TOWARDS A FORMAL DESCRIPTION OF FORAMINIFERAL ASSEMBLAGE FORMATION IN NEAR SHORE ENVIRONMENTS: QUALITATIVE AND QUANTITATIVE CONCEPTS

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Abstract

The use of intertidal foraminifera in reconstructing former sea levels 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 and taphonomic processes. A corresponding mathematical model is described and shown to explain empirical dead test distributions in terms of empirically-defined standing crops and sedimentation rates, together with model estimates of standing crop turnover and/or taphonomic decay rates. This approach provides a quantitative basis 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, emphasizing the need for a detailed and coherent framework for understanding the mechanics assemblage formation if interpretations are to be clear and conclusive.

Keywords

Foraminifera, taphonomy, infauna, assemblage, model

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 is 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, crude trends in species 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 recognise the final foraminiferal product of deposition and burial at specific intertidal elevations (e.g. Berkeley et al., 2009a). 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 form. A formal description of foraminiferal assemblage formation, in particular of the interaction of ecological and taphonomic 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; Schink and Guinasso, 1977; Hippensteel and Martin, 1999), 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. A number of illustrative contributions to this end have been made. Loubere (1989), for example, numerically simulated the interplay between infauna, sedimentation and bioturbation, although this was tested only qualitatively against empirical data, and the principal equations were not described. Loubere et al. (1993) identified the primary components of foraminiferal assemblage formation and discussed their variability with depth into the sediment (Figure 1). This paper aims to address this shortfall by presenting a conceptual and mathematical description of assemblage formation during burial.

2. A conceptual model of foraminiferal test accumulation

The model outlined below builds upon fundamental concepts from established approaches to foraminiferal assemblage formation as well as the modelling of other shallow sedimentological phenomena (e.g. radionuclide activities, early diagenesis, bioturbation). Firstly, the notion of test 'continuity' – the balance of test inputs and losses occurring through time within a discrete volume of sediment - is established as a basic axiom, with the implication that ultimate accumulation reflects the net balance of inputs and losses. Secondly, burial is conceptualised using the sedimentary volume as a reference frame which is considered to migrate away from the sediment-water interface (SWI) through time as a result of continual sediment deposition above (Berner, 1980). Thirdly, empirical observations and assumptions describing the ways in which test dynamics may vary systematically with depth (and therefore through time) are used to conceptualize assemblage "maturation" during burial.

2.1 The assemblage forming system

At the most general scale, the sediment column can be divided into two primary units: an upper *dynamic zone* in which test production (including infauna), taphonomic destruction and mixing (bioturbation) occur; and a deeper *historical zone* where these processes cease to operate and in which assemblages are effectively fossilised (Figure 1). The upper dynamic zone can be considered a generalisation of the concept of the *taphonomically active zone*

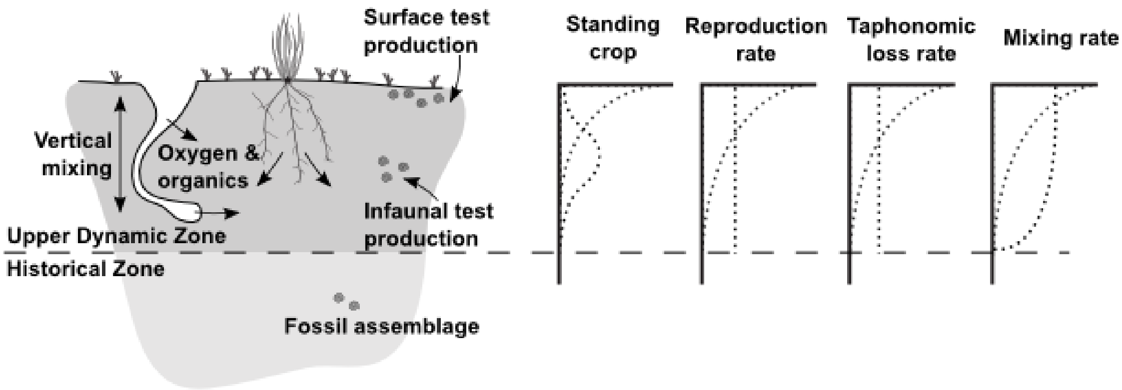

Figure 1: The two primary zones comprising the assemblage forming system. The “dynamic zone” is defined as the upper sedimentary interval within which all test production and appreciable taphonomic losses occur. The introduction of organic material and oxygen into subsurface sediments is likely to influence 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 show notional depth-distributions of rates of test input, loss and mixing (adapted from Loubere et al., 1993).

(TAZ; Davies et al., 1989; Powell, 1992; Flessa et al., 1993; Martin et al., 1996; Meldahl et al., 1997; Olszewski, 2004; Powell et al., 2012), which describes the tendency for taphonomic processes to be concentrated close to the sediment surface. The respective depths to which test production, taphonomic destruction and bioturbation occur are, in principle, independent, but these processes may share some common influences (e.g. sedimentary oxygen penetration, organic matter supply) or indeed directly influence one another (Aller, 1982; Jorissen et al., 1995; Moodley et al., 1998; de Stigter et al., 1998; Barbieri, 2001; Licari et al., 2003; Debenay et al., 2004; Geslin et al., 2004; Berkeley et al., 2007). Consequently, their depth ranges may broadly coincide. The dynamic zone may plausibly range from a few centimetres (e.g. Alve and Murray, 2001) to over a metre in depth (Hippensteel et al., 2000;

Berkeley et al., 2008, 2009a). A model is thus required which describes the process by which assemblages form in the upper dynamic zone and enter the historical zone.

2.2 Test dynamics and continuity

Implicit in many studies of foraminiferal assemblage formation is a basic, intuitive identity: *dead tests = produced tests - destroyed tests*. Murray (1991), for example, described fossil assemblage formation as proceeding according to three stages: (1) inputs from a living assemblage; (2) an *original* dead assemblage arising from the death of the living community; and (3) a taphonomically altered dead assemblage. An important corollary to this identity is that taphonomic losses from (or introductions to) assemblages can be identified on the basis of discrepancies between living and dead assemblages (e.g. Murray, 1989; Green et al., 1993; Murray and Alve, 1999; Wang and Chappell, 2001).

Applying this principle to a finite volume of sediment enables the accumulation of foraminiferal tests to be formally conceptualised (Figure 2A). Tests enter the volume via test production, and are removed via taphonomic loss. From considerations of material balance, tests which enter the volume within a given interval of time must either leave the volume or accumulate within the volume. Therefore, we can rewrite the original identity in terms of rates with respect to time,

change in dead test concentration = rate of test production – rate of test loss (1)

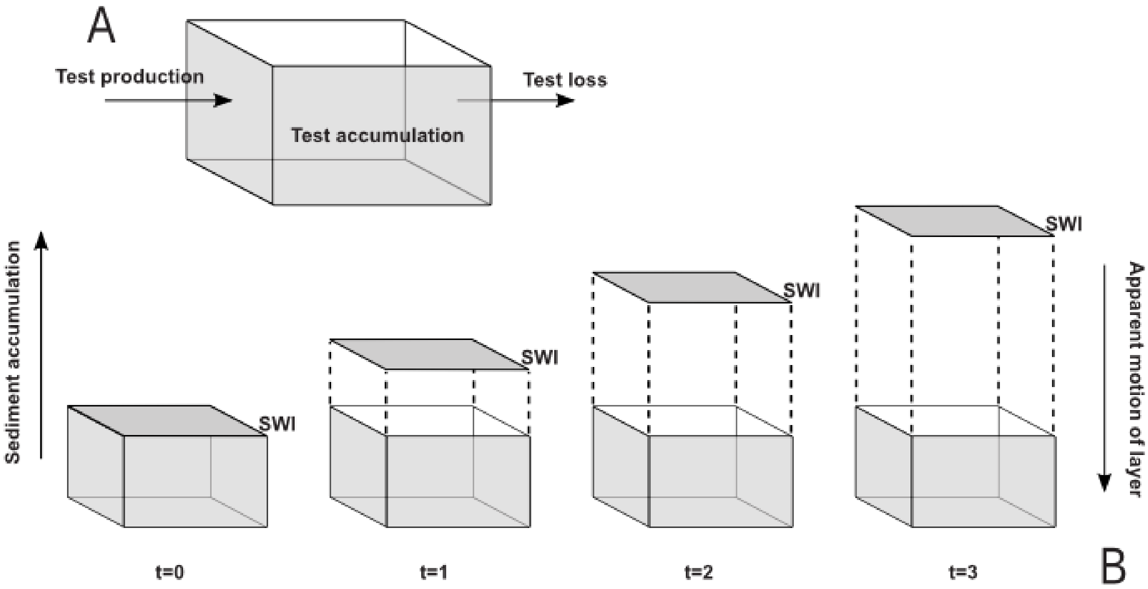

Figure 2: (A) Test accumulation in a volume of sediment based on considerations of material balance: tests enter the volume via test production and are removed by taphonomic losses. Accumulation of tests within the volume through time equals the difference between additions and losses; (B) Apparent advection of a sedimentary volume undergoing burial. As sediment accumulates, the sediment-water interface (SWI) – together with the upper Dynamic Zone – migrates upwards. A given volume of sediment is therefore seen to migrate *downwards* with respect to the SWI and through the Dynamic Zone.

This statement of test 'continuity' can be considered a basic axiom of foraminiferal assemblage formation and shows that, through time, the dead assemblage within the volume represents the cumulative balance of all previous inputs and losses.

2.3 Assemblage burial

Considering test accumulation within a single sedimentary interval represents a model of assemblage formation within a stationary or 'static' reference frame. Such an approach implies that sedimentation is negligible, that assemblages can be explained solely in terms of processes *currently* acting, and taken to its logical conclusion, that these processes continue to act within the volume indefinitely. Such a model is appropriate when considering short-term assemblage dynamics (e.g. Green et al., 1993) or surficial sediments only (Murray, 1989; Culver et al., 1996; Edwards and Horton, 2000; Wang and Chappell, 2001; Horton and Murray, 2006), but in the context of palaeo-environmental applications, it is necessary to consider the effect of burial.

Continual sedimentation results in a gradual upward migration of the sediment-water interface (SWI). From the reference frame of a particular volume of sediment, despite remaining at the same *absolute* stratigraphic level at which it was first deposited (ignoring uplift, subsidence and compaction), burial can be viewed as an advection *away* from the SWI (Berner, 1980, Boudreau, 1996). It follows that a previously deposited volume of sediment passes *through* the subsurface zones of foraminiferal production and taphonomic processes during burial (Figure 2B). The central concept of successive and cumulative test inputs and losses through time therefore occurs within a *shifting reference frame* of increasing depth.

Rates of test production and taphonomic processes are likely to vary with depth into the sediment (Figure 1; Loubere et al., 1993). It is well known that living populations vary with depth depending on the microhabitat preferences of species (e.g. Matera and Lee, 1972; Goldstein and Harben, 1993; Goldstein et al., 1995; Ozarko et al., 1997; Saffert and Thomas, 1998; Duchemin et al., 2005; Berkeley et al., 2008; Culver et al., 2013). Some authors have suggested that standing crop turnover rates also decline with depth below the SWI, perhaps due to decreasing oxygen availability and organic matter quality (Loubere et al., 1993; de Stigter et al., 1999). The probability of taphonomic loss may also decline beneath the SWI (e.g. Alexandersson, 1978; Aller, 1982; Cummins et al., 1986; Powell, 1992; Loubere et al., 1993; Olszewski, 2004), with the depth to which taphonomic processes act defining the TAZ (Davies et al., 1989).

Given the relationship between depth and time in sedimentary systems, the introduction of burial has several important consequences. Firstly, since dead test concentrations represent cumulative net test inputs through time, a dead assemblage is the product of the entire sedimentary interval through which a layer has migrated during burial. Secondly, the finite depth range of test production and taphonomic processes results in assemblage formation becoming a finite process in time. Finally, rates of test inputs and loss experienced by a layer during burial vary according to the particular production and taphonomic conditions at different sedimentary depths (Loubere et al., 1993). The cumulative balance of depth-dependent test inputs and losses through a given path of burial is equal to the dead assemblage formed.

2.4 Model resolution

The size of the sedimentary volume under consideration bears directly on the resolution at which assemblage formation is understood. Green et al. (1993) applied their detailed analysis of test dynamics in Long Island Sound to the bulked upper 7 cm of deposits, but a number of considerations suggest that a higher resolution is required for understanding the formation of intertidal foraminiferal assemblages. Firstly, cored assemblages used for palaeo-environmental analyses - the formation of which is of principal interest - are typically collected from samples on the order of 1 cm thick. Secondly, test accounting must be undertaken at a scale which is at least as small as the dynamic zone (i.e. the maximum depth of infauna and taphonomic processes) if the transition of assemblages into the historical zone - and thereby the formation of *fossil* assemblages - is to be described. The depth of the dynamic zone may be as small as a few centimetres (e.g. Alve and Murray, 2001). A more subtle consideration concerns the fact that *surface assemblage zones* (e.g. Scott and Medioli, 1978; Patterson, 1990; Horton et al., 1999, 2003, 2005; Woodroffe et al., 2005; Hawkes et al., 2010; Leorri et al., 2010; Callard et al., 2011) and *subsurface* a*ssemblage forming processes* (infauna, taphonomic loss, bioturbation; Goldstein and Watkins, 1999, Hippensteel et al., 2002; Berkeley et al., 2008, 2009a; Culver et al., 2013) occur on similar *vertical* scales of centimetres to decimetres. This raises questions about how subsurface assemblage formation affects the *perceived* environmental resolution of the sedimentary record (see Section 4.2). For example, what is the environmental resolution of a surface assemblage with an elevational range of 5 cm but which is underlain by 10 cm of infaunal test production?

Assemblage formation must, therefore, be understood at least at a scale of just a few centimetres if changes in environmental resolution brought about by processes acting during burial are to be recognised. This equally implies that it must be possible to resolve progressive assemblage formation *within* the dynamic sedimentary zone in which test production and loss occurs. Assemblage formation can thus be considered in terms of the changes which occur within an arbitrarily thin sediment layer, from the point at which it was originally deposited at the surface, through burial within the dynamic zone, to its arrival within the historical zone.

3. A mathematical model of foraminiferal test accumulation

3.1 Characterising test production and loss

Rates of foraminiferal production are difficult to estimate (Murray and Alve, 2000). In order to simplify the problem, several authors (e.g. Loubere, 1989; Loubere et al., 1993; Jorissen and Wittling, 1999) have divided production into an empirically-defined standing crop and a multiplicative factor representing reproduction or 'turnover' rate. This approach defines the total (e.g. annual) production rate of tests as being *proportionate* to the standing crop. Many studies have observed considerable seasonality in standing crop abundances and composition (Scott and Medioli, 1980; Buzas, 1989; Alve and Murray, 2001; Hippensteel et al., 2002; Duchemin et al., 2005; Debenay et al., 2006) and thus the relationship between the standing crop at any given time and annual production is not obvious. Moreover, seasonal patterns are not necessarily reproduced in successive years (Buzas et al., 2002; Morvan et al., 2006). However, since sedimentation occurs on timescales considerably longer than foraminiferal life spans, assemblages are time-averaged over many generations (Martin, 1999; Olszewski, 1999). Therefore, it is reasonable to assume that total test input does approach proportionality to average standing crop abundances, at least over the long-term (Buzas et al., 2002). Implying proportionality between standing crops and absolute test production is essentially similar to the notion that dead assemblages average out short-term fluctuations in live assemblages, producing an average signal for a given environment (e.g. Saffert and Thomas, 1998; Horton, 1999; Buzas et al., 2002; Horton et al., 2005).

According to this formulation, test production comprises an input of a specific *absolute* number of tests per time interval. Taphonomic loss, however, is usually considered as a *probabilistic* process, by which each specimen has an equal probability of destruction during any given time interval (e.g. Cummins et al., 1986; Loubere and Gary, 1990; Powell, 1992; Olszewski, 1999, 2004; Tomašových et al., 2006). It follows that the absolute number of tests destroyed within a given time interval is a specific *proportion* of the tests which exist. Thus, while test production can be conceptualised as an *additive* process where successively produced cohorts of tests are *added* to those which were previously produced (Martin, 1999), taphonomic loss results in a *proportionate* loss of tests, which is *compounded* through time.

3.2 Mathematical description

As stated by equation 1, considerations of test continuity necessitate that the rate at which dead tests accumulate through time is equal to the rate of test production minus the rate of test destruction, i.e.,

$$\frac{dC}{dt} = P - L \quad (2)$$

where *C* is the concentration of dead tests, *P* the rate of test production, and *L* the rate of test destruction. Given the discussion above, the terms *P* and *L* can be characterised as,

$$P = aR \quad (3)$$

$$L = -\lambda C \quad (4)$$

where *a* is the concentration of living specimens, *R* the reproduction (or turnover) rate, and λ the rate of taphonomic destruction (Table 1). Combining equations 2-4 gives,

$$\frac{dC}{dt} = aR - \lambda C \quad (5)$$

This is the simplest description of the relationship between test accumulation (*C*) through time, and standing crop (*a*). It shows that differences between the numbers of living (i.e., *a*)

symbol	Description	notional unit(s)
C	Concentration of dead foraminiferal tests	cm^{-3}
P	Rate of test production	$cm^{-3}\ yr^{-1}$
L	Rate of test loss	$cm^{-3}\ yr^{-1}$
a	Concentration of living foraminifera	cm^{-3}
R	Rate of standing crop turnover	yr^{-1}
λ	Taphonomic decay rate	yr^{-1}
x	Sedimentary depth	cm
$a(x)$	Concentration of living foraminifera at depth, x	cm^{-3}
$R(x)$	Rate of standing crop turnover at depth, x	yr^{-1}
$\lambda(x)$	Taphonomic decay rate at depth, x	yr^{-1}
w	Sedimentation rate	$cm\ yr^{-1}$
R_0	Rate of standing crop turnover at the sediment surface	yr^{-1}
α	Decay parameter for standing crop turnover with depth	cm^{-1}
C_0	Concentration of dead foraminiferal tests at the sediment surface	cm^{-3}
λ_1	Taphonomic decay rate in the zone of test production	yr^{-1}
λ_2	Taphonomic decay rate below the zone of test production	yr^{-1}
$\tau(x)$	Test residence time	yr

Table 1: Model components used in the derivation and illustrative examples of the model

and dead specimens (C) within sediments depends on either the intrinsic reproduction rate (R; e.g. de Stigter et al., 1999; Jorissen and Wittling, 1999), and/or their susceptibility to taphonomic loss (λ; e.g. Murray, 1989).

Equation 5 describes test accumulation within a stationary reference frame, implying that rates of production (aR) and test loss (λ) remain constant through time and continue indefinitely. Since sedimentation rate (*w*) is a change in *depth* divided by change in *time* (i.e., $w = dx/dt$), substituting depth (*x*) for time (*t*) into equation 5 gives,

$$\frac{dC}{dx} = \frac{a(x)R(x) - \lambda(x)C}{w} \tag{6}$$

This expression now describes dead test concentration, *with depth below the SWI*, in terms of standing crop, and rates of reproduction, taphonomic loss and sedimentation. Given that the parameters *a*, *R*, and *λ* are all specified as functions of depth, this is the most general description of dead test accumulation. In accordance with the *ergodic theorem* (see Olszewski, 2004), this model can be considered to represent the accumulation of tests either within a single layer through time (i.e. with increasing depth during burial), or within all layers at one time (since they simply correspond to layers at successive stages of burial). The variables *C*, *a*, *R* and *λ* may be taken to represent the properties of an individual species or the assemblage as a whole.

3.3 Applications to empirical data

Several applications of the model to empirical data are described below which yield estimates of model parameters and provide insights in the dynamics of assemblage formation.

3.3.1 Estimating standing crop turnover in the absence of taphonomic losses

Jorissen and Wittling (1999) yielded estimates of species standing crop turnover by assuming that taphonomic losses were nil or negligible. On the basis of the model presented, this approach can be extended through burial to estimate the rates of standing crop turnover implied by a cored series of dead assemblages, inclusive of the effects of infaunal test production.

In the absence of taphonomic processes ($\lambda(x) = 0$), equation 6 reduces to,

$$\frac{dC}{dx} = \frac{a(x)R}{w} \tag{7}$$

which can be solved to give,

$$C(x) = \frac{R}{w}\int a(x)dx \tag{8}$$

Equation 8 shows that the concentration of dead tests (C) at a given depth (x) is proportionate to the *cumulative standing crop* to that depth (represented by the integral $\int a(x) dx$). Furthermore, dead test accumulation exceeds the cumulative standing crop by a factor corresponding to the ratio of standing crop turnover and sedimentation rates (R/w). Where sedimentation rate (w) is known, R can be calculated from corresponding standing crop and dead test concentration profiles.

Buzas (1974) presented downcore data on living and dead abundances of the agglutinated species *Ammobaculites exiguus* from the Rhode River, Maryland. Of the four cores analysed, all had infaunal populations down to a depth of 9 cm (the maximum depth examined). At this depth, the average concentration of dead tests was 2595 per cm^3, while the average depth-

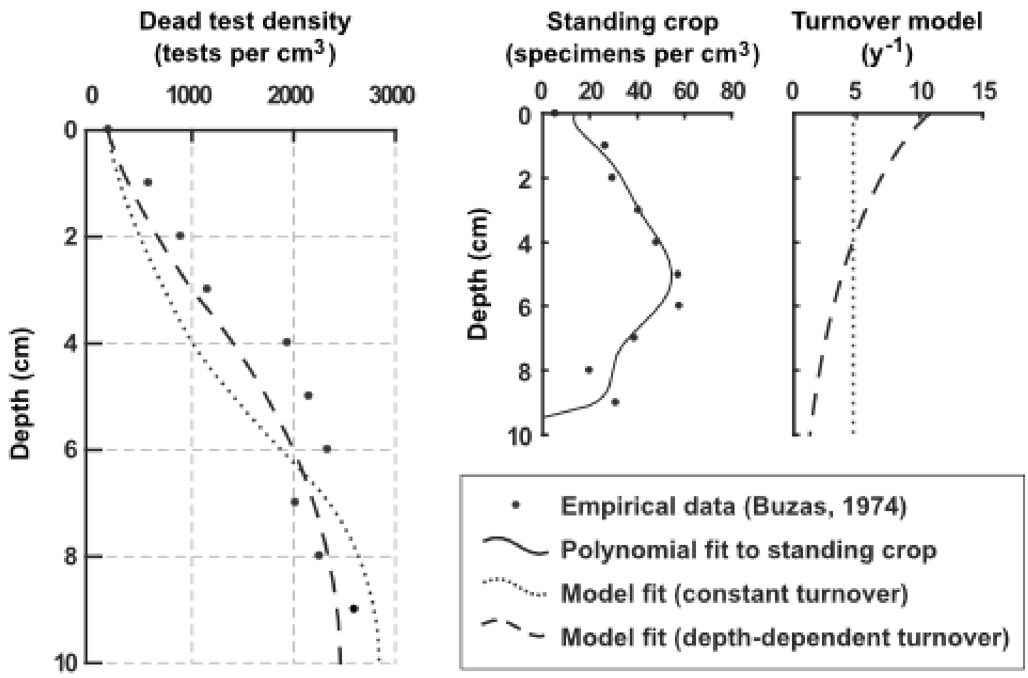

Figure 3: Calculation of standing crop turnover rates for *A. exiguus* from the Rhode River, Maryland (Buzas, 1974): empirical dead test (left) and live specimen (middle) concentrations, with hypothesized depth-profiles for standing crop turnover rate (right). Fitted curves show applications of the model using constant (dotted) and exponentially decreasing (dashed) function of standing crop turnover rate with depth. The dead test concentration profile is seen to be better explained by a standing crop turnover rate which decreases with depth.

integrated living population was 336 specimens per cm^2. Assuming a sedimentation rate of 0.6 cm y^{-1} (estimated by Arnold et al. (2000) from the nearby Severn River), equation 8 estimates an average standing crop turnover rate for the upper 9 cm of sediment of 4.64 y^{-1}. This is within the range of turnover rates estimated for other near-shore sediments (Murray, 1983). Given the assumption of no taphonomic loss, this represents a *minimum* estimate for turnover rates.

A potential caveat to this analysis is that reproduction (R) may be preferentially concentrated near to the SWI (Loubere et al., 1993; de Stigter et al., 1999). This would have the effect of producing a ‘true’ test input which is skewed towards shallow layers from an apparent infaunal standing crop. Indeed, a plot of test accumulation based on equation 8 and a constant turnover rate of 4.64 y^{-1} provides a reasonable fit to the dead test concentration profile (R^2 = 0.86), but model values within the upper 6 cm are consistently under-estimated (Figure 3). This suggests that standing crop turnover occurs more rapidly than the calculated rate within these upper sediments, a hypothesis which can be tested by modelling turnover as a decreasing function of depth.

Incorporating reproduction as a function of depth, equation 8 takes the more general form,

$$C(x) = \frac{1}{w}\int a(x)R(x)dx \tag{9}$$

with test accumulation now proportionate to depth-integrated ‘true production’ ($\int a(x)\, R(x)\, dx$), more accurately reflecting the schematic model suggested by Loubere et al. (1993). Postulating an exponential decrease in turnover rates with depth is the simplest extension to the constant model, increasing the model by just one parameter and permitting turnover rates to decrease asymptotically. Therefore, we may model $R(x)$ as,

$$R(x) = R_0 exp(-\alpha x) \tag{10}$$

where R_0 is the turnover rate at the sediment surface (i.e. $x = 0$), and α is a parameter which describes the decrease in turnover rates with depth x. Combining equations 9 and 10, a least squares, numerical estimate of these two parameters yields R_0 = 8.20 and α = 0.162, suggesting that turnover rates decline from ~8.2 y^{-1} at the sediment surface to ~1.9 y^{-1} at a depth of 9 cm (Figure 3). The improved fit to the observed data (R^2_{adj} = 0.94) can be seen as evidence that turnover rates do decrease with depth into the sediment.

3.3.2 Estimating taphonomic decay rates in the absence of test production

Rates of taphonomic loss can be isolated where test production is considered absent or negligible (e.g. Green et al., 1993). This assumption is perhaps most valid where specimens of a given species are found in dead assemblages but not in associated living assemblages and can therefore be considered to have been transported (e.g. Alve and Murray, 1994; Murray and Alve, 1999; Wang and Chappell, 2001). Assuming that surface assemblages are in equilibrium with these transport processes, and that these effects have impacted consistently over time (Hayward et al., 2004), transported tests represent an ideal opportunity to isolate the effect of taphonomic processes and constrain their rates. In this case (i.e. $a(x) = 0$), and assuming the simplest case where rates of taphonomic loss remain constant with depth (i.e. $\lambda(x) = \lambda$), the appropriate form for the general equation 6 is,

$$\frac{dC}{dx} = \frac{-\lambda}{w}C \qquad (11)$$

which can be solved to give,

$$C(x) = C_0 exp\left(\frac{-\lambda}{w}x\right) \qquad (12)$$

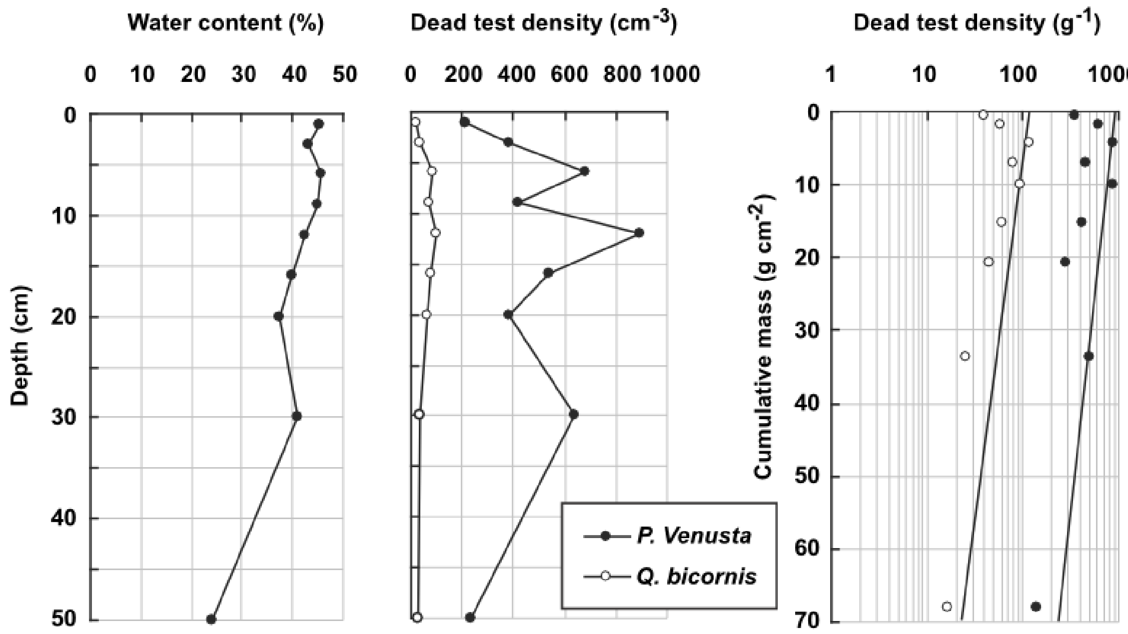

Figure 4: Calculation of taphonomic decay rates for *P. vensuta* and *Q. bicornis* in upper mudflat sediments at Cocoa Creek: sedimentary water content (left), volumetric dead test densities (middle), and test densities per weight of dry sediment (right). Both species are seen to decrease significantly (and exponentially) in abundance with depth into the sediment, which can be interpreted as representing compounding taphonomic losses at a constant downcore rate.

where C_0 is the concentration of tests at the sediment surface (i.e. $x = 0$). Thus, systematically transported species should show a constant abundance downcore (well preserved) or an exponential decrease according to the ratio λ/w. Under known sedimentation rates (w), the taphonomic decay coefficient (λ) can be estimated.

The calcareous species *Pararotalia venusta* and *Quinqueloculina bicornis* were identified in dead assemblages collected from an intertidal mudflat site in Queensland, but were not present within the living community (Berkeley et al., 2008, 2009a). As such they can be tentatively considered to be transported species. High water-content within upper sediment horizons of cores collected from the site caused *volumetric* test densities to *increase* with depth towards the comparatively compacted lower horizons. Correcting for these variations, the test concentrations of these two transported species decline significantly with depth into the sediment (*P. venusta*, $P < 0.05$; *Q. bicornis*, $P < 0.01$; Figure 4). In accordance with the conceptual model, these decreases are considered to represent compounding taphonomic test losses occurring during burial. Given a mass accumulation rate of 0.4317 g y^{-1} calculated using ^{210}Pb activities (Berkeley et al, 2009a), equation 12 estimates taphonomic decay rates of 0.0087 y^{-1} and 0.0103 y^{-1} for *P. venusta* and *Q. bicornis* respectively. Dissolution was argued to be the dominant taphonomic agent for calcareous tests at Cocoa Creek (Berkeley et al., 2009b) and therefore the relative magnitudes of these rates are consistent with expectations based on mineralogy (*P. venusta*, low-Mg calcite; *Q. bicornis*, high-Mg calcite; Peebles and Lewis, 1991). Given the assumption of no test production, these rates represent *minimum* estimates of taphonomic decay.

3.3.3 Standing crop turnover and taphonomic decay rates in a 'tiered' system

Vance et al. (2006) investigated living and dead foraminiferal distributions in the Albermarle estuarine system, North Carolina, for the purpose of assessing their utility as palaeoenvironmental indicators. Core ALB01S3C2, taken in Albermarle Sound, exhibited a consistent biofacies downcore in terms of assemblage composition. However, dead test abundances increased considerably within the upper 14 cm, where the living fauna was concentrated, but declined below this depth (Figure 5). According to the conceptual model outlined here, this pattern can be interpreted as reflecting a gradual accumulation of tests during passage of sediments through the living zone (upper 14 cm), followed by a net decline in test abundances below this depth where taphonomic processes act in the absence of further test production. Thus, the sediment column can be divided into two units; an upper horizon (*x* < 14 cm) where test production and taphonomic processes occur; and a lower horizon (*x* > 14 cm) in which only taphonomic processes operate. Assuming that rates of standing crop turnover (*R*) and taphonomic loss (λ) remain constant with depth, the appropriate forms for equation 6 are,

$$\frac{dC}{dx} = \frac{a(x)R - \lambda_1 C}{w}, \qquad x < 14cm \qquad (13)$$

$$\frac{dC}{dx} = \frac{-\lambda_2}{w} C, \qquad x > 14cm \qquad (14)$$

where λ_1 and λ_2 are the taphonomic decay coefficients within the upper and lower horizons respectively.

Assuming that decay rates are constant with depth and similar in both depth intervals (i.e. $\lambda_1 = \lambda_2$), applying an estimate for λ from the lower horizon to the upper horizon enables the estimation of standing crop turnover rates. This is analogous to the use of sedimentation rates estimated from deeper, non-bioturbated layers within the overlying bioturbated zone in order to obtain bio-diffusion parameters (e.g. Osaki et al., 1997; Dellapenna et al., 1998; Smoak and Patchineelam, 1999; Widdows et al., 2004).

Figure 5 shows the living and dead distributions of the agglutinated species *Ammotium salsum* within the core presented by Vance et al. (2006). Using the calculated sedimentation rate of 0.13 cm y^{-1} (Vance et al., 2006), equation 12 (the solution to equation 14) estimates a taphonomic decay coefficient of 0.0175 y^{-1} for the interval below 14 cm. A least squares, numerical fit to the entire data using this estimate reproduces the observed dead test

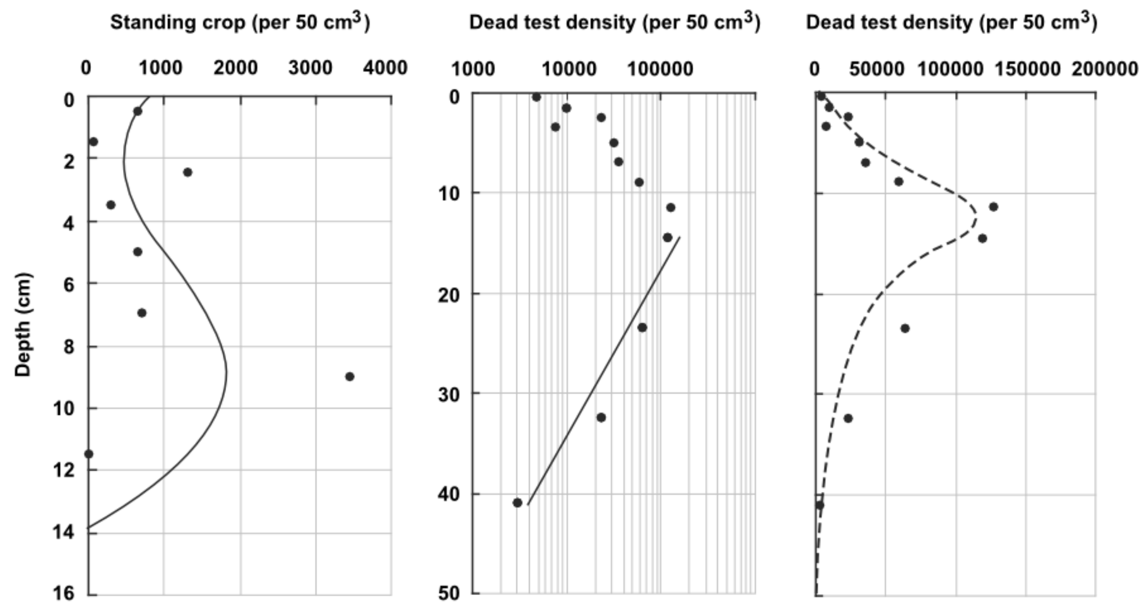

Figure 5: Calculation of standing crop turnover and taphonomic decay rates for *Ammotium salsum* at Albemarle Sound, Virginia (Vance et al., 2006): empirical standing crop with polynomial curve fit (left), logarithmic plot showing exponential decline in test abundance below the living zone (middle), and model fit to empirical dead test concentrations (right). Note, depth scale is not the same on all plots.

concentration profile (R^2_{adj} = 0.85) and constrains standing crop turnover rate to 1.927 y^{-1}. This is at the low end of estimates from other studies (Murray, 1983), and may reflect the assumption of constant taphonomic decay rates over the entire cored interval, which may plausibly be greater at shallower depths.

4. Discussion

.4.1 Conceptual model

According to the conceptual model of assemblage development outlined, test inputs and losses occur during passage of a thin layer of sediment through the shallow sediment horizons where the living community is concentrated and taphonomic processes are most intense. A number of implications emerge from this formulation.

Firstly, assemblage formation is a *cumulative* process such that assemblages asymptotically approach their final character towards deeper levels. Burial through the dynamic zone can therefore be seen as a process of gradual assemblage 'maturation' (*sensu* Sadler, 1993). Surface assemblages from a given environment are likely to be (but are not necessarily) the most dissimilar of all assemblages within the dynamic zone to the character of the eventual mature, fossil assemblage. Similar conclusions have been reported elsewhere (Loubere, 1989, Olszewski, 1999), and have led some authors to advocate the use of assemblages taken from the base of the taphonomically-active zone as the most appropriate modern analogues (Loubere, 1989; Goldstein and Watkins, 1999).

Dead assemblages are the product of the entirety of the test production and taphonomic conditions experienced during burial. As shown elsewhere (Berkeley et al., 2007; Leorri and Martin, 2009), one implication of this is that species' *depth-integrated* standing crops provide the best *a priori* estimate of a species contribution to subsurface dead assemblages. In general, the direct comparison of living and dead assemblages from single horizons is not warranted: living assemblages represent only the most recent test production conditions experienced by the associated dead assemblage. Conceivable exceptions to this rule include surface assemblages and cases where taphonomic destruction occurs rapidly in relation to sedimentation (Hippensteel et al., 2000).

A further consequence of the importance of cumulative production is that, in the absence of taphonomic processes, the depth of test input is irrelevant for controlling the absolute or relative abundance of tests within a mature assemblage. Instead, species microhabitat preferences simply affect the stage, during burial, at which tests are added to a layer. A logical implication of this is the characteristic downcore dead test abundance profiles for 'shallow-' and 'deep-' infaunally produced species described by Loubere (1989). It also follows that, where a living community is made up of different microhabitat types (i.e. is 'stratified'; Berkeley et al., 2007), dead assemblage composition is likely to change during burial, while a more vertically homogenous community results in dead test assemblages which do not change markedly with depth, regardless of the extent to which the living community as a whole lives infaunally (Loubere et al., 1993; Jorissen and Wittling, 1999; Licari and Mackensen, 2005). Taphonomic processes are likely to complicate these patterns, particularly where taphonomic decay rates vary across the depth range of infaunal production (Loubere and Gary, 1990).

4.2 Mathematical model

Equation 6 formally specifies the components of the conceptual model and describes the relationship between them. This mathematical formulation yields a number of conclusions relating to assemblage formation and the interpretation of assemblage data.

According to equation 6, changes in the concentration of dead foraminiferal tests with depth into the sediment reflect changes in the *net* balance of test inputs and losses. Where test inputs exceed losses ($aR > \lambda C$), tests continue to accumulate within a given sediment layer and dead test concentrations exhibit an *increase* with depth (Figure 6). If test losses are greater than test inputs ($aR < \lambda C$) a layer of sediment experiences a net loss of tests and a *decreasing* dead test concentration profile results. The latter situation occurs - by definition - where test production is absent, for example, in the case of transported species, or below the maximum depth of (infaunal) test production. A constant dead test abundance profile represents an equilibrium between test inputs and losses of which the historical zone (aR =

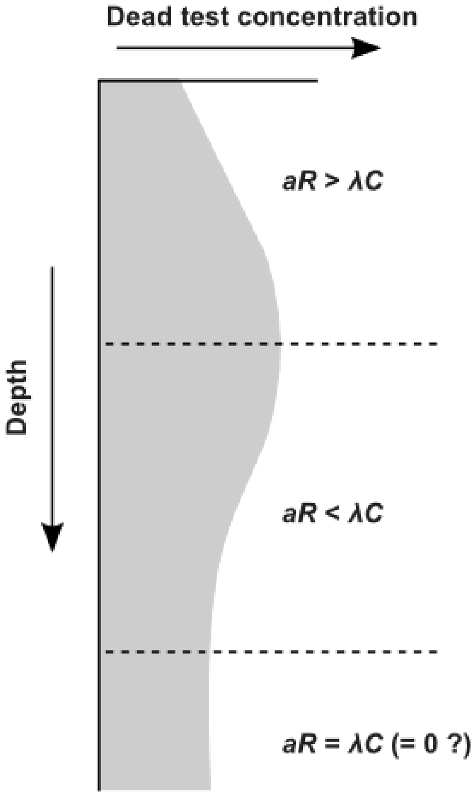

Figure 6: A hypothetical dead test concentration profile illustrating the possible inferences regarding test production and loss. Dead test concentrations which *increase* with depth reflect test inputs to a volume of sediment undergoing burial being greater than test losses. A decreasing dead test concentration profile results where test losses exceed test inputs. Constant dead test concentrations imply a balance between test inputs and losses.

$\lambda C = 0$) represents a special case (Figure 6). The precise rate at which test concentrations change with depth is dependent on sedimentation rate (w). Test input is proportionate to standing crop turnover rate (R) and inversely proportionate to sedimentation rate (equation 6), which is consistent with the models of shell accumulation proposed by Kidwell (1985, 1986).

It follows that the effects of infaunal test production and taphonomic processes cannot be identified on the basis of trends in dead test abundances alone, which indicate only their net, combined effect. The model presented does, however, provide a framework in which these components can potentially be separated. By applying the model to counterpart standing crop and dead test concentration profiles, implied rates of standing crop turnover and/or taphonomic losses can be estimated. This approach is conceptually similar to previous work which attributes differences between living and dead assemblages to the effects of reproduction or taphonomy (Murray, 1989; Jorissen and Wittling, 1999; Murray and Alve, 1999; de Stigter et al., 1999; Wang and Chappell, 2001) but additionally takes into consideration the *cumulative* nature of test production, the *compounding* nature of taphonomic losses, and the dimension of burial, including the rate of burial and the depth-dependency of processes (e.g. infauna).

Data on living and dead foraminiferal assemblages and sedimentation rates are relatively easily obtainable, making rates of standing crop turnover ($R(x)$) and taphonomic loss ($\lambda(x)$) the principal uncertainties in the understanding of assemblage formation. In such cases, a large range of possible combinations of these values may adequately explain the same sequence of dead test concentrations. These dual unknowns therefore complicate any application of this and other models, and could be considered the central problem in understanding assemblage formation. As shown, however, the model presented has the ability to explain empirical dead test concentrations where reasonable, simplifying assumptions are made, and yields estimates for standing crop turnover and taphonomic decay rates. Such estimates can be compared against independent observations (e.g. culture/dissolution experiments, taphonomic analyses) or form the basis for quantitative comparisons between species, habitats (e.g. low- versus high-intertidal) or sites.

Given the ambiguity of multiple unknown factors, it is crucial that interpretations of buried foraminiferal assemblages are associated with a well-specified, mechanistic conception of assemblage formation if they are to be clearly understood and conclusive. The conceptual and mathematical models presented represent a coherent system of definitions, relations and assumptions which provide a framework within which ideas relating to assemblage formation can be described, understood and evaluated. For example, Hippensteel et al. (2000) described estimates of residence time for agglutinated tests within the sediments of a Delaware salt marsh ranging from a few years to two centuries. Residence times were calculated separately for successive sediment horizons, using the formula,

$$\tau(x) = \frac{C(x)}{a(x)} \qquad (15)$$

where $\tau(x)$ is the residence time of tests at a given horizon, x, and $a(x)$ and $C(x)$ are the living and dead specimen concentrations, respectively, at the same horizon. By comparing dead test concentrations with living populations from *the same depth*, Hippensteel et al. (2000) effectively considered dead assemblages to be the product of production and taphonomic processes operating solely within each respective horizon. In terms of the conceptual model described here, this means that assemblage formation at each depth occurs within discrete, static reference frames. The appropriate model form for this situation therefore omits sedimentation (equation 5), and can be solved to give,

$$C(t) = \frac{aR}{\lambda}[1 - exp(-\lambda t)] \qquad (16)$$

This expression implies that, through time (i.e. $t \rightarrow \infty$), the concentration of dead tests converges to a maximum - corresponding to aR/λ - at which taphonomic losses are in equilibrium with test inputs from the living population. Under these conditions, and given that residence times are the reciprocal of decay constants (i.e. $1/\lambda$), equation 16 reduces to an expression for test residence time which is directly equivalent to the method of Hippensteel et al. (2000):

$$\tau = \frac{1}{\lambda} = \frac{C}{aR} \quad (17)$$

As such, the residence times calculations of Hippensteel et al. (2000) can be considered a special case of our model in which: (1) rates of taphonomic decay are sufficiently high relative to sedimentation ($\lambda >> w$) that the earlier contributions of tests from overlying horizons during burial are negligible; (2) dead test concentrations are at steady-state (test inputs = test losses); and (3) observed living populations represent the entirety of annual production (i.e. $R = 1$). Hippensteel et al. (2000) therefore approached the problem of multiple unknowns (standing crop turnover and taphonomic decay rates) by normalizing against a standing crop turnover rate of 1. This example demonstrates the value of a detailed framework for understanding assemblage formation in reconciling and contextualising interpretations of empirical data.

4.3 Future development

The model presented is a generalised but minimal description of assemblage formation. Test production and taphonomic loss represent perhaps the core processes required in any model of foraminiferal assemblage formation, although other processes (e.g. bioturbation, compaction, varying sedimentation rates) are likely to be important in some cases. As shown in the example applications, the generalised nature of equation 6 enables the introduction of assumptions, empirical models or other modelling techniques which may be appropriate to particular modelling problems or constraints. Furthermore, the conceptual and mathematical ideas described in this paper are compatible with a range of existing modelling techniques (e.g. bioturbation, diagenesis; Berner, 1980; Boudreau, 1996). The application of the model to a broader range of problems and data, and the integration of additional features, should be a research priority.

In intertidal areas, foraminiferal faunas vary with elevational changes on the order of centimetres to decimetres (Scott and Medioli, 1978; Patterson, 1990; Horton et al., 1999, 2003, 2005; Hawkes et al., 2010; Leorri et al., 2010; Callard et al., 2011), similar to the vertical scales on which post-depositional processes operate. The ultimate challenge in understanding assemblage formation is the differentiation of these two effects such that environmental changes can be isolated and the palaeo-environmental record accurately interpreted. The model presented here explains foraminiferal test accumulation entirely in terms of systematic processes occurring during burial, and thereby assumes non-varying background conditions, i.e. “environmental steady-state”. This assumption is a necessary condition for the isolation and recognition of post-depositional effects specifically. Conventional approaches to the analysis of infaunal and taphonomic effects, wherein surface assemblages are compared with those occurring below within the same core (e.g. Jonasson and Patterson, 1992; Goldstein and Harben, 1993; Goldstein et al.,1995; Culver et al.,1996; Ozarko et al.,1997; Goldstein and Watkins, 1998, 1999; Patterson et al., 1999; Hippensteel et al., 2000; Culver and Horton, 2005; Tobin et al., 2005; Leorri and Martin, 2009; Culver et al., 2013), similarly imply that each assemblage originated under the same conditions as those at the contemporary surface (otherwise the comparisons are ambiguous).

This presents a paradox: if cored sequences of foraminiferal assemblages can be considered to represent environmental steady-state for the purposes of post-depositional studies, how can they be considered to provide a record of *environmental transitions* in palaeoenvironmental studies? The paradox is resolved by recognising that successive assemblages within a single core can only be considered to have originated at a similar elevation when buried under vertical aggradation (i.e. sediment accumulation rate equal to the rate of sea level rise). Where shorelines exhibit different modes of development (e.g. progradation, retrogradation), successively older deposits *with the same origin* do not occur directly beneath one another (Culver & Horton, 2005), and the post-depositional modification of a particular biofacies is not represented within a single core. Tracking assemblages *along strata* is a more general approach to controlling for environmental transitions and isolating the post-depositional signal, and enables a direct link to be made between surface assemblages, progressively modified subsurface assemblages, and the eventual 'mature' assemblages which enter the fossil record (Berkeley et al. 2009a). Applying the concepts and methods described in this paper along the appropriate "burial trajectories" (rather than reflexively downcore) represents a novel but potentially effective approach to differentiating the various influences on the formation of the palaeoenvironmental record.

5. Conclusions.

The use of intertidal foraminifera in reconstructing former sea levels 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.

Assemblage formation can be conceptualised in terms of the balance of test inputs and losses through a volume of sediment undergoing burial. Tests are added to a volume of sediment via test production (including infaunal production) and removed via taphonomic processes. During burial, the conditions of test production and loss experienced by a given volume of sediment vary until burial within the "historical zone" where - by definition - an assemblage is "fossilised". Assemblage "maturation" is the asymptotic process by which a parcel of sediment accumulates dead foraminiferal tests during passage through the upper sedimentary zones of test production and taphonomic processes.

A mathematical model of assemblage maturation is shown to explain empirical dead test distributions in terms of empirically-defined standing crops and sedimentation rates, together with model estimates of standing crop turnover and/or taphonomic decay rates. This approach provides a quantitative basis 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, emphasizing the need for a detailed and coherent framework for understanding the mechanics assemblage formation if interpretations are to be clear and conclusive.

The model presented is highly flexible and extensible. The next major challenge is the integration of additional processes such as bioturbation and the application of the model within a framework which reconciles post-depositional processes and environmental transitions.

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