BIODIVERSITY AND FUNCTIONALITY OF AQUATIC ECOSYSTEMS

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Summary

Life evolved in aquatic ecosystems and the marine environment has been stable and better buffered against environmental change than terrestrial systems. It is therefore not surprising that marine ecosystems contain areas of high biodiversity and abundance. However, the theories that have been derived to explain the relationship between ecosystem function and biodiversity have largely been developed through work of a terrestrial nature. In recent years this bias is being reversed and more aquatic scientist are working in freshwater, transitional and marine environments to examine the generic applicability of diversity/functionality relationships. In some ways, these scientists are at an advantage to their terrestrial colleagues in that it is arguably more realistic to establish short-term experimental systems under aquatic conditions than in air. In addition, metrics of ecosystem function are often easier to record in water than in air. This short review introduces some of the advances made using aquatic models but considers some of the limitations inherent in such work and provides an indication of the challenges to come.

1. Why research on aquatic systems has lagged behind

The life form and functionality of aquatic organisms varies from terrestrial forms principally because of the physical and dynamic implications of life in an aquatic medium. Terrestrial life evolved in aquatic environments and invaded land. In doing so, organisms adapted to a "dry" existence although dependence on water is still manifest in the life cycle of terrestrial organisms. As terrestrial organisms ourselves, it is not surprising that the study of the biodiversity/functionality relationship of terrestrial systems has outstripped that of aquatic systems. However, it can be argued from an evolutionary (the origin of life and the establishment of an oxygenic atmosphere), spatial distribution (surface coverage or volume), or functional role (carbon fixation, nutrient recycling) perspective that the aquatic habitat is of more global importance than the terrestrial one. The mechanisms that drive the functionality of aquatic systems are also different in scale to those of terrestrial systems. Water is a much more viscous medium than air and this has important implications for biogeochemical processes and organismal behavior. Transport processes lean towards the inertial and are thus more likely to be governed by advection rather than diffusion over any significant distances, and this establishes processes that show rapid (advective) exchange rates, supports the development of steep physical and chemical gradients and rapid biological processing. The ecosystem services provided by aquatic systems are well-recognized and are central to the global biogeochemical balance. This fact has always provided impetus to the study of aquatic ecosystem dynamics but these studies now attempt to incorporate socio-economic as well as ecological values. This has led to the concept of ecosystem services and a more widespread recognition of the "value" that humankind "obtains" from the natural cycling, or functionality, of biological systems. The economic valuation of ecosystem services is keenly contested (Pagioloa *et al* 2004) but the figures that arise serve to emphasize the relative importance of aquatic ecosystem services. The importance of aquatic systems on a global scale is unarguable and understanding the interplay between the organisms that inhabit this system and the ecosystem service they provide is an intellectually challenging and important consideration. However, the strategies used to conserve and protect habitats may vary between terrestrial and aquatic systems. Improved understanding of the functionality/diversity relationship in aquatic systems will contribute toward sensible conservation and/or sustainable exploitation strategies. The purpose of this short review is to highlight research questions and approaches to the understanding of the diversity/functionality relationship as applied to aquatic ecosystems.

2. The nature of aquatic habitats

The major subdivision of aquatic habitats is based on the salinity of the medium. This gives rise to three major aquatic habitat types: Fresh water systems, transitional and brackish waters, and marine systems. Fresh water is defined as having a salinity of less than 0.5 while sea water is generally regarded as having a salinity of >30 but these definitions are narrow and open to regional interpretation. For example, the Baltic Sea is an enclosed water body with a limited connection to the North Sea via a narrow sound between Denmark and Sweden. Salinity is often below 30 and the environment could be regarded as brackish rather than marine although in many other ways the system is more like a sea than a brackish lake. Marine systems are generally considered to show higher levels of biodiversity than freshwater systems which are in turn more diverse than transitional (brackish) waters. This is an expression of the well-known Remane's curve (Figure 1). The use of salinity as an axis here is debatable and this curve may obscure more complex analysis of the system involved. The reduction in biodiversity for transitional systems is usually explained through the physiological problems of living where salinity varies on a regular (tidal) basis but this is now recognized as too simplistic. The restricted nature of the habitat, the relatively short geological life span of transitional waters and the unstable nature of the substratum may be equally if not more important than salinity *per se* as a first order parameter controlling biodiversity.

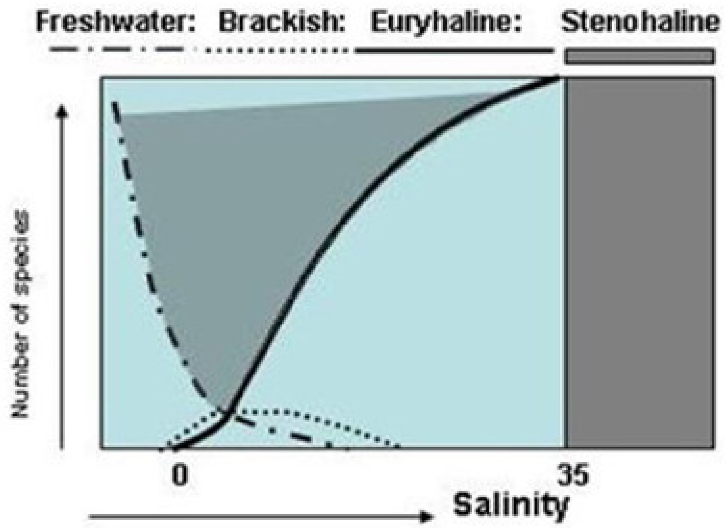

Figure 1. Schematic representation of Remane's curve. The number of species is plotted against salinity and shows a region of reduced diversity (grey shaded area) where fresh water and sea water meet. These "transitional waters" are often considered to be depauperate.

2.1. Fresh water ecosystems

Fresh waters are usually divided into standing (lentic) systems with no overall direction displacement of the medium and flowing (lotic) system where there is a measurable and consistent directional flow. A recurrent question concerning the biodiversity of freshwaters is why the number of freshwater species is relatively low in comparison to marine systems. A number of suggestions have been put forward (Moss 1998) including:

- The directional flow acting as a barrier to species migration and colonization;
- The relative variability of physicochemical conditions in freshwaters, and
- Relative geological youth of freshwater systems

The first and second possibilities seem unlikely but the final possibility has some support (Moss 1998). Circumstantial evidence of the importance of geological age in the evolution of specialist forms, and therefore the increase in speciation is given in circumstances where freshwater systems are known to have an extended geological stability. Examples of "ancient lakes" are commonly cited: Lake Chilwa (Malawi) and Lake Baikal (Russia). These systems have a long geological record and harbor endemic species showing evidence of specialization and unexpectedly high diversity.

2.2. Marine ecosystems

Marine systems have been stable for far longer than most terrestrial systems and some show extremely high levels of biodiversity with typical examples being coral reef systems and seagrass meadows. However, most marine habitats are relatively poorly studied simply because of the difficulty in sampling the deep systems which comprise the vast majority of the marine system. The relative heterogeneity of habitat in marine systems, geological age, volume and therefore buffering capacity has allowed the diversification and maintenance of varied biological forms. As sampling methods have improved there has been a re-interpretation of deep sea, and even coastal biodiversity but the actual level of biodiversity to be found in the ocean is a matter of debate.

2.3. Transitional waters

Transitional waters are often restricted in diversity as a result of a combination of factors but young geological age and high frequency of disturbance and physiological stress are probably especially influential. The ecosystem services that arise include storage of sediment, flood defense and storm buffering, maintenance of water quality and support of coastal and marine food chains. While the systems are considered depauperate, however, many organisms have become adapted to either reside permanently in transitional system or exploit them at certain stages of their life cycle (e.g. juvenile fish). In addition not all functional groups are depauperate. Many surveys neglect the smaller organisms that exploit the available resources under conditions where competition from larger forms is restricted by the physical setting (shear and drag). A high diversity of cryptic consumers are found among the meiofauna associated with the surface sediments while the role of primary producer falls to the microphytobenthos (unicellular algae) which show a wide variety of forms, several hundreds of species coexisting in one system (see Figure 2).

Figure 2. Light micrographs and sketches showing some of the diversity of

microphytobenthos in a small sample of the surface of intertidal cohesive sediment. Eight different species of diatom are shown with varying morphological features but similar functional roles.

This varied group of microbial eukaryotes have been used to investigate simple biodiversity/functionality questions in ecology and ecosystem response (Defew et al. 2002, Hagerthey et al. 2002). These cryptic forms highlight the problem that research on "biodiversity" rarely concerns the total diversity of the system but is usually biodiversity in the "eye of the beholder" (Bengtsson, 1998). This particularly applies as organism become smaller and more cryptic: for example the meiofauna; protista; bacteria; and viruses, of which we know very little in terms of overall distribution and abundance. This remains a major challenge in terms of biodiversity research.

A second advantage of aquatic ecosystems is that assemblages are often more malleable and open to experimental manipulation. This applies to soft sediment deposits as well as benthic sessile systems and many advances are now being made using field manipulation of natural assemblages. Scale relationships in these systems are still problematic and interpretation of such experiments requires recognition of such limitations.

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Biographical Sketch

Prof David M. Paterson holds a personal chair in Coastal Ecology at the University of St Andrews with 20 years of experience in research on coastal systems. His PhD at Bath University (UK) concerned the non-target effects of herbicides in aquatic systems. From Bath, he moved to the School of Biology at Bristol University in 1984 as a Post-doctoral Associate to examine the influence of microphytobenthos on cohesive sediment dynamics. At Bristol, he developed novel ways of examining sediment stability in the laboratory and field, and also the structure of transient biofilms on intertidal sediments (low-temperature scanning electron microscopy). In 1988 he was awarded a Royal Society Research Fellowship which he held at Bristol for 5 years before moving to St Andrews University as a lecturer. Here he established the Sediment Ecology Research Group (SERG) and continued his work on the dynamics and ecology of intertidal systems. He was promoted to Reader in 1996 and to a Chair in Coastal Ecology in 2000. SERG now has a strong record of national and international funding, innovation and scholarship in coastal science. Professor Paterson has specialised in interdisciplinary research at the interface between sedimentology, hydrodynamics and biology and has coordinated a number of successful interdisciplinary projects (EU and National). He has 90 full publications and three edited books. His experience encompasses: the investigation of biodiversity/ecosystem effects in depauperate systems; physical/biological coupling in coastal system particularly the phenomena of bio-stabilisation and bioturbation; and the structure and function of microbial mats. Recent initiatives include the use of remote sensing in the study of estuarine systems, the use of fluorescence techniques to measure aspects of microbial photo-physiology under field conditions, and the study of living stromatolite systems

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