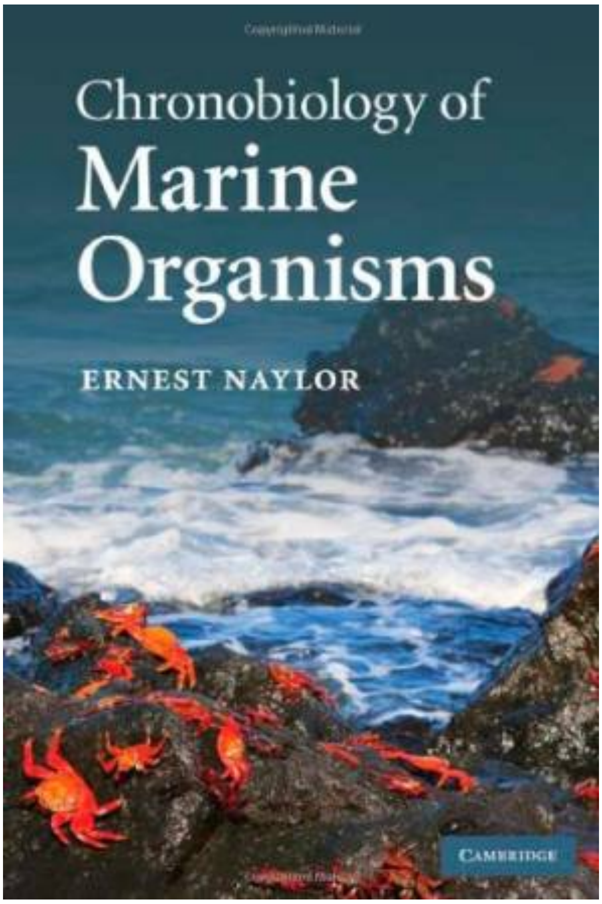
EN: On appointment to my first academic post in Swansea and reading in preparation for lectures I became aware of Frank Brown's provocative work suggesting that biological rhythms were controlled by "residual periodic variables". Many of the papers on biological rhythms at that time (mid-1950s) were based on questionable statistical analysis of bulked data and it seemed to me that it would be interesting to test for spontaneous rhythmicity in individual animals. I knew something of the biology of *Carcinus* (active at high tide and secretive at low tide, particularly during daytime) so a hypothesis could be proposed to test whether they continued with this kind of behaviour in controlled recording conditions in the laboratory. They did, and my first Chronobiology paper was born! I was particularly pleased with the outcome of these experiments since it allowed one to challenge the "residual periodic variables" hypothesis. The spontaneous tidal and daily rhythms faded after a few cycles in laboratory conditions and one would not expect that to happen if they were cued by cosmic cycles not under experimental control.

Part II: The history of (marine) Chronobiology

TK: Your reply makes the transition to the second subject that I would like to discuss with you – the history of Chronobiology and its major concepts. Chronobiology as a distinct discipline formed in the 1950s and 1960s. Today, Colin Pittendrigh, Jürgen Aschoff and Erwin Bünning are widely recognised as the founding fathers of Chronobiology and the Chronobiology Meeting at Cold Spring Harbour in 1960 seems to be a major reference point for many chronobiologists. What are your memories of these early days of the discipline?

EN: The pioneering studies of Pittendrigh, Aschoff and Bünning consolidated the endogenous nature of biological clocks and began to characterize some of their properties. I knew these authors only from exchange of reprints and I was not sufficiently established in the field to have participated in the Cold Spring Harbor symposium. Needless to say, however, the published proceedings became essential reading for me and for my students as I began to establish a group. The symposium was a milestone in the establishment of Chronobiology as a discipline.

TK: In these early days of Chronobiology, which approaches were taken to identify the substrates of the newly discovered endogenous biological clocks?



EN: Once it was established that clocks were truly endogenous, albeit phased by exogenous factors, our approach was to consider the problem to be a physiological one. Were the clocks neural phenomena or could they be isolated through the methodology of classical endocrinology? Was clock control hormonal and, by ablation and injection experiments, could its site be located at the organ or cellular level? Another approach that seemed important was to consider the life-style significance of the behavioural rhythms that we studied. Recognizing the difficulties of carrying out experiments to confirm that biological rhythmicity was of survival value, it has nevertheless always seemed to me to be important to consider the possible adaptive value of behavioural tidal rhythms.

At the same time it was being shown by other workers that circadian phenomena were highly persistent and emphasis was being placed on their physical characteristics, with terms such as “oscillator”, “transient”, “phase shift”, “phase response” etc. entering the terminology. All approaches eventually converged as in more recent years clock genes and molecular clock mechanisms came to be characterised, initially, particularly in insect circadian rhythms.

TK: In this context, it seems to me that in the early years of Chronobiology the different biological clocks – circatidal, circadian, circalunar and circannual – received almost equal scientific attention. Today the field focuses largely on circadian clocks. Is this due to the fact that the genetic and molecular basis only of circadian clocks is increasingly described? Or do you see other reasons, e.g. that non-circadian clocks do not seem relevant for human biology or medicine?

EN: Certainly there came to be increasing recognition of the relevance of Chronobiology in the fields of human biology and medicine, as well as in the fields of animal and plant cultivation, which probably contributed to the surge in studies of circadian rhythms and their molecular basis. In addition, however, it was also apparent that there were differences between circadian and circatidal rhythms, notably that circatidal rhythms were typically less persistent than circadian rhythms in constant conditions, which may have been discouraging for some potential investigators. Indeed, tidal, circasemilunar, circalunar and annual rhythms, eventually came to be regarded as “enigmatic”. Some reports of these “enigmatic” rhythms were often regarded as anecdotal and sometimes referred to as being in the “realms of mysticism”. This was a view which Carl Hauenschild sought to dispel as early as the Cold Spring Harbor Symposium in 1960 but it recurred beyond that time. Initially, too, circatidal rhythms were considered by some to be no more than paired circadian rhythms operating in antiphase.

TK: Possibly emanating from the “pre-eminence” of circadian clocks in Chronobiology, there are long-standing debates of whether circadian clocks are involved in seasonal timing (e.g. the “Bünning hypothesis”) and circalunar timing (e.g. the “beat hypothesis”), or whether the circadian and the circatidal oscillator may even be identical (circatidal rhythms being based on two circadian oscillators coupled in antiphase). In most cases, there is experimental evidence for and against these hypotheses. Only in recent years, molecular studies on Eurydice and Platynereis have shown that in these species the circatidal or circalunar clocks respectively keep ticking when the circadian clock is abolished. How do you see these long standing debates?

EN: I have argued for separate circatidal and circadian clockwork (against Palmer’s dual circadian clock hypothesis) and consider that recent molecular studies are confirming my interpretation. Moreover, studies by Ugolini, Wilcockson and others bring support to the interpretation of separate circalunar and circadian clocks, adding *Talitrus* to the supporting cast of *Eurydice* and *Platynereis* in the wider debate concerning moon-related and sun-related biological rhythms.

TK: Do you think there is a single circatidal clock or do you think nature has invented circatidal clocks repeatedly, based on different principles?
And do you expect circadian clocks to play a role in circannual and circalunar timing systems?

EN: Until further studies have been made the most economical hypothesis to work with is that common circatidal clockwork prevails. Also, I see it as reasonable to suppose from modern studies that circadian clockwork can have a role to play in circalunar and circannual timing mechanisms.

TK: When I think of the pioneers in the study of circatidal clocks, I think of Naylor, Enright and Palmer. When I do the same for circalunar clocks, I think of Bünning, Hauenschild and Neumann. Did I forget someone? What were the connections between the six (or more) of you?

EN: I am flattered to be included as one of your three pioneers of circatidal clocks. Jim Enright, Jack Palmer and I of course met at international meetings and I visited Jim's lab in the US for discussion and to give a seminar. Jack and I corresponded at times and probably met more frequently at meetings, including the first airing in Italy of our debate concerning circatidal/circadian v. dual circadian hypotheses.
My closest contact with the circalunar pioneers was with Dietrich Neumann. He visited my lab to talk with my students and to lecture. I visited him in Köln, and we regularly exchanged reprints and met at meetings. Incidentally, on a visit to Woods Hole I just missed seeing Frank Brown, one of the pioneers in the "exogenous/endogenous" debate, though I did see his recording facilities.

TK: In your eyes, what were the milestones in the study if circatidal and circalunar clocks?

EN: From my point of view the milestones in the circatidal and circalunar stories were when such rhythms were demonstrated unequivocally, without the use of questionable statistics, and in the context of the observed behaviour of the animals concerned in their natural environment. Full characterisation of the sites of the relevant clockwork must I think await further studies by molecular biologists.

TK: If you had to make a bet, what would you expect are the molecular or cellular substrates of circatidal and circalunar clocks?

EN: Such evidence as there is so far suggests that brain/neural tissue is the best bet.

Part III: Biology and beyond

TK: During your scientific career you have worked on a large number of different species. In contrast to that we see that currently molecular (Chrono)biology focuses on a small number of model species. Concerning a balance between the extremes of exploring the full range of diversity in biological systems and trying to extract the principles of biological systems from a small number of tractable model species, where do you see biological science today? And where do you think it should be?

EN: The reductionist approach is essential in elaborating the nature of a biological process. However, this approach should not exclude development of understanding of the lifestyle of the model organisms being studied. It seems to me that a holistic approach is critical if valid new questions are to be posed. Such an approach permits wider comparisons to be made which, with appropriate "model hopping", are able to lead to the development of general principles relating to biological systems.

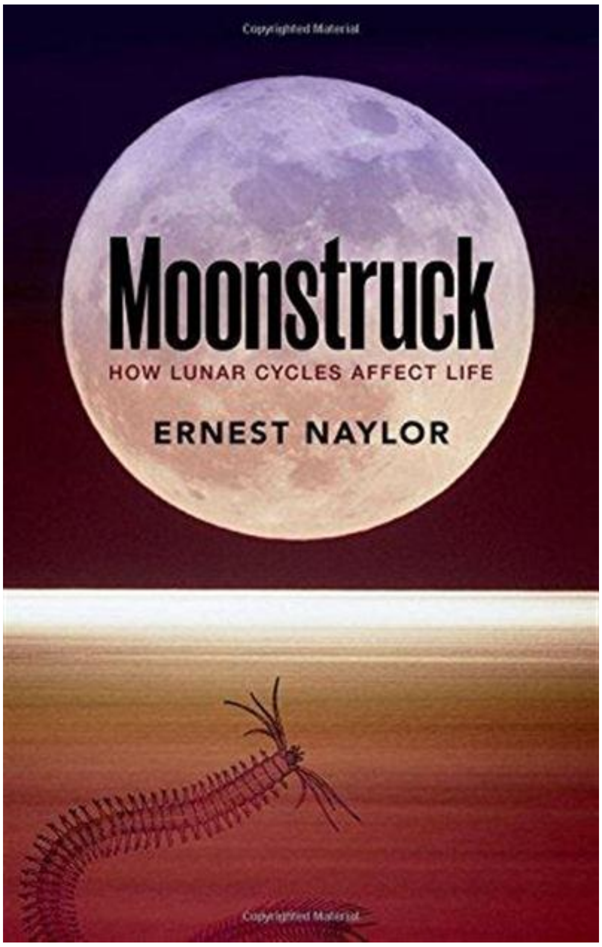
TK: In 2005 you published and article on the implications of Chronobiology for marine resource exploitation and management. Generally, there is increasing pressure for science to be economically or medically relevant. The value of "curiosity-driven" basic research seems to be less and less recognised. What is your position in this area of conflict?

EN: My research career, from Ph.D. days onwards, has been essentially "curiosity-driven" and it is the case that increasingly throughout that time funding pressure for "relevant" research has steadily increased. Clearly, where specific and tractable "relevant" problems can be identified, then attempts should be made to seek support for research with such aims, and I have on several occasions been successful with funding applications for "relevant" projects involving a Chronobiology approach. However, in my view, "blue skies" research should not be neglected by society. Such research fosters the spirit of scientific enquiry, which is essential since how else are new questions posed for "relevant" studies to be formulated?

In my 2005 paper that you refer to I was trying to emphasise that fundamental research had revealed how the Chronobiology of organisms should be taken into account when addressing issues of living resource exploitation, management and cultivation. In the same way, it was widely understood that correct synchronization of an organism's endogenous biological oscillators is fundamental to its optimal physiological performance and survival. Moreover, it had been demonstrated how Chronobiology has impacted on therapeutic application of medicinal drugs. In my view a society totally dependent upon applications-led research will eventually stifle original thought; some "blue skies" research should be afforded by society to foster creativity.

TK: You have recently published your first popular science book "Moonstruck", in which you attempt to bring into the public domain notions of circalunar and circatidal rhythms. What was your motivation to write a popular science book? Was part of it a feeling of responsibility of the scientist towards the general public? And if so, what defines this responsibility in your eyes: Educating the public? Justifying how the tax money was spent?

EN: The notions of inbuilt "biological clocks" and "circadian rhythms" are well established in the public domain, particularly as society has been able to test these notions "experimentally" as individuals move quickly between time zones during air travel. In contrast, it seemed that there was little general appreciation that there might be tidal and lunar clockwork in living organisms. I sought to enhance public appreciation of such phenomena against a perceived background of scepticism, which partly emanates from modern appraisal of ancient moon myths and legends. My motivation was less to do with a justification of expenditure of tax money and more to do with informing the public of discoveries of science that emerge from basic research in the field of Chronobiology. By implication, though, I hope that the book indicates aspects of such research in Chronobiology that have yielded new questions for Applied Science, thus highlighting the need for curiosity-driven and applications-led research to be advanced (and funded by society) in parallel.



TK: A third question on science and responsibility: As early as in the 1950s you discovered that species from southern latitudes can successfully reproduce in the Swansea docks, because the water there is warmed by a power station. Today, this finding seems like a prophetic piece on the effects of global warming. What do you think are the contributions science can make to the challenges of environmental change and nature conservation? Can or should science even set up protection agendas or its own protection initiatives?

EN: I think the role of science is to provide data and interpretations of those data for decision making at the political level of society. For scientists to seek to establish executive agencies, other than through the political process, would be counterproductive.

TK: You are now looking back onto more than 60 years in science. Has the profession of the scientist changed over these years? If so, in which respects did it change?

EN: As a graduate student in the early 1950s I had considerable independence to pursue curiosity driven research (not in Chronobiology!) and I was sole author of the six publications emanating from my Ph.D. thesis. Subsequently in UK it has become increasingly the case that proposed doctoral thesis projects, like major research proposals, are assessed by grant agencies, some of which are directive in their funding. Graduate students, too, often work in the group of a project leader who has appropriate equipment and grant funding. The best students succeed eminently in such structured groups but the breadth of enquiry, more widely in science, could be affected by such funding models if blue skies projects were not also funded.

TK: If you had to make a recommendation to students of biology, deciding to pursue a scientific career, what would it be?

EN: My recommendation to biology students has always been as follows: If you have motivation and aspiration for a subject such as medicine or veterinary science, then pursue that aim. If not, avoid a fashionable course that you think might lead to a job if you are unsure whether you will enjoy that course. In that case it is better to pursue a subject that you are interested in and excited about. In that way you will obtain the best qualifications that you are capable of and you will be in the best situation possible for you to seek employment of your choosing after graduation.

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