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Paradigms in estuarine ecology – A review of the Remane diagram with a suggested revised model for estuaries

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ABSTRACT

Most estuarine ecology textbooks have included the so-called Remane diagram which is derived from German studies in the Baltic Sea region during the early part of the 20th Century. The model shows how aquatic species diversity changes from freshwater to more marine areas. In essence it aims to show the relative proportions of each component of the fauna (freshwater, brackish and marine) and how these change along a salinity gradient. These combined components decrease in diversity with a progression from both the freshwater and marine ends of the spectrum, with the 5–7 salinity area being dominated by a small number of true brackish/estuarine species. The way in which the Remane diagram has been interpreted (and misinterpreted) and used (and misused) in the literature is discussed here. We primarily investigate whether the model needs to be modified to help provide an understanding of current biotic distribution patterns within estuaries and how these patterns might be influenced by climate change. Using global estuarine examples for a variety of taxa we discuss the appropriateness of the Remane model beyond the zoobenthos (on which the model was originally based) and provide a revised model that is more suited to estuaries worldwide. Comment is also provided on the way in which a more appropriate estuarine biodiversity model can influence future estuarine ecotone and ecocline studies.

1. Introduction

There have been recent attempts to define paradigms showing the fundamental properties of estuaries by attempting to both summarise and allow the further investigation of those properties (e.g. Elliott and Whitfield, 2011; Basset et al., in press). As one such paradigm, many estuarine ecology textbooks (e.g. Hedgpeth, 1967; Beadle, 1972; McLusky and Elliott, 2004) have included the so-called Remane diagram (Fig. 1), the basic model of which can be traced back to Remane (1934). The original diagram is a conceptual model designed to show species diversity distribution along a salinity continuum (in this case, for rivers entering Baltic waters) and displays the numbers of species with different salinity tolerances (freshwater, brackish and marine) which comprise the communities across that continuum. In this review we examine the basis for the creation and widespread acceptance of the Remane diagram and assess whether it has application for estuaries worldwide. Based on more recent information from estuarine systems on different continents, we have constructed a more appropriate model for use in describing the relationship between salinity and biotic trends in estuaries.

2. Review of the Remane diagram

According to the species diversity terminology used on the *Y*-axis of the Remane diagram by Remane (1934), the model suggests (although no scale is given) that the marine and freshwater components comprise an equal number of species. These components decrease with the progression into transitional waters and the space is then also occupied by a small but significant number of 'brackish' species, which peak at a salinity of about 6 (Fig. 1). It is important to note that salinities are here presented according to the practical salinity scale and thus no units are given (Lewis, 1980); to provide comparison with previous work it should be noted that up to a salinity of 42 the practical salinity units (psu) equate to parts per thousand (ppt or ‰), or g l^{-1}.

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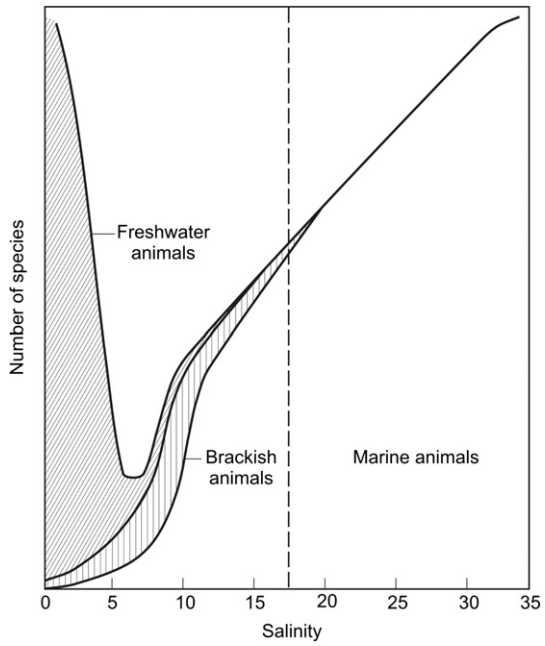

Fig. 1. A redrawn version of the original Remane diagram (Remane, 1934). The slanted hashed area represents freshwater species, vertical hashed area corresponds to brackish species, and white area below the curve marine species. The vertical dashed line represents a salinity of approximately 50% seawater.

Adolf Remane's figure legend does not confirm that we are dealing with absolute numbers for the marine, brackish and freshwater components, but the low maximum value for brackish species (Fig. 1) seems to suggest that actual numbers are being used in the diagram (rather than a scaling of species diversity for each component out of 100%). Greater clarity, however, is provided by the Remane and Schlieper (1958) version of the earlier diagram which shows the *Y*-axis scaled as a "per cent" (Fig. 2). This most likely refers to the percentage of freshwater and marine animals, relative to the total number of freshwater and marine animals, respectively. In this diagram, the inclusion of brackish animals is somewhat confusing, but most likely is a subset of the marine taxa (see below).

The Remane model suggests that the diversity of freshwater taxa declines rapidly between a salinity of 0.5–5, with minimum

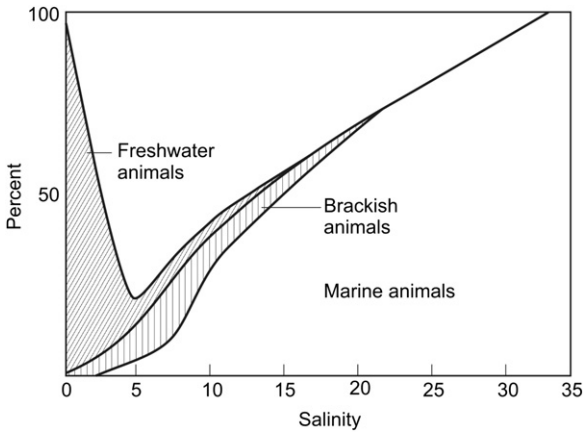

Fig. 2. A redrawn version of the Remane and Schlieper (1958) diagram, as depicted in McLusky and Elliott (2004), showing that the *Y*-axis has now been scaled according to percentage (not number).

species richness occurring at 5–7 (Fig. 1), a critical physico-chemical range for aquatic organisms according to Telesh and Khlebovich (2010). At a salinity of 6, brackish species are the dominant component in the Baltic, but this ratio changes considerably above 7 when marine species become overwhelmingly dominant. Very few brackish species are recorded above a salinity of 17 (approximately 50% seawater) and none are recorded above 20. Remane (1934) classified all waters between 0.1 and 17 salinity as "brackish" and therefore his brackish group of species is effectively confined to this salinity range.

Remane (1934) does not define what is meant by marine, brackish and freshwater species. Whilst marine and freshwater taxa obviously have a distribution that ranges from the marine and freshwater environments into brackish waters respectively, the brackish species quoted by Remane are presumed to be a subset of marine and freshwater taxa that have adapted to life in brackish waters. The implication from the Remane diagram is that all these groups of species are euryhaline to varying degrees and that this is the primary driver in terms of their occurrence along the salinity gradient. It is likely, however, that stenohaline taxa are also included in the Remane marine component since there is an immediate decrease in species diversity as salinities decline below 35 (Fig. 1). In addition, the marked decrease in freshwater taxa as salinities increase suggests a similar intolerance by certain freshwater species to saline waters.

In essence the "brackish" sector of the Remane diagram is a reflection of the stress-subsidy continuum (Elliott and Quintino, 2007), showing the inability of many freshwater and marine species to tolerate low salinities, whereas true brackish species are highly euryhaline and capable of thriving under wide variations in salinity. This property is likely to become increasingly significant in relation to climate change and rises in sea level when estuaries and river systems may undergo major changes. Therefore understanding the vulnerability of freshwater and marine taxa in estuaries and the role and colonization potential of truly brackish species has never been more important.

The Remane (1934) paper appears to be written almost verbatim (in an older form of colloquial German) from an oral presentation, and does not provide the kind of detail currently expected of scientific publications. There is also a lack of basic information, e.g. to what extent intertidal and/or sub-tidal sampling was used to compile species lists and one is left to assume that a similar sampling protocol was used in the different study areas. The model appears to be based primarily on benthic invertebrates although comment is made about similar patterns in other taxa, but no figures or tables are presented. The fact that the Remane diagram legend does not refer specifically to invertebrate diversity, and the author indicates that his paper is a general overview on the "problems and phenomena of brackish water biology", indicates that the diagram was intended for general rather than specific use. Hence the ease with which it has been used as a paradigm to cover the biota in all estuaries.

The Remane (1934) paper covered four broad regions, viz. the German North Sea, Belt Sea, southern Baltic up to northern Gotland, and the remaining northern areas of the Baltic. Remane only refers generally to the actual salinity in the different sampling areas, with surface salinities in the northern Baltic given as 4–6, southern and central Baltic 6–8, Kiel Bay 13–20 and North Sea 30–35. Based on the evidence presented it would appear that no samples were collected from estuaries *sensu stricto*, although Barnes (1974) considers the Baltic to be a single large stable 'estuary'. Remane refers to the Baltic Sea as a large brackish water area that is connected to the ocean (the North Sea) and that this makes it particularly interesting because of the gradual decrease in salinity from the Kattegat and Belt Sea up to the Gulf of Bothnia