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Towards a formal description of foraminiferal assemblage formation in shallow-water environments: Qualitative and quantitative concepts

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ABSTRACT

The use of foraminifera in palaeoenvironmental reconstructions (e.g. sea level) may be complicated by processes such as infaunal test production, taphonomic degradation and bioturbation which act to modify contemporary analogue (surface) assemblages during and subsequent to burial. Understanding the palaeoenvironmental significance of these processes is limited by the absence of a clear theoretical description of the mechanics of foraminiferal assemblage formation. A conceptual framework is proposed which describes assemblage formation in terms of the balance of test inputs and losses within a volume of sediment undergoing burial through the upper sedimentary zones of test production, taphonomic processes and bioturbation. A corresponding mathematical model is described and shown to explain empirical dead test distributions in terms of empirically-defined standing crops, sedimentation and mixing rates, together with model estimates of standing crop turnover and/or taphonomic decay rates. This approach provides a quantitative basis for understanding assemblage formation and for comparing assemblage forming processes between species, environments and study sites. Rates of standing crop turnover and taphonomic loss are identified as the primary unknowns in the study of foraminiferal assemblage formation. These multiple unknowns make interpretations of cored data ambiguous, emphasising the need for a detailed and coherent framework of theory and assumptions for understanding the mechanics assemblage formation if interpretations are to be clear and conclusive.

1. Introduction

There has been much discussion in the past two decades about the applicability of surface sediment foraminiferal assemblages from intertidal environments as modern environmental analogues for the reconstruction of Holocene relative sea level changes. Such assemblages typically occur in species zonations which reflect tidal elevation, and therefore clearly exhibit an environmental signature related to relative sea level prior to their burial (Scott and Medioli, 1978; Patterson, 1990; Scott and Leckie, 1990; Jennings and Nelson, 1992; Horton et al., 1999, 2003, 2005; Edwards et al., 2004; Barbosa et al., 2005; Woodroffe et al., 2005; Hawkes et al., 2010; Leorri et al., 2010; Callard et al., 2011). The recognition that these assemblages may be modified by processes which act during burial (infaunal test production, taphonomic degradation, bioturbation) has led some authors to question their utility as simple palaeoenvironmental analogues (Denne and Sen Gupta, 1989; Jonasson and Patterson, 1992; Goldstein and Harben, 1993; Ozarko et al., 1997; Patterson et al., 1999; Goldstein and Watkins, 1999; Hippensteel et al., 2000, 2002; Berkeley et al., 2007; Leorri and Martin, 2009). The detection of post-depositional effects and the isolation of the 'true' environmental signal are a fundamental challenge that needs to be overcome before intertidal foraminiferal records can be reliably interpreted.

Prevailing approaches to studying post-depositional processes typically focus on downcore (<1 m) trends in absolute test concentrations or relative species abundances from either dead or 'total' (living plus dead) foraminiferal assemblages, sometimes with qualitative reference to associated surface and infaunal living populations (Goldstein and Harben, 1993; Culver et al., 1996; Ozarko et al., 1997; Goldstein and Watkins, 1998; de Rijk and Troelstra, 1999; Hippensteel et al., 2000; Hayward et al., 2004; Culver and Horton, 2005; Tobin et al., 2005; Culver et al., 2013). However, these approaches are limited in the extent to which they establish the influence of post-depositional processes on the palaeoenvironmental record. For example, simple trends in species relative or absolute abundances may be attributed to *either* infaunal production *or* taphonomic degradation, but remain ambiguous in cases where both (or other) processes operate. In addition, these approaches provide no framework for discriminating post-depositional effects from subsurface assemblage variations which reflect changing depositional conditions over time (e.g. elevation relative to mean sea level). It is striking to note that, of all of the studies which address post-depositional assemblage formation, few have attempted to

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recognise the final foraminiferal product of deposition and burial at specific intertidal elevations (e.g. Berkeley et al., 2009). The precise palaeoenvironmental consequences of post-depositional processes – i.e. recognisable, systematic changes in assemblage composition or environmental resolution – remain poorly evaluated.

These limitations reflect a poorly-defined understanding of how foraminiferal assemblages develop. A formal description of foraminiferal assemblage formation, in particular of the interaction of ecological, taphonomic and physical processes during burial does not exist. This contrasts with other sedimentary phenomena, for example radionuclide decay (Dellapenna et al., 1998), early diagenesis (Berner, 1980; Boudreau, 1996) and bioturbation (Guinasso and Schink, 1975; Officer and Lynch, 1989), which employ a rich and well-specified theoretical underpinning for relating sedimentary components and processes during burial. Despite the potential suitability of these methods to the study of foraminiferal assemblage formation, the appropriate conceptual and quantitative foundations have not been established.

Comparisons of the relative species abundances in live and dead assemblages represent perhaps the simplest quantitative models of assemblage formation in use. Such approaches have shown significant differences between in situ test production and test accumulation in surface sediments, implying a role for taphonomic or other processes (Murray, 1989; Culver et al., 1996; Murray and Alve, 1999; Edwards and Horton, 2000; Wang and Chappell, 2001; Vance et al., 2006). Green et al. (1993) formalised this approach by defining a system of equations linking rates of foraminiferal production, death, and test dissolution to variations in the concentrations of live and dead foraminifera in Long Island Sound. Their study identified complete, seasonal loss of tests (through dissolution) within the bulked upper 7 cm of sediment, associated with test residence times of ~86 days. Hippensteel et al. (2000) similarly inferred residence times for tests at a succession of depths (0–60 cm) in salt marsh deposits using ratios of live and dead test concentrations, finding greater persistence of tests at depth. Common to each of these cases is the explanation of dead assemblages in terms of the concomitant living assemblage (and their discrepancies), with no reference to the action of burial.

Loubere et al. (1993) identified standing crops, together with rates of reproduction, taphonomic loss and sedimentary mixing, as the primary components of foraminiferal assemblage formation, and discussed their variability with depth into the sediment (Fig. 1). The precise mechanisms by which these components combine to produce downcore variations in foraminiferal abundances have not been clearly defined but some instructive contributions have been made. Loubere (1989) numerically simulated the interplay between infauna and sedimentation, showing that: (1) downcore increases in dead test concentrations are controlled by species' preferred living depths; and (2) that downcore variations in assemblage composition can arise from a "stratified" living community. Although clearly quantitative in nature, Loubere's (1989) model was tested only qualitatively against empirical data and the governing equations were not described, making the findings, for practical purposes, of only qualitative value. Berkeley et al. (2007) argued that, in the absence of taphonomic losses, test accumulation during burial is proportionate to the depth-integrated standing crop. Leorri and Martin (2009) tested this hypothesis, finding the cumulative-standing-crop model to be a good predictor of species' dead test abundances beneath the surface of a Delaware salt marsh, notwithstanding some discrepancies. Such discrepancies could be interpreted as representing cumulative taphonomic losses (Loubere and Gary, 1990; Ozarko et al., 1997) under identical logic to that employed in concomitant live-dead comparisons.

Although several authors have postulated an increased likelihood of preservation for foraminiferal tests produced at depth (Loubere and Gary, 1990; Loubere et al., 1993; Goldstein and Watkins, 1999), the interplay of infaunal test production and taphonomic processes *during burial* remains a significant ambiguity. Conceptual and quantitative techniques for dealing with taphonomic processes are well established in other contexts where concentrations and time-averaging of skeletal material are known to reflect an interaction between the rates and maximum depths of taphonomic processes and bioturbation, together with rates of burial (Loubere, 1989; Flessa et al., 1993; Meldahl et al., 1997; Olszewski, 1999, 2004; Tomašových et al., 2006). These approaches have been shown to be applicable to coastal foraminifera (e.g. Martin et al., 1996; Hippensteel and Martin, 1999) but an integrated framework incorporating the effects of infaunal test production is missing.

This paper aims to address this shortfall by formally presenting a model of assemblage formation during burial. Specifically, we present: (1) a conceptual model of test accumulation; (2) a formal mathematical description of test accumulation in terms of standing crop, reproduction rate, taphonomic decay rate, mixing rate and sedimentation rate; and (3) examples of the model applied to empirical data.

2. A conceptual model of foraminiferal test accumulation

The model outlined below builds upon fundamental concepts from established approaches to foraminiferal assemblage formation and the modelling of other shallow sedimentological phenomena

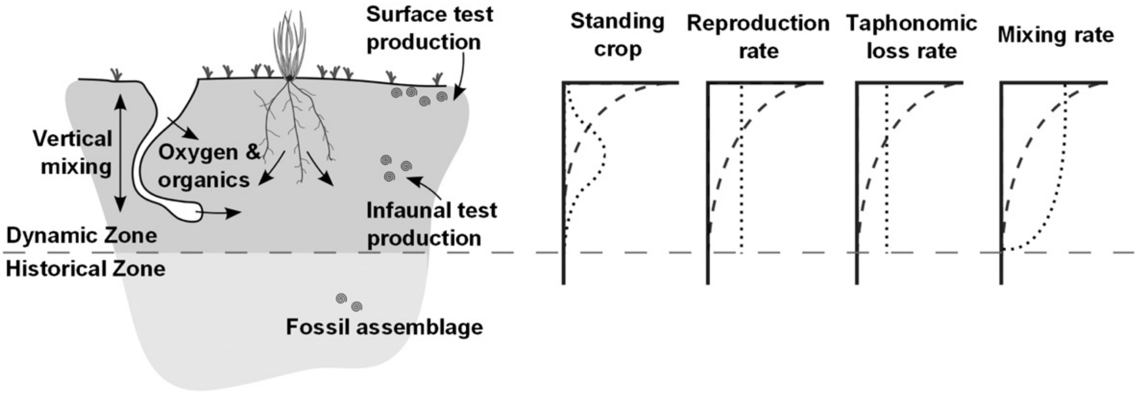

Fig. 1. The two primary zones comprising the assemblage forming system. The "dynamic zone" is defined as the upper sedimentary interval within which all test production and appreciable taphonomic losses occur. The introduction of organic material and oxygen into subsurface sediments is likely to influence the depth to which foraminiferal populations live and taphonomic processes (e.g. mineralization of organic cements, calcareous dissolution) operate (Berkeley et al., 2007). The "historical zone" represents the depth beyond which no further assemblage forming processes operate and wherein assemblages are effectively fossilised. The schematic plots describe some ways in which standing crops and rates of reproduction, test loss and mixing might be expected to vary with depth into the sediment (adapted from Loubere et al., 1993). Peak concentrations in the standing crop of foraminiferal species may occur, for example, at the sediment surface (dashed line) or at some depth below (dotted line), thereby defining the 'microhabitat' of the species. Rates of reproduction (standing crop 'turnover'), taphonomic decay and sedimentary mixing (e.g. bioturbation) may plausibly be expected to decrease asymptotically with depth into the sediment (dashed lines) or be more approximately constant or 'lumpy' (Loubere et al., 1993) over a particular depth range (dotted lines). These examples are not exhaustive.