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A testable linear model for diversity trends in estuaries

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Summary

1. In 1934, Adolf Remane constructed a diagram to describe changes in the number of species along a full salinity gradient within the Baltic. Despite fundamental differences in tidal regimes, the Baltic model has been applied directly to estuaries, becoming subsequently the textbook model for estuarine diversity trends.
2. Despite its ubiquity, the Remane diagram has many inconsistent features, making it unsuitable as a quantitative tool for comparing diversity trends between estuaries, including poor definition of *x*-axis (salinity), *y*-axis (number of species) and variations in sample location (subtidal/intertidal) than can greatly influence the resulting diversity/salinity relationship. Consequently, diversity trends within and between estuaries remain to be tested robustly.
3. The major environmental factor influencing the distribution of organisms in estuaries is salinity variation, rather than absolute salinity tolerance as in the Baltic. As salinity range demonstrates a quadratic relationship with mean salinity, an alternative linear model is therefore suggested utilizing mean salinity range at any one point in the estuary (*x*-axis) and mean α-diversity of macroinvertebrates (*y*-axis) obtained from subtidal samples to allow comparison with river systems and to minimize salinity variability between interstitial and overlying water.
4. The model was tested on an extensive subtidal data set from the Thames estuary (salinity 0–35), significant negative linear relationships between salinity range and α-diversity being apparent for annual and seasonal data sets. Significant models were also possible for both 'marine' and 'freshwater' halves of the estuary and for meiofauna α-diversity.
5. The linear model allows formal, statistical investigation of the differences in diversity trends between estuaries and the development of testable hypotheses on aspects of estuarine diversity, including the causes of the species minimum in estuaries. It also has potential as a management tool enabling the definition of sites of concern that fall below their predicted diversity.
6. The new model of diversity now requires testing in systems additional to the Thames in order to determine whether this relationship is a macroecological phenomenon or restricted to the test system.

Key-words: benthic invertebrates, salinity range, Thames.

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Introduction

In 1934, Adolf Remane produced a diagram to describe the hypothetical distribution of benthic invertebrate diversity along a marine–freshwater salinity gradient (Fig. 1), based on his observations in the Baltic and associated systems. This model has two components, namely the relative distribution of freshwater, brackish-water and marine species within the Baltic system and the overall diversity trend, in terms of number of species, associated with the progressive decrease in salinity. Both aspects of the diagram have received some discussion and modification (e.g. Hedgpeth 1967; Odum 1988; Barnes 1989), but the Remane diagram (Remane & Schlieper 1971) has now become the recognized textbook model for diversity patterns in tidal estuaries (e.g. McLusky 1971; Sumich

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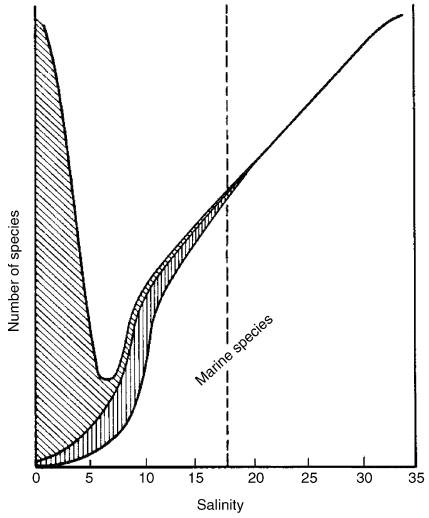

Fig. 1. The Remane diagram (from Remane & Schlieper 1971). Vertical hashed area corresponds to brackish water species, slanted hashed area freshwater species.

1992; Nybakken 2001). This is despite the diagram being a hypothetical construct for the Baltic system which is generally tideless (Segerstråle 1957), or at best weakly tidal in outer fjords. Subsequent influential publications (e.g. Friedrich 1969; Wolff 1983) have stated that the pattern has been confirmed in a range of brackish systems, including estuaries, but examples quoted are rarely more than descriptive, or qualitative, comparisons (e.g. Wolff 1973), often showing marked departure from the Remane model (e.g. Boesch, Diaz & Virnstein 1976). The Remane diversity model therefore remains to be tested quantitatively in estuaries.

The problems of testing estuarine diversity patterns using the textbook Remane diagram (Remane & Schlieper 1971) as a quantitative tool result from inadequate definitions of the model itself, particularly which parameters need to be measured in order to test observations against the model. These inconsistencies arise due partly to the transfer of the model from tideless brackish-water to strongly tidal estuaries and involve definitions of axes, habitat to be sampled and taxon to be targeted. To compare empirically, for example, diversity trends in two separate estuaries, these terms need to be consistent and meaningful. The *y*-axis (Fig. 1) is labelled 'number of species', but it is unclear how this should be defined for quantitative use. For example, this could be measured in terms of mean number of species in a sample at a location (i.e. α-diversity) or a qualitative count of the total number of species in a particular salinity band (some measure of regional diversity at the estuary scale). Diversity measure can alter the shape of plotted curves dramatically, Wagner (1999) demonstrating very different patterns for estuarine fish communities depending, in this case, on whether α- or β-diversity was assessed.

Definition of the *x*-axis is particularly problematic in estuaries. The lack of tides in the Baltic allows the stable salinity gradient to be mapped (e.g. McLusky 1971), the salinity at any one spatial location being relatively consistent and predictable, particularly at below-annual timescales. This is not the case in estuaries, salinity at any given point varying widely over both tidal (McLusky 1971) and seasonal (Attrill & Thomas 1996) time periods, so categorizing fixed estuarine sites in terms of a single salinity value is difficult, even inappropriate. A site may be classified into vastly different salinity bands depending on which criteria are used for salinity assessment (e.g. high tide, low tide, mean over tidal cycle, mean annual salinity, interstitial salinity, etc.). To enable a quantitative comparison of diversity trends in estuaries, the definition of the *x*-axis needs to be specific and consistent. A secondary aspect of the Remane model that has received some discussion is the position and cause of the species minimum, termed artenminimum (e.g. Deaton & Greenberg 1986; Wagner 1999). In the original diagram this minimum falls between salinities of 5–8, which led to suggestions that hydrochemical characteristics at these salinities cause an ecophysiological barrier (Khlebovich 1968) and thus are characterized by a minimum number of species (Kinne 1971, who termed this boundary the horohalinicum). While the existence of this boundary has since been disproved (Deaton & Greenberg 1986), these authors also state that the existence of the artenminimum at salinities of 5–8 within estuaries and stable brackish waters suggests that the species minimum cannot be explained in terms of fluctuations in physical factors. This second direct application of the Remane diagram to estuaries has also led to the adoption of the original *x*-axis, without consideration of what a salinity range of '5–8' actually means in an estuary, and thus may have led to spurious conclusions about the role of physical variation.

A further inconsistency apparent when attempting to apply the Remane diagram to estuaries is the location of sample site, i.e. in the intertidal or subtidal regions, a factor that appears to have been ignored when the diagram has been transferred from the Baltic to estuaries. Due to the minimal tidal movement in the Baltic, the original model was naturally constructed using all subtidal sites, whereas traditionally most work in estuaries has concentrated on intertidal mudflats. Diversity trends plotted for estuaries therefore can have a combination of intertidal (e.g. mid-estuary) and subtidal (e.g. freshwater reaches) sites. Application of the Remane model to estuaries assumes that sites in the same salinity regime will have similar levels of diversity, but this is not necessarily the case (Fig. 2); sites only 100 m apart bordering the low tide mark can have significantly different levels of diversity. Consistency in sample location is therefore an important factor if trends are to be compared between estuaries.

While the Remane diagram has many limitations in terms of its quantitative use in estuaries, it has persisted because, despite some criticism, no suitable alternative

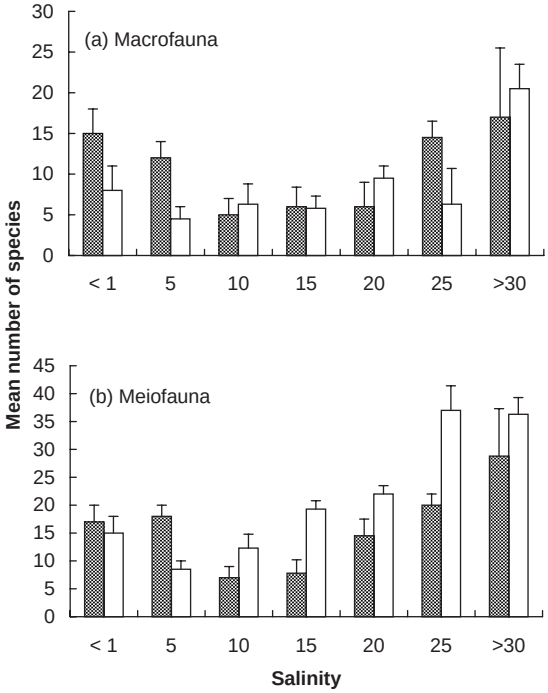

Fig. 2. Comparison of mean subtidal (solid bars) and intertidal (clear bars) diversity for sites in the Thames estuary over the full salinity range, where sites have both subtidal and adjacent intertidal components. (a) Macrofaunal assemblage (n = 13); (b) meiofaunal assemblage (n = 4).

has been suggested. The aim of this paper therefore is to present an alternative model for diversity trends in estuaries that can be consistently applied. This will allow quantitative comparisons between estuaries and the testing of a priori hypotheses affecting estuarine diversity.

Materials and methods

Data utilized in constructing models for this paper were obtained from a 4-year (1989–92) survey of the benthic macroinvertebrate communities along the full length of the Thames Estuary, UK (Attrill 1998). This survey was implemented by the (then) National Rivers Authority (now Environment Agency) and involved quarterly surveys at 28 sites covering the full 110 km of the estuary, from the freshwater river Thames (Attrill, Rundle & Thomas 1996) to the North Sea (Attrill *et al*. 1996). Sites were located in both intertidal (12 sites) and subtidal (16 sites) regions, with a set of sites having both components. Three to four replicates were obtained from each site, the sampling methodology being detailed by Attrill (1998). All macroinvertebrates in samples were identified to species and enumerated. For the first year of the survey, coincident meiofauna samples (species level ID) were taken at each site (see Attrill *et al*. 1996 for methodology). Salinity measurements (expressed as dimensionless PSU) were obtained from weekly boat-run samples (Attrill, Power & Thomas 1999), the EA half-tide correction model (IMER 1984) allowing low- and high-tide salinity to be determined for each site. Sediment particle size was determined using a Malvern laser Master-Sizer (Attrill 1998).

During the early 1990s the Thames catchment experienced severe drought conditions, affecting both water quality (Attrill & Power 2000a) and mobile invertebrate populations (Attrill & Power 2000b). Additionally, meiofauna samples were only obtained for the first year of the survey. Data analyses for model construction were therefore restricted to the first year's data (April 1989–March 1990), giving a candidate data set of 112 site-samples (replicated). Linear regression methods were used to examine the significance of relationships between invertebrate diversity and selected environmental variables. Statistical assumptions of the technique include normally distributed residuals and homoscedastistic variances. The Shapiro–Wilk statistic was utilized to test for normality in the residuals (d'Agostino 1986), while homoscedastistic residual variances were confirmed by examining plots of the standardized residuals (Draper & Smith 1981). Associations between environmental variables were assessed by calculating Spearman's rank correlation coefficient, while the significant differences between regression lines was investigated using analysis of co-variance (ANCOVA).

CONCEPTUAL FRAMEWORK OF THE MODEL

Brackish water organisms exist at far lower salinities in the Baltic than in estuaries. The bivalve *Macoma balthica* (L.), for example, penetrates the Baltic as far up as the Gulf of Bothnia (salinity = 3, McLusky 1971), whereas in estuaries such as the Thames it is confined to the outer reaches (salinity ≈ 20, Attrill 1998). This is due to the contrasting environmental stresses affecting the organisms. Due to the stable salinity regime, the distribution of organisms in the Baltic tends to correspond closely to their lower lethal salinity limit (McLusky 1971); in estuaries the fluctuating salinities (and other associated parameters) add a level of stress that prevents organisms maximizing their potential distribution (Carriker 1967). The distribution of organisms within estuaries (and thus diversity patterns) are therefore influenced more highly by variation than by absolute salinity regimes (Wolff 1983). A measure of environmental variability, particularly associated with the prime stressor of salinity, would therefore seem a more valid parameter to utilize in models of estuarine diversity. One such measure that is easily determined in estuaries is salinity range at any one static point, the difference between mean low-tide salinity and mean high-tide salinity demonstrating a quadratic relationship with mean salinity (Fig. 3). The quadratic nature of the relationship is the inverse of the putative estuarine diversity trend (Fig. 1), so potentially provides the opportunity to develop a linear model which will encompass all estuarine taxa rather than dividing the system into freshwater and marine

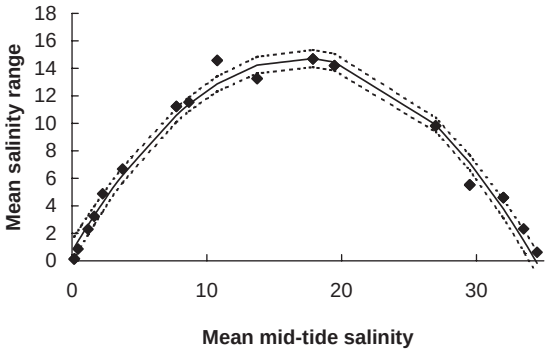

Fig. 3. Relationship between mid-tide salinity and salinity range in the Thames estuary. ◆ = data points, solid line = model ($y = 0{\cdot}69 + 1{\cdot}65x - 0{\cdot}05x^2$, $r^2 = 0{\cdot}969$, $P < 0{\cdot}001$, SW = 0·966), dotted lines = 95% CIs.

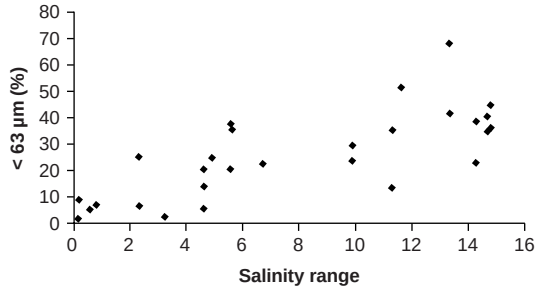

Fig. 4. Relationship between mean annual salinity range and percentage mud in the Thames estuary. Spearman's rank correlation coefficient = 0·746, $n = 28$.

components. Additionally, salinity range provides a good predictor of other stressors in the estuarine system, particularly particle size of the sediment (Fig. 4), the existence of fine material in suspension and the extensive mud banks characteristic of estuaries being considered as important as salinity in determining organism distribution (Carriker 1967; Wolff 1983; Barnes 1989). Therefore, salinity range can be used as an analogue for a set of variable conditions within the estuary that may be influencing organisms at any particular point; it is not intended that salinity range alone is to be considered causative of any pattern observed.

A criticism of the Remane diagram was the poor definition of axes and sample location, so the construction of any model based on salinity range therefore requires a priori definition of terms. Salinity range will be defined as the salinity range at a sample point over the time period of the sampling under investigation, expressed as the difference between mean low-water salinity and mean high-water salinity. Macroinvertebrate species diversity will be defined as mean α-diversity, i.e. the mean number of species present in replicate samples taken at each location during each sampling visit. Only subtidal samples will be included to give consistency along the estuary, and allow comparison with river samples. The use of subtidal samples

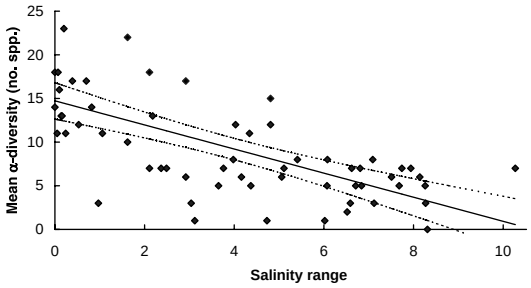

Fig. 5. Scattergram of salinity range with α-diversity for subtidal sites in the Thames estuary sampled over four seasons, together with fitted regression (solid line) plus 95% CIs (dotted lines). See Table 1 for regression details.

is also important in order to allow comparative consistency between sampled estuary water and interstitial water in contact with infauna. Interstitial salinity is recognized as being far less variable than overlying water over a tidal cycle (McLusky 1971), although it will vary seasonally with large-scale changes in river flow (Wolff 1973). However, there is no evidence that this is the case for subtidal areas, Wolff (1973, p. 34) stating that 'in general it may be assumed that the salinity in the topmost layer of the [subtidal] sediment closely follows the salinity of the overflowing water'. For the Thames data set, subtidal samples were limited to < 20 m to prevent sampling an exceptional, and unusual, high-diversity site deep in the shipping channel of the outer estuary (Attrill *et al*. 1996) and to provide a realistic depth framework for further studies.

RESULTS OF MODEL CONSTRUCTION

Mean macroinvertebrate α-diversity demonstrated a significant negative linear relationship with salinity range when samples for the full year were utilized (Fig. 5), salinity range explaining over 40% of the variation in diversity (Table 1). Robust models were also evident when the data were divided into individual seasons (Fig. 6, Table 1), salinity range within the sample season explaining up to 63% of α-diversity variation. Similar significant trends were also apparent when the estuary was split into two, investigating the relationship from the point of maximum salinity range to both freshwater and fully marine conditions (Fig. 7, Table 1). The model was also consistent for meiofaunal diversity (Fig. 8, Table 1). The residuals of all models presented in Table 1 showed no evidence of heteroscedasticity and were found to be normally distributed.

Discussion

The results demonstrate that a robust, linear model of diversity trends in estuaries is possible when macroinvertebrate α-diversity is related to mean salinity range, with all regressions explaining 39–61% of variation in diversity. The general model is consistent for all

Table 1. Details of regressions constructed for relationships between invertebrate α-diversity (y) and salinity range (x). SW = Shapiro–Wilk statistic to test for normality in regression residuals

Community component/time period	n	Regression equation	R^2	P	SW
Macroinvertebrates					
All samples combined (full year, Fig. 5)*	59	$y = 13{\cdot}86 - 1{\cdot}24x$	0·425	< 0·001	0·990
Spring (untransformed, Fig. 6)	15	$y = 17{\cdot}39 - 1{\cdot}90x$	0·451	0·006	0·879†
Spring (ln-ln data)	15	$y = 2{\cdot}27 - 0{\cdot}32x$	0·509	0·003	0·967
Summer (Fig. 6)	15	$y = 14{\cdot}46 - 1{\cdot}25x$	0·390	0·012	0·958
Autumn (Fig. 6)	15	$y = 17{\cdot}11 - 1{\cdot}94x$	0·613	< 0·001	0·943
Winter (Fig. 6)	15	$y = 13{\cdot}50 - 0{\cdot}91x$	0·385	0·014	0·939
Max. salinity range – river (full year, Fig. 7)*	25	$y = 12{\cdot}75 - 1{\cdot}16x$	0·529	< 0·001	0·916
Max. salinity range – sea (full year, Fig. 7)	33	$y = 16{\cdot}21 - 1{\cdot}66x$	0·453	< 0·001	0·979
Meiofauna					
Annual mean (Fig. 8)	15	$y = 23{\cdot}57 - 1{\cdot}08x$	0·553	0·002	0·960

†Critical value (α = 0·05) for SW statistic when n = 15 is 0·881. *Single outlier removed allowing normalization of residuals.

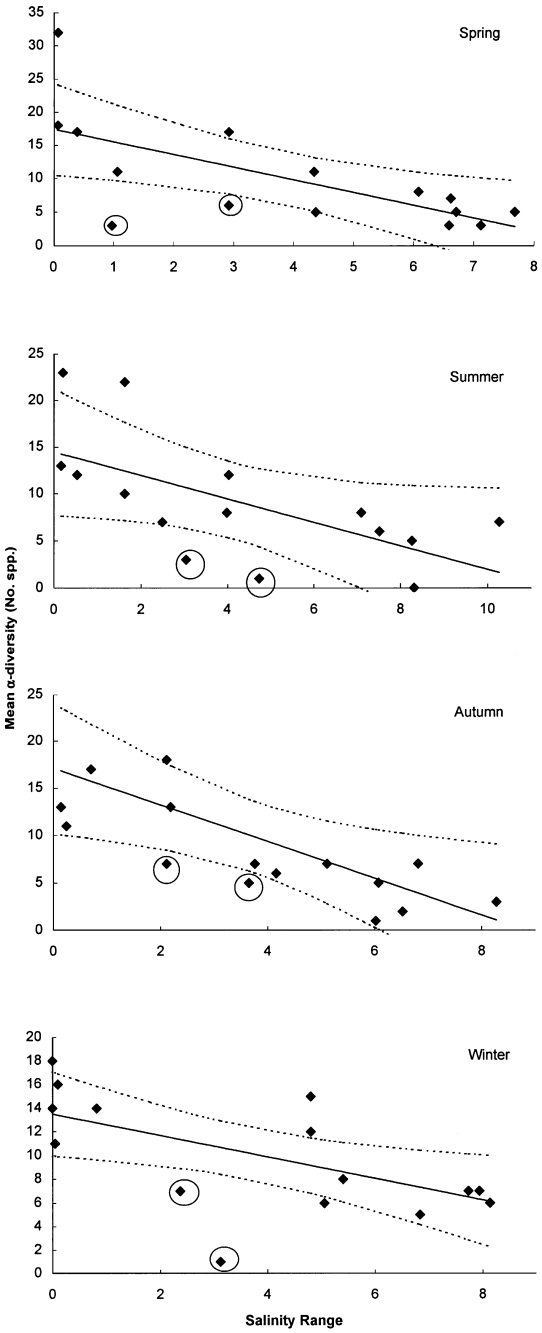

Fig. 6. Scattergrams of salinity range with α-diversity for subtidal sites in the Thames estuary where data are split into individual seasons. Fitted regression lines and CIs as for Fig. 5, regression details in Table 1. Circles highlight points that fall below the lower CI, i.e. those with much lower than predicted diversity, providing a potential management tool (see text).

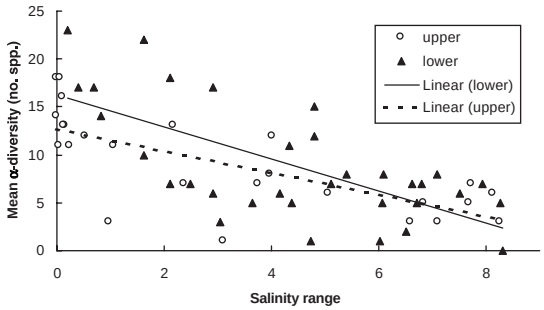

Fig. 7. Scattergram of data in Fig. 5 where sites have been divided into the upper (freshwater) and lower (marine) parts of the estuary, the cut-off point being the site of maximum salinity range. Regression lines fitted for both sectors differ in both slope and intercept (ANCOVA, $P < 0{\cdot}001$), but illustrate the relative consistency of the trend (see Table 1 for details).

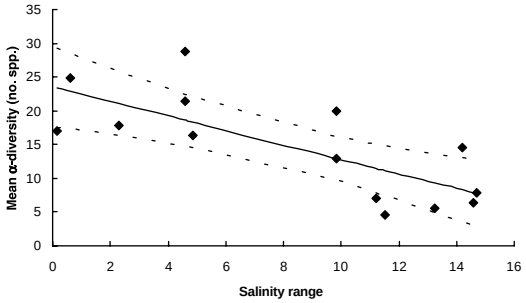

Fig. 8. Scattergram of salinity range with meiofauna α-diversity for subtidal sites in the Thames estuary. Fitted regression lines as Fig. 5, see Table 1 for regression details.

seasons, despite large apparent changes in physico-chemical parameters (Attrill & Thomas 1996). Additionally, a significant relationship was also evident for meiofaunal diversity, highlighting that the salinity range model is applicable to other components of the biota. The existence of a linear model will therefore allow diversity trends in estuaries to be compared statistically (e.g. by ANCOVA) and thus provide an opportunity for more rigorous ecological investigations, previously unfeasible using the Remane diagram. For example, Fig. 7 presented the trends for two halves of the estuary, namely the 'marine' and 'freshwater' ends. While both components demonstrated significant negative relationships with salinity range that supported the general model, there were small but significant differences in the lines when tested using ANCOVA, revealing that freshwater-based systems at the top end of the Thames estuary were slightly less diverse than marine equivalents under zero salinity range at the estuary mouth, the intercepts of the lines differing by approximately 3·5 species. However, the gradient of the line for the 'freshwater' section is lower than that for the 'marine' component (b = 1·16 and 1·66, respectively), in direct contrast to the Remane diagram where the drop in species from river to mid-estuary is far more severe than that for marine species (Fig. 1). The comparative responses of two different components of the biota can also be compared by assessing differences in the models for macroinvertebrates and meiofauna. The slope for meiofauna is shallower than that for macroinvertebrates (Figs 5 and 8, Table 1, ANCOVA $P < 0{\cdot}001$), suggesting that the reduction in meiofaunal diversity with increasing salinity range is not as severe as that for macroinvertebrates, supporting earlier qualitative conclusions (Gerlach 1954; Remane & Schlieper 1971). Warwick & Gee (1984) and Montagna & Kalke (1992) have suggested that macrofauna predation is a potential factor controlling meiofaunal diversity, so responses of the two assemblages to the environment may not be independent. However, the comparative consistency of the models for these two assemblages in the Thames provides no evidence that the macrofauna are either boosting or reducing meiofauna diversity suggesting that, at the whole-estuary scale, environmental variability is probably having a dominant influence.

The linear model also provides information on the possible causes of the estuarine species minimum (artenminimum) stated to be in salinities between 5 and 8 (e.g. Kinne 1971). While the existence of a putative ecophysiological barrier at these salinities appears not to be the case (Deaton & Greenberg 1986), experiments targeted at exploring this phenomenon have been undertaken at fixed salinities rather than attempting to test the effect of constantly varying conditions (e.g. Khlebovich 1968; Deaton & Greenberg 1986). The results of such experiments produce interesting curves for potential stressors, such as ion ratios, at different salinities, yet the x-axis will reflect fixed salinities as apparent in, for example, the Baltic rather than a subtidal benthic site in an estuary. While experiments involving varying salinities are logistically difficult, discussion on the artenminimum in estuaries has been rather misguided due to the assumption that the Remane diagram (in particular its x-axis) is an accurate model of estuarine diversity. The linear model reveals a species minimum at the point of maximum salinity range, suggesting that fluctuations in the main physical factors may explain the arteminimum in estuaries, in contrast to the Deaton & Greenberg's (1986) statement. Certainly, the linear model provides a framework for future experimental work in estuaries, concentrating on salinity range, and that perhaps it is time to separate estuaries and other brackish water systems in terms of searching for general mechanisms controlling species diversity.

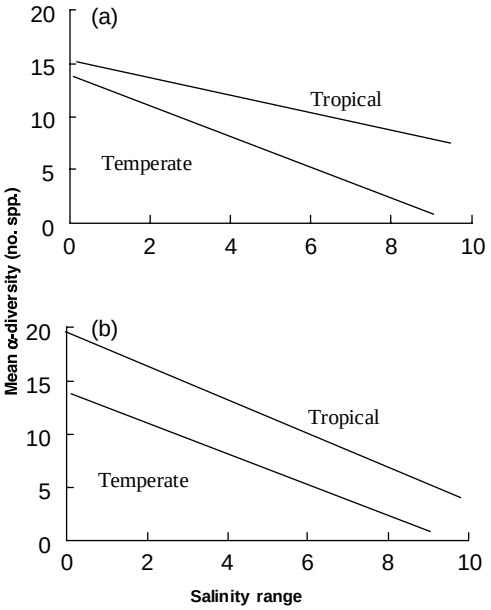

Fig. 9. Examples of an a priori scenario suitable for testing. A comparison of a tropical vs. a temperate estuary to test hypothesis that estuaries at low latitudes are more diverse: (a) postulated pattern if tropical system is more diverse only in the mid-estuary region; (b) postulated pattern if tropical system is more diverse along its full length.

The linear model will also allow testing of a priori hypotheses about estuarine diversity and direct comparisons between systems. For example, it has been suggested that tropical estuaries are more diverse than temperate estuaries (e.g. Sanders 1968; Wolff 1973, 1983) due perhaps to the impact of successive glaciations on high-latitude systems (Attrill, Stafford & Rowden 2001). The significance of diversity differences can be tested using the linear model, allowing the development of scenarios on how differences in diversity could be expressed (Fig. 9). In scenario Fig. 9a, intercepts would be different, but slopes similar, whereas in scenario 9b only slopes would differ. Similarly, scenarios for the putative impact of pollution on estuarine systems compared with unimpacted controls can be developed and tested. The model could also provide a useful management

tool for application within an estuarine system, enabling sites of concern to be highlighted. In Fig. 6, two points consistently fall below the lower 95% CI for the model, corresponding to two sites whose diversity constantly falls well below that predicted for their location. Further investigation reveals these to be sites in the southern, outer Thames estuary where a combination of sediment mobility (due to circulation patterns) and the deposition of decaying seagrass material decreases macroinvertebrate diversity (Attrill 1998). It is interesting to note that the equivalent sites do not show the same pattern for meiofauna, suggesting a specific impact on the larger fauna consistent with such mechanical disturbance (e.g. Warwick *et al*. 1990).

Conclusions

Analysis of data from the Thames estuary has highlighted the existence of a linear trend between species diversity and salinity range in this system, creating a testable model for use in other estuaries. However, it is clear that this suggested model now requires extensive testing and validating in order to determine whether this is a macroecological phenomenon or restricted in this form to the Thames. In particular, it will be interesting to test the model in estuaries with different levels of salinity range. Due to the length of the Thames estuary, anthropogenic narrowing (Tinsley 1998) and a comparatively large freshwater input the highest mean salinity range at any one point was rarely above 10; other estuaries with different morphological characteristics could exhibit much higher salinity ranges. The Thames macroinvertebrate models intercept with the x-axis at salinity ranges between 10 and 12, the meiofauna model having a much higher intercept (21·8), suggesting the maximum salinity range for these respective components in the Thames system. The patterns for similar sets of species in estuaries with higher salinity ranges would be interesting and allow information to be generated on comparative responses of estuarine taxa to salinity variation. Certainly the model would allow this to be investigated and tested and may result, for example, in a standardized x-axis (e.g. scaled 0–100 for minimum to maximum salinity range). Validating the model for other biotic components, such as fish, would also help support the generality of the trend.

For further testing it appears suitable to construct models for subtidal samples taken within a season and compare the mean α-diversity with mean salinity range for the season in question. The linear nature of the model will therefore allow the patterns in other estuaries, and for other taxa, to be compared with that constructed for the Thames.

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References

d'Agostino, R.B. (1986) Test for the normal distribution. *Goodness-of-Fit Techniques* (eds R.B. d'Agostino & M.A. Stephens), pp. 367–419. Marcel Dekker, New York.

Attrill, M.J. (1998) The benthic macroinvertebrate communities of the Thames estuary. *A Rehabilitated Estuarine Ecosystem: the environment and ecology of the Thames Estuary* (ed. M.J. Attrill), pp. 85–113. Kluwer Academic Publishers, Dordrecht.

Attrill, M.J. & Power, M. (2000a) Modelling the effect of drought on estuarine water quality. *Water Research*, **34**, 1584–1594.

Attrill, M.J. & Power, M. (2000b) Effects on invertebrate populations of drought-induced changes in estuarine water quality. *Marine Ecology Progress Series*, **203**, 133–143.

Attrill, M.J., Power, M. & Thomas, R.M. (1999) Modelling estuarine Crustacea population fluctuations in response to physico-chemical trends. *Marine Ecology Progress Series*, **178**, 89–99.

Attrill, M.J., Ramsay, P.R., Thomas, R.M. & Trett, M.W. (1996) An estuarine biodiversity hot-spot. *Journal of the Marine Biological Association*, **76**, 161–175.

Attrill, M.J., Rundle, S.D. & Thomas, R.M. (1996) The influence of drought-induced low freshwater flow on an upper-estuarine macroinvertebrate community. *Water Research*, **30**, 261–268.

Attrill, M.J., Stafford, R. & Rowden, A.A. (2001) Latitudinal diversity patterns in estuarine tidal flats: indications of a global cline. *Ecography*, **24**, 318–324.

Attrill, M.J. & Thomas, R.M. (1996) Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora, Cnidaria, Crustacea: Decapoda) in relation to hydrological parameters. *Marine Ecology Progress Series*, **143**, 25–36.

Barnes, R.S.K. (1989) What, if anything, is a brackish water fauna? *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **80**, 235–240.

Boesch, D.F., Diaz, R.J. & Virnstein, R.W. (1976) Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. *Chesapeake Science*, **17**, 246–259.

Carriker, M.R. (1967) Ecology of estuarine benthic invertebrates: a perspective. *Estuaries* (ed. G.H. Lauff), pp. 443–487. AAAS, Washington DC.

Deaton, L.E. & Greenberg, M.J. (1986) There is no horohalinicum. *Estuaries*, **9**, 20–30.

Draper, N.R. & Smith, H. (1981) *Applied Regression Analysis*, 2nd edn. John Wiley & Sons, New York.

Friedrich, H. (1969) *Marine Biology*. Sidgwick & Jackson, London.

Gerlach, S.A. (1954) Das supralitoral der sandigen Meeresküsten als Lebensraum einer Mikrofauna. *Kieler Meeresforschungen*, **10**, 121–129.

Hedgpeth, J.W. (1967) Ecological aspects of the Laguna Madre, a hypersaline estuary. *Estuaries* (ed. G.H. Lauff), pp. 408–419. AAAS, Washington DC.

Institute for Marine Environmental Research (IMER) (1984) Predicted effects of proposed changes in patterns of water abstraction on the ecosystems of the lower River Thames and its tidal estuary. Institute for Marine Environmental Research Miscellaneous Publications 9. IMER, Plymouth.

Khlebovich, V.V. (1968) Some peculiar features of the hydrochemical regime and the fauna of mesohaline waters. *Marine Biology*, **2**, 47–49.

Kinne, O. (1971) Salinity: animals–invertebrates. *Marine Ecology*, Vol. 1. *Environmental Factors* (ed. O. Kinne), pp. 821–996. John Wiley & Sons, New York.

McLusky, D.S. (1971) *Ecology of Estuaries*. Heinemann, London.

Montagna, P.A. & Kalke, R.D. (1992) The effect of freshwater inflow on macrofaunal and meiofaunal populations in the Guadalupe and Nueces estuaries. *Estuaries*, **15**, 307–326.

Nybakken, J.W. (2001) *Marine Biology: an ecological approach*, 5th edn. Benjamin Cummings, San Francisco.

Odum, W.E. (1988) Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics*, **19**, 147–176.

Remane, A. (1934) Die Brackwasserfauna. *Zoologischer Anzeiger (Supplement)*, **7**, 34–74.

Remane, A. & Schlieper, C. (1971) *Biology of Brackish Water*. E. Schweiserbart'sche Verlagsbuchhandlung, Stuttgart.

Sanders, H.L. (1968) Marine benthic diversity: a comparative study. *American Naturalist*, **102**, 243–282.

Segerstråle, S.G. (1957) Baltic Sea. *Treatise on Marine Ecology and Paleoecology*, Vol. 1 (ed. J.W. Hedgpeth), pp. 751–800. Geological Society of America Memoir 67.

Sumich, J.L. (1992) *An Introduction to the Biology of Marine Life*. Wm. C. Brown, Dubuque, IA.

Tinsley, D. (1998) The Thames estuary: a history of the impact of humans on the environment and a description of the current approach to environmental management. *A Rehabilitated Estuarine Ecosystem: the environment and ecology of the Thames Estuary* (ed. M.J. Attrill), pp. 5–26. Kluwer Academic Publishers, Dordrecht.

Wagner, C.M. (1999) Expression of the estuarine species minimum in littoral fish assemblages of the lower Chesapeake Bay tributaries. *Estuaries*, **22**, 304–312.

Warwick, R.M. & Gee, J.M. (1984) Community structure of estuarine meiobenthos. *Marine Ecology Progress Series*, **18**, 97–111.

Warwick, R.M., Platt, H.M., Clarke, K.R., Agard, J. & Gobin, J. (1990) Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton harbour, Bermuda. *Journal of Experimental Marine Biology and Ecology*, **138**, 119–142.

Wolff, W.J. (1973) The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Schledt. *Zoologische Verhandelingen*, **126**, 1–242.

Wolff, W.J. (1983) Estuarine benthos. *Ecosystems of the World 26: estuaries and enclosed seas* (ed. B.H. Ketchum), pp. 151–183. Elsevier, Amsterdam.

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