Book Review

Advances in Littorinid Biology. Proceedings of the Fourth International Symposium on Littorinid Biology, Roscoff, France 1995

Editors P.J. Mill and C.D. McQuaid
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Littorinids are abundant world-wide, often very common, and frequently occur in the upper zones of intertidal shores. They also exhibit a wide range of life history patterns, and many species are polymorphic. These characteristics make them ideal targets for addressing a wide range of ecological, evolutionary and practical problems, and they have attracted considerable attention from researchers. This is evidenced by a succession of international symposia devoted to the group. The all-encompassing title of the fourth symposium, *Advances in Littorinid Biology*, reflects the considerable range of research fields covered by the 20 papers drawn together in the proceedings.

Broadly speaking, the papers fall into six groups, dealing respectively with morphology, shell shape, physiology, pollution, genetics and ecology. Two of the papers have a purely morphological slant. The first, by Uthe, deals with the structure of the larval cephalic sensory organ as revealed by transmission and scanning electron microscopy. While presenting a detailed description, the paper presents no concrete evidence of the function of this organ, other than to suggest rather vaguely that it may serve in chemoreception. The second morphological paper, by Mak, describes the structure of the egg capsules of five species of littorinids from Hong Kong and shows that they are sufficiently distinct to be used as taxonomic characters. All five species are, however, relatively easily distinguished by their shells, so this finding does not revolutionise taxonomic methods for distinguishing these species.

No less than five papers concern shell shape and its variation; a topic that has long fascinated littorinologists because of the considerable variation within many species. Clines of shell shape are described by Mill and Grahame for *Littorina saxatilis* in Britain, although no reasons are suggested for these. In a paper by Fletcher, differences in shell strength are demonstrated for *L. mariae* and *L. obtusata*, the former being stronger. Shell strength tends to increase down-shore. In *L. mariae* it declines as wave action increases (an effect often attributed to low intensities of predation in wave-beaten areas) but in *L. obtusata* the opposite pattern is exhibited. The rather banal conclusion is drawn that shell strength is explained mainly by the weight of the shell (i.e., its thickness). Britton describes how shell ornamentation varies with size in *L. striata*, small individuals being more nodular and occurring on basaltic rocks that reach high surface temperatures. As an explanation, nodular texturing is assumed (but not demonstrated) to increase re-radiation. On the other hand, nodular shells lose water faster during desiccation than do striate shells, albeit at a very low rate compared with most other species. Extreme morphological variations of shell shape are described by Lewis and Williams for *L. obtusata* from Britain and Iceland, but parallel genetic analyses show all variants to be extremely similar – to a level at which they must be considered conspecific even although the Icelandic forms are sometimes regarded as a separate species. A final paper in this group, by Caley *et al.*, compares shell shape in a large sample of the species complex called 'rough periwinkles' from various parts of Europe, Britain, Iceland and the East Coast of America, and shows that even with large shells an accuracy of only 88% can be achieved in their classification on the basis of shell measurements.

Four papers deal with different aspects of physiology. A particularly stimulating paper is that by McMahon *et al.* on metabolic temperature compensation, which concludes that *Littorina saxatilis* and *L. obtusata* fail to show any acclimation when exposed to different temperatures. Pointing out that this may be a general pattern in littorinids, the authors go on to argue that this is perfectly understandable, given the extensive diurnal temperature range to which high-shore littorinids are subjected. However, they do describe how these species can undertake a near-instantaneous suppression of metabolic rate and enter diapause at high temperatures, thus offsetting the thermal stresses attending their environment. Two papers deal with nitrogen excretion, one by Aldridge *et al.* demonstrating a lack of temperature acclimation, and the other by Smith *et al.* showing that uric acid production varies with shore level and that this pattern is phenotypic. A fourth paper, by Davies and Hutchinson, shows that X-ray microanalysis reveals calcium carbonate crystals in the mucous trails of three species (the first documentation for marine species), but notes that the quantities are too small to play a role in calcium regulation.

Pollution formed the focus of three papers. Bauer *et al.* show that tributyltin (TBT) causes malformations of the oviduct, leading to sterilisation, and that an index of this effect can be correlated directly with TBT load. Huet *et al.* describe imposex in three prosobranchs related to TBT, and Calvo-Ugarteburu *et al.* examine changes in planimetric measures of the digestive epithelium as an index of stress, concluding that some measures need to be discarded because they are influenced by reproductive condition, but that others remain valid indicators.

Somewhat surprisingly, genetic analyses formed the heart of only a single paper, by Zaslavskaya, who used allozyme comparisons to assign four Russian species to subgenera, and to recognise a previously unidentified species.

Five papers had an ecological or evolutionary ring to them. Hughes presents a little gem of a paper (is it coincidence that it was the opening paper?), which applies life-history theory to a comparison of populations, ecotypes and siblings of 'rough periwinkles'. After eliminating the effects of body size, he was able to show no differences in trade-offs between resource allocation or reproductive effort. However, life histories could be related to habitat. A shift from primitive oviparity to ovoviviparity led to colonisation of salt-marshes, estuaries and pebble beaches, all habitats too hazardous for naked egg masses. Similarly, a shift from a perennial to an

annual life history is linked to the small size necessary for the occupation of empty barnacle shells. These changes in life history attributes are thus associated with a broadening of habitats available to littorinids. This still leaves unexplained why oviparous forms should persist in the face of presumed competition with ovoviviparous forms.

Another ecological paper, by Williams, describes differences in zonation between *L. rnariae* and *L. obtusata* and demonstrates that they are at least partly determined by active movements. Animals transplanted into the 'wrong' zones migrated back to their normal zones, possibly influenced by the presence of their respective host algae. Takada describes down-shore migration of *L. brevicula* in winter (the period when breeding takes place). The interest in this paper lies in the fact that only part of the population migrates down-shore, so that assortative mating occurs between the migrants and the animals that remain in the high-shore. Sexual selection is demonstrated in a paper by Rolán-Alvarez *et al.* dealing with the strikingly polymorphic *L. saxatilis*, which has an ornamented and banded upper-shore form and a smooth unbanded lower-shore form. Mating between the two is non-random, and sexual selection against intermediate (hybrid) forms further limits gene flow between the morphs. Finally, Johannesson and Johannesson describe how they capitalised on the local extinction of *L. saxatilis* by a dense bloom of toxic flagellates to explore how long recolonisation takes in a species that lacks any pelagic larval stage. They show that populations on larger islands were reduced to extremely low levels (< 1%) but recovered in 2–4 years, but those on small islands were completely wiped out and it may take up to 33 years for them to be completely recolonised.

My overall impression of these symposium proceedings was one of disappointment. On the one hand, the editors have done a good job of quickly and efficiently handling the papers and arranging publication soon after the symposium. On the other hand, I felt that many of the papers lacked challenging conceptual content, and there was little feeling of cohesion between the papers. They were just an assemblage of papers on littorinids (even to the extent that there is no index for the volume). One gets no feeling that the symposium generated any synergy. No clear themes run through the proceedings, and there is no sense of 'what have we learnt, and where are we going?'. I also had to wince at the price. Converting from Dollars or Pounds to Rands doesn't help, but one has to query whether a price of over R600 is justified, particularly as this book is being reprinted from *Hydrobiologia* Vol. 309.

G.M. BRANCH
Zoology Department, University of Cape Town.