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

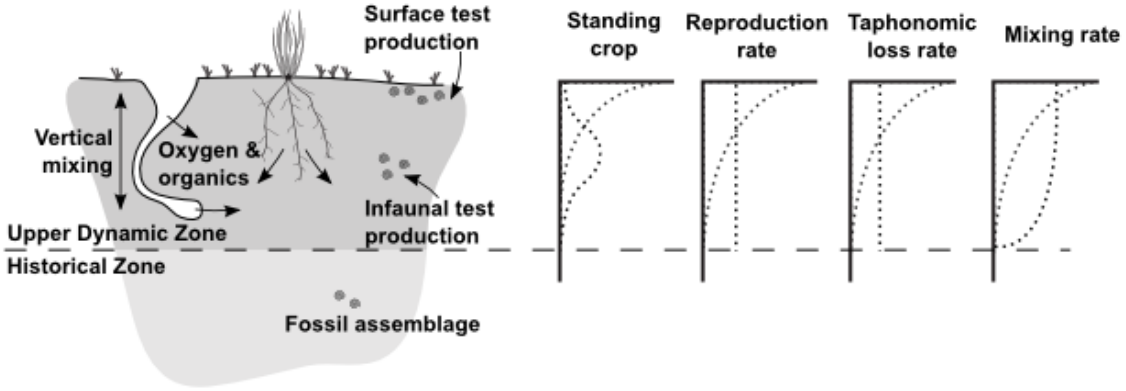
with depth into the sediment (Figure 1). This paper aims to address this shortfall by presenting a conceptual and mathematical description of assemblage formation during burial.

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*



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120 Figure 1: The two primary zones comprising the assemblage forming system. The "dynamic
121 zone" is defined as the upper sedimentary interval within which all test production and
122 appreciable taphonomic losses occur. The introduction of organic material and oxygen into
123 subsurface sediments is likely to influence the depth to which foraminiferal populations live
124 and taphonomic processes (e.g. mineralization of organic cements, calcareous dissolution)
125 operate (Berkeley et al, 2007). The "historical zone" represents the depth beyond which no
126 further assemblage forming processes operate and wherein assemblages are effectively
127 fossilised. The schematic plots show notional depth-distributions of rates of test input, loss
128 and mixing (adapted from Loubere et al., 1993).

129

130 (TAZ; Davies et al., 1989; Powell, 1992; Flessa et al., 1993; Martin et al., 1996; Meldahl et
131 al., 1997; Olszewski, 2004; Powell et al., 2012), which describes the tendency for
132 taphonomic processes to be concentrated close to the sediment surface. The respective depths
133 to which test production, taphonomic destruction and bioturbation occur are, in principle,
134 independent, but these processes may share some common influences (e.g. sedimentary
135 oxygen penetration, organic matter supply) or indeed directly influence one another (Aller,
136 1982; Jorissen et al., 1995; Moodley et al., 1998; de Stigter et al., 1998; Barbieri, 2001; Licari
137 et al., 2003; Debenay et al., 2004; Geslin et al., 2004; Berkeley et al., 2007). Consequently,
138 their depth ranges may broadly coincide. The dynamic zone may plausibly range from a few
139 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,

$$\textit{change in dead test concentration} = \textit{rate of test production} - \textit{rate of test loss} \quad (1)$$

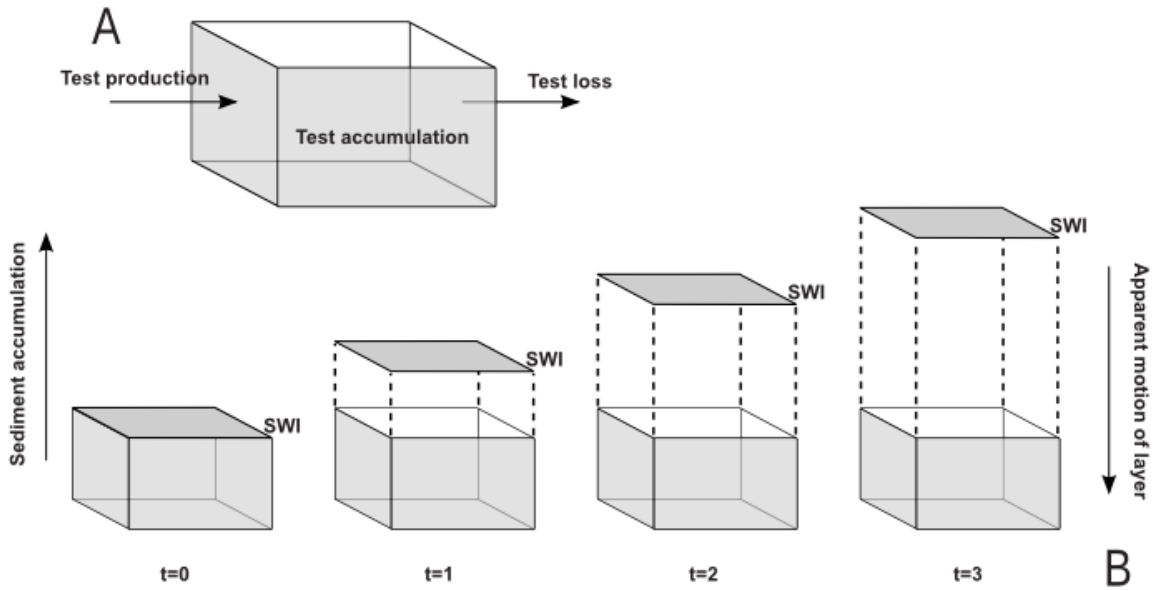


Figure 2: (A) Test accumulation in a volume of sediment based on considerations of material balance: tests enter the volume via test production and are removed by taphonomic losses. Accumulation of tests within the volume through time equals the difference between additions and losses; (B) Apparent advection 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

178 processes *currently* acting, and taken to its logical conclusion, that these processes continue
179 to act within the volume indefinitely. Such a model is appropriate when considering short-
180 term assemblage dynamics (e.g. Green et al., 1993) or surficial sediments only (Murray,
181 1989; Culver et al., 1996; Edwards and Horton, 2000; Wang and Chappell, 2001; Horton and
182 Murray, 2006), but in the context of palaeo-environmental applications, it is necessary to
183 consider the effect of burial.

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

192 Rates of test production and taphonomic processes are likely to vary with depth into the
193 sediment (Figure 1; Loubere et al., 1993). It is well known that living populations vary with
194 depth depending on the microhabitat preferences of species (e.g. Matera and Lee, 1972;
195 Goldstein and Harben, 1993; Goldstein et al., 1995; Ozarko et al., 1997; Saffert and Thomas,
196 1998; Duchemin et al., 2005; Berkeley et al., 2008; Culver et al., 2013). Some authors have
197 suggested that standing crop turnover rates also decline with depth below the SWI, perhaps
198 due to decreasing oxygen availability and organic matter quality (Loubere et al., 1993; de
199 Stigter et al., 1999). The probability of taphonomic loss may also decline beneath the SWI
200 (e.g. Alexandersson, 1978; Aller, 1982; Cummins et al., 1986; Powell, 1992; Loubere et al.,
201 1993; Olszewski, 2004), with the depth to which taphonomic processes act defining the TAZ
202 (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

293

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

295

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

299 Equation 5 describes test accumulation within a stationary reference frame, implying that
300 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,

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

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,

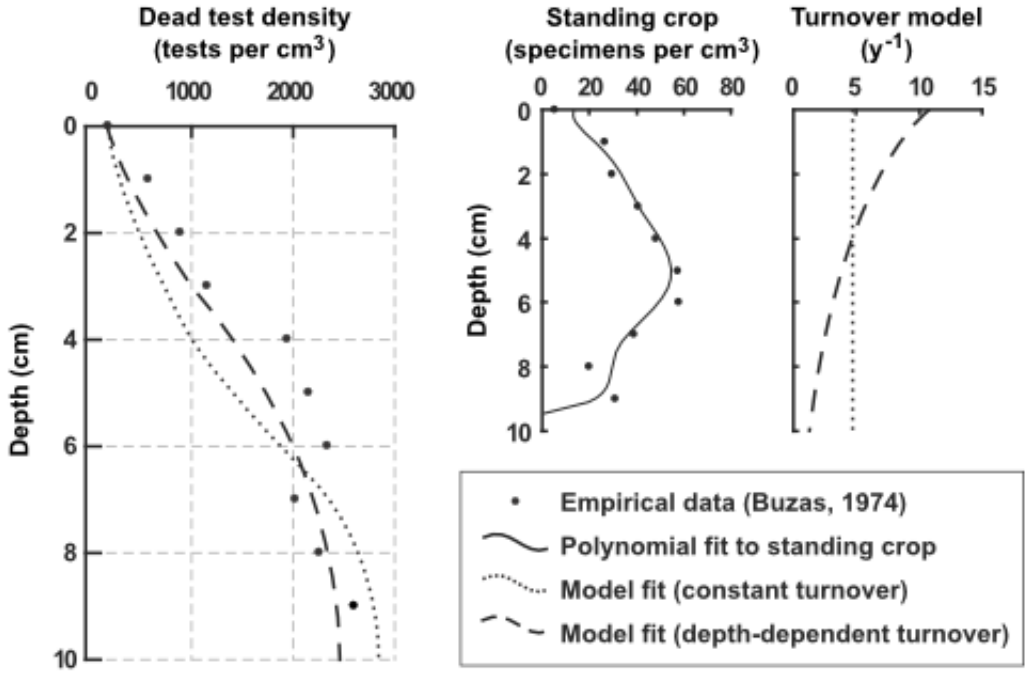
$$\frac{dC}{dx} = \frac{a(x)R}{w} \tag{7}$$

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-



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

348

349 integrated living population was 336 specimens per cm^2. Assuming a sedimentation rate of
350 0.6 cm y^{-1} (estimated by Arnold et al. (2000) from the nearby Severn River), equation 8
351 estimates an average standing crop turnover rate for the upper 9 cm of sediment of 4.64 y^{-1}.
352 This is within the range of turnover rates estimated for other near-shore sediments (Murray,
353 1983). Given the assumption of no taphonomic loss, this represents a *minimum* estimate for
354 turnover rates.

355 A potential caveat to this analysis is that reproduction (*R*) may be preferentially
356 concentrated near to the SWI (Loubere et al., 1993; de Stigter et al., 1999). This would have

357 the effect of producing a 'true' test input which is skewed towards shallow layers from an
358 apparent infaunal standing crop. Indeed, a plot of test accumulation based on equation 8 and a
359 constant turnover rate of 4.64 y^{-1} provides a reasonable fit to the dead test concentration
360 profile (R^2 = 0.86), but model values within the upper 6 cm are consistently under-estimated
361 (Figure 3). This suggests that standing crop turnover occurs more rapidly than the calculated
362 rate within these upper sediments, a hypothesis which can be tested by modelling turnover as
363 a decreasing function of depth.

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

365

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

366

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

372

$$R(x) = R_0 exp(-\alpha x) \qquad (10)$$

373

374 where R_0 is the turnover rate at the sediment surface (i.e. x = 0), and α is a parameter which
375 describes the decrease in turnover rates with depth x. Combining equations 9 and 10, a least
376 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,

$$\frac{dC}{dx} = \frac{-\lambda}{w} C \tag{11}$$

which can be solved to give,

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

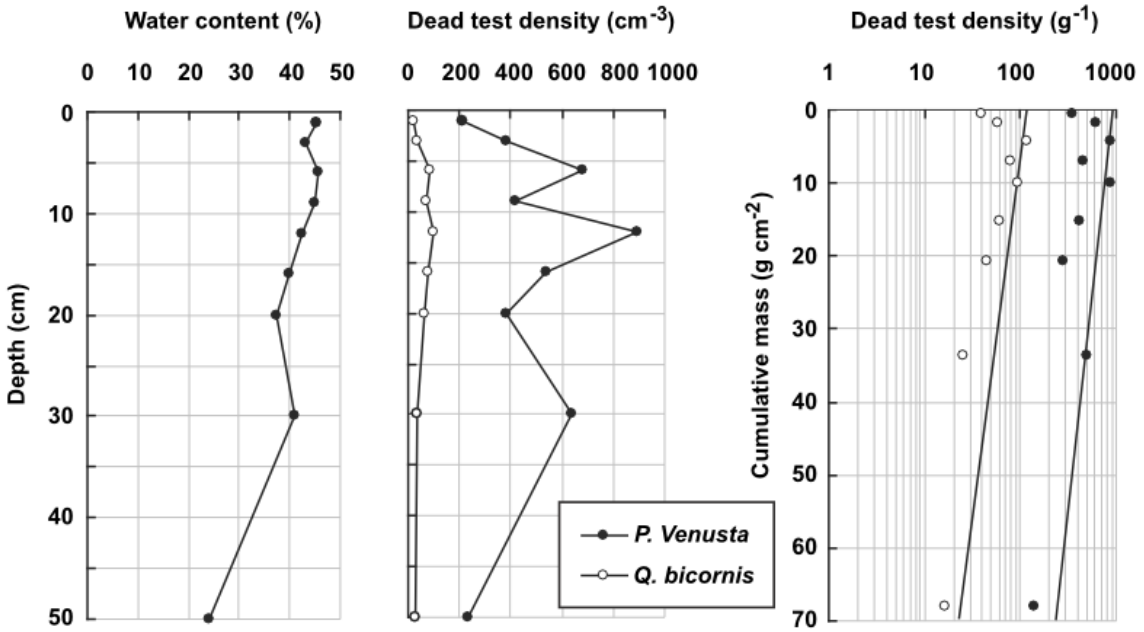


Figure 4: Calculation of taphonomic decay rates for *P. vensuta* and *Q. bicornis* in upper mudflat sediments at Cocoa Creek: sedimentary water content (left), volumetric dead test densities (middle), and test densities per weight of dry sediment (right). Both species are seen to decrease significantly (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

436 test production. Thus, the sediment column can be divided into two units; an upper horizon (x
437 < 14 cm) where test production and taphonomic processes occur; and a lower horizon (x > 14
438 cm) in which only taphonomic processes operate. Assuming that rates of standing crop
439 turnover (R) and taphonomic loss (λ) remain constant with depth, the appropriate forms for
440 equation 6 are,

441

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

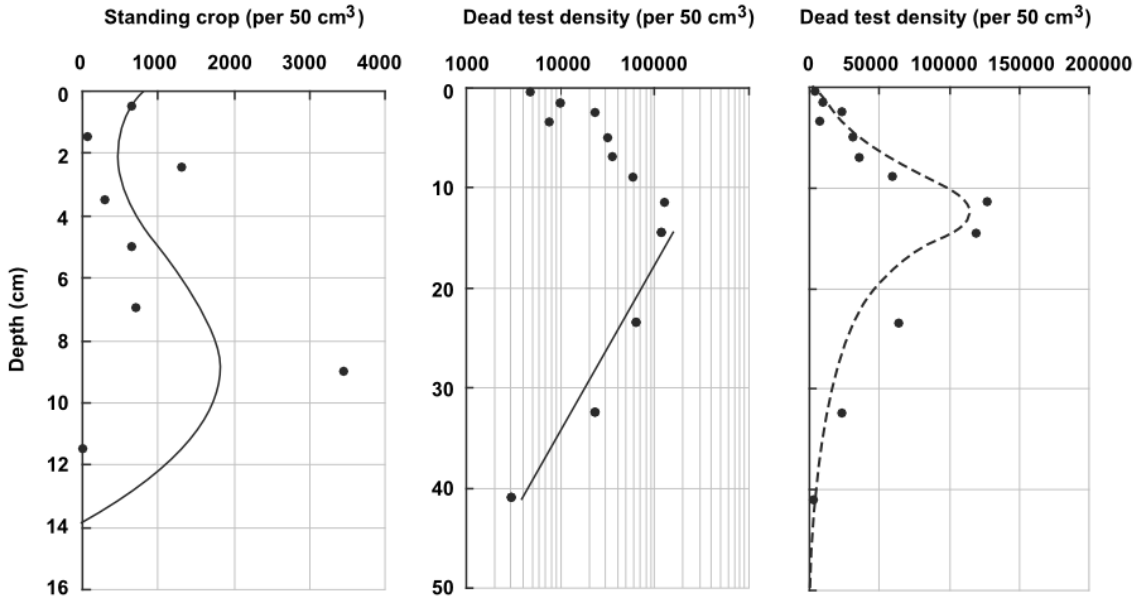
$$\frac{dC}{dx} = \frac{-\lambda_2}{w} C, \qquad x > 14cm \tag{14}$$

442

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

445 Assuming that decay rates are constant with depth and similar in both depth intervals (i.e. λ_1
446 = λ_2), applying an estimate for λ from the lower horizon to the upper horizon enables the
447 estimation of standing crop turnover rates. This is analogous to the use of sedimentation rates
448 estimated from deeper, non-bioturbated layers within the overlying bioturbated zone in order
449 to obtain bio-diffusion parameters (e.g. Osaki et al., 1997; Dellapenna et al., 1998; Smoak
450 and Patchineelam, 1999; Widdows et al., 2004).

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



456

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

462

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

467

468 **4. Discussion**

469 *.4.1 Conceptual model*

470 According to the conceptual model of assemblage development outlined, test inputs and
471 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).

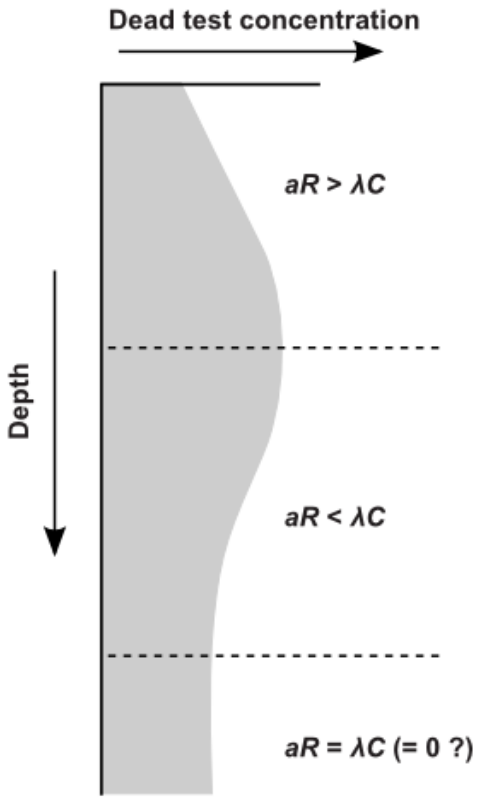
A further consequence of the importance of cumulative production is that, in the absence of taphonomic processes, the depth of test input is irrelevant for controlling the absolute or relative abundance of tests within a mature assemblage. Instead, species microhabitat preferences simply affect the stage, 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 ($aR =$



520

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

526

527 $\lambda C = 0$) represents a special case (Figure 6). The precise rate at which test concentrations
528 change with depth is dependent on sedimentation rate (w). Test input is proportionate to
529 standing crop turnover rate (R) and inversely proportionate to sedimentation rate (equation 6),
530 which is consistent with the models of shell accumulation proposed by Kidwell (1985, 1986).

531 It follows that the effects of infaunal test production and taphonomic processes cannot be
532 identified on the basis of trends in dead test abundances alone, which indicate only their net,
533 combined effect. The model presented does, however, provide a framework in which these
534 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,

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

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,

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

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

580 expression for test residence time which is directly equivalent to the method of Hippensteel et
581 al. (2000):

582

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

583

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

594

595 *4.3 Future development*

596 The model presented is a generalised but minimal description of assemblage formation. Test
597 production and taphonomic loss represent perhaps the core processes required in any model
598 of foraminiferal assemblage formation, although other processes (e.g. bioturbation,
599 compaction, varying sedimentation rates) are likely to be important in some cases. As shown
600 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

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

641

642 **5. Conclusions**.

643 The use of intertidal foraminifera in reconstructing former sea levels may be complicated by
644 processes such as infaunal test production, taphonomic degradation and bioturbation which
645 act to modify contemporary analogue (surface) assemblages during and subsequent to burial.
646 Understanding the palaeoenvironmental significance of these processes is limited by the
647 absence of a clear theoretical description of the mechanics of foraminiferal assemblage
648 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.

671 **References**

672 Alexandersson, E.T., 1978, Destructive diagenesis of carbonate sediments in the eastern
673 Skagerrak, North Sea: Geology, v. 6, p. 324-327.

674

675 Aller, R.C., 1982, Carbonate dissolution in nearshore terrigenous muds: the role of physical
676 and biological reworking: Journal of Geology, v. 90, p. 79-95.

677

678 Alve, E. and Murray, J.W., 1994, Ecology and taphonomy of benthic foraminifera in a
679 temperate mesotidal inlet: Journal of Foraminiferal Research, v. 24, p. 18-27.

680

681 Alve, E. and Murray, J.W., 2001, Temporal variability in vertical distributions of live
682 (stained) intertidal foraminifera, southern England: Journal of Foraminiferal Research, v. 31,
683 p. 12-24.

684

685 Arnold, R.R., Cornwell, J.C., Dennison, W.C. and Stevenson, J.C., 2000, Sediment-based
686 reconstruction of submersed aquatic vegetation distribution in the Severn River, a sub-estuary
687 of Chesapeake Bay: Journal of Coastal Research, v. 16, p. 188-195.

688

689 Barbieri, R., 2001, Taphonomic implications of foraminiferal composition and abundance in
690 intertidal mudflats, Colorado River Delta (Mexico): Micropaleontology, v. 47, p. 73-86.

691

692 Barbosa, C.F., Scott, D.B., Seoane, J.C.S. and Turcq, B.J., 2005, Foraminiferal zonations as
693 base lines for quaternary sea-level fluctuations in south-southeast Brazilian mangroves and
694 marshes: Journal of Foraminiferal Research, v. 35, p. 22-43.

695

696 Berkeley, A., Perry, C.T., Smithers, S.G., Horton, B.P. and Taylor, K.G., 2007, A review of
697 the ecological and taphonomic controls on foraminiferal assemblage development in
698 intertidal environments: Earth-Science Reviews, v. 83, p. 205-230.

699

700 Berkeley, A., Perry, C.T., Smithers, S.G., and Horton, B.P., 2008, The spatial and vertical
701 distribution of living (stained) benthic foraminifera from a tropical, intertidal environment,
702 north Queensland, Australia: Marine Micropaleontology, v. 69, p. 240–261.

Berkeley, A., Perry, C.T., Smithers, S.G., Horton, B.P., and Cundy, A.B., 2009a, Foraminiferal biofacies across mangrove-mudflat environments at Cocoa Creek, north Queensland, Australia: Marine Geology, v. 263, p. 64–86.

Berkeley, A., Perry, C.T., and Smithers, S.G., 2009b, Taphonomic signatures and patterns of test degradation on tropical, intertidal benthic foraminifera: Marine Micropaleontology, v. 73, p. 148–163.

Berner, R. A., 1980, Early Diagenesis: A Theoretical Approach: Princeton University Press, Princeton, 241 p.

Boudreau, B.P., 1996, Diagenetic models and their implementation: modelling transport and reactions in aquatic sediments: Springer-Verlag, Berlin, 424 p.

Buzas, M.A., 1974, Vertical distribution of Ammobaculites exiguus in the Rhode River, Maryland: Journal of Foraminiferal Research, v. 4, p. 144-147.

Buzas, M.A., 1989, The effect of quartz versus calcareous sand on the densities of living foraminifera: Micropaleontology, v. 35, p. 135-141.

Buzas, M.A., Hayek, L.C., Reed, S.A. and Jett, J.A., 2002, Foraminiferal densities over five years in the Indian River lagoon, Florida: a model of pulsating patches: Journal of Foraminiferal Research, v. 32, p. 68-93.

Callard, S.L., Gehrels, W.R., Morrison, B.V. and Grenfell, H. R., 2011, Suitability of salt-marsh foraminifera as proxy indicators of sea level in Tasmania: Marine Micropaleontology, v. 79, p. 121-131.

Culver, S.J. and Horton, B.P., 2005, Infaunal marsh foraminifera from the Outer Banks, North Carolina, USA: Journal of Foraminiferal Research, v. 35, p. 148-170.

735 Culver, S.J., Woo, H.J., Oertel, G.F. and Buzas, M.A., 1996, Foraminifera of coastal
736 depositional environments, Virginia, USA: distribution and taphonomy: Palaios, v. 11, p.
737 459-486.

738

739 Culver, S.J., Leorri, E., Corbett, D.R., Mallinson, D.J., Shazili, N.A.M., Mohammad, M.N.,
740 Parham, P.R and Yaacob, R., 2013, Infaunal mangrove swamp foraminifera in the Setiu
741 Wetland, Terengganu, Malaysia: Journal of Foraminiferal Research, v. 43, p. 262-279.

742

743 Cummins, H., Powell, E.N., Stanton, R.J. and Staff, G., 1986, The rate of taphonomic loss in
744 modern benthic habitats: how much of the potentially preservable community is preserved?:
745 Palaeogeography, Palaeoclimatology, Palaeoecology, v. 52, p. 291-320.

746

747 Davies, D.J., Powell, E.N. and Stanton, R.J., 1989, Relative rates of shell dissolution and net
748 sediment accumulation – a commentary – can shell beds form by the gradual accumulation of
749 biogenic debris on the sea-floor?: Lethaia, v. 22, p. 207-232.

750

751 Debenay, J-P., Guiral, D. and Parra, M., 2004, Behaviour and taphonomic loss in
752 foraminiferal assemblages of mangrove swamps of French Guiana: Marine Geology, v. 208,
753 p. 295-314.

754

755 Debenay, J-P., Bicchi, E., Goubert, E. and du Chatelet, E.A., 2006, Spatio-temporal
756 distribution of benthic foraminifera in relation to estuarine dynamics (Vie Estuary, Vendee,
757 France): Estuarine, Coastal and Shelf Science, v. 67, p. 181-197.

758

759 Dellapenna, T.M., Kuehl, S.A. and Schaffner, L.C., 1998, Sea-bed mixing and particle
760 residence times in biologically and physically dominated estuarine systems: a comparison of
761 lower Chesapeake Bay and the York River subestuary: Estuarine, Coastal and Shelf Science,
762 v. 46, p. 777-795.

763

764 Denne, R.A. and Sen Gupta, B.K., 1989, Effects of taphonomy and habitat on the record of
765 benthic foraminifera in modern sediments: Palaios, v. 4, p. 414-423.

766

767 de Rijk, S. and Troelstra, S., 1999, The application of a foraminiferal actuo-facies model to
768 saltmarsh cores: Palaeogeography, Palaeoclimatology, Palaeoecology, 149, 59-66.

de Stigter, H.C., Jorissen, F.J. and van der Zwaan, G.J., 1998, Bathymetric distribution and microhabitat partitioning of live (rose Bengal stained) benthic foraminifera along a shelf to bathyal transect in the southern Adriatic Sea: Journal of Foraminiferal Research, v. 28, p. 40-65.

de Stigter, H.C., van der Zwaan, G.J. and Langone, L., 1999, Differential rates of benthic foraminiferal test production in surface and subsurface sediment habitats in the southern Adriatic Sea: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 67-88.

Duchemin, G., Jorissen, F.J., Redois, F. and Debenay, J-P., 2005, Foraminiferal microhabitats in a high marsh: consequences for reconstructing past sea levels: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 226, p. 167-185.

Edwards, R.J. and Horton, B.P., 2000, Reconstructing relative sea-level change using UK salt-marsh foraminifera: Marine Geology, v. 169, p. 41-56.

Edwards, R.J., Wright, A.J. and van de Plassche, O., 2004, Surface distribution of salt-marsh foraminifera from Connecticut, USA: modern analogues for high-resolution sea level studies: Marine Micropaleontology, v. 51, p. 1-21.

Flessa, K.W., Cutler, A.H. and Meldahl, K.H., 1993, Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat: Paleobiology, v. 19, p. 266-286.

Geslin, E., Heinz, P., Jorissen, F. and Hemleben, C., 2004, Migratory responses of deep-sea benthic foraminifera to variable oxygen conditions: laboratory investigations: Marine Micropaleontology, v. 53, p. 227-243.

Goldstein, S.T. and Harben, E.B., 1993, Taphofacies implications of infaunal foraminiferal assemblages in a Georgia salt marsh, Sapelo Island: Micropaleontology, v. 39, p. 53-62.

801 Goldstein, S.T. and Watkins, G.T., 1998, Elevation and the distribution of salt-marsh
802 foraminifera, St. Catherine's Island, Georgia: a taphonomic approach: Palaios, v. 13, p. 570-
803 580.

804

805 Goldstein, S.T. and Watkins, G.T., 1999, Taphonomy of salt marsh foraminifera: an example
806 from coastal Georgia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 103-
807 114.

808

809 Goldstein, S.T., Watkins, G.T., and Kuhn, R.M., 1995, Microhabitats of salt marsh
810 foraminifera: St. Catherine's Island, Georgia, USA: Marine Micropaleontology, v. 26, p. 17-
811 29.

812

813 Green, M.A., Aller, R.C. and Aller, J.Y., 1993, Carbonate dissolution and temporal
814 abundances of foraminifera in Long Island Sound sediments: Limnology and Oceanography,
815 v. 38, p. 331-345.

816

817 Guinasso, N.L. and Schink, D.R., 1975, Quantitative estimates of biological mixing rates in
818 abyssal sediments: Journal of Geophysical Research – Oceans and Atmospheres, v. 80, p.
819 3032-3043.

820

821 Hawkes, A.D., Horton, B.P., Nelson, A.R. and Hill, D.F., 2010, The application of intertidal
822 foraminifera to reconstruct coastal subsidence during the giant Cascadia earthquake of AD
823 1700 in Oregon, USA: Quaternary International, v. 221, p. 116-140.

824

825 Hayward, B.W., Scott, G.H., Grenfell, H.R., Carter, R. and Lipps, J.H., 2004, Techniques for
826 estimation of tidal elevation and confinement (similar to salinity) histories of sheltered
827 harbours and estuaries using benthic foraminifera: examples from New Zealand: Holocene, v.
828 14, p. 218-232.

829

830 Horton, B.P., 1999, The distribution of contemporary intertidal foraminifera at Cowpen
831 Marsh, Tees Estuary, UK: Implications for studies of Holocene sea-level changes:
832 Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 127-149.

833

Horton, B.P. and Murray, J.W., 2006, Patterns in cumulative increase in live and dead species from foraminiferal time series of Cowpen Marsh, Tees Estuary, UK: Implications for sea-level studies: Marine Micropaleontology, v. 58, p. 287-315.

Horton, B.P., Edwards, R.J. and Lloyd, J.M., 1999, UK intertidal foraminiferal distributions: implications for sea-level studies: Marine Micropaleontology, v. 36, p. 205-223.

Horton, B.P., Larcombe, P., Woodroffe, S.A., Whittaker, J.E., Wright, M.R. and Wynn, C., 2003, Contemporary foraminiferal distributions of a mangrove environment, Great Barrier Reef coastline, Australia: implications for sea-level reconstruction: Marine Geology, v. 198, p. 225-243.

Horton, B.P., Whittaker, J.E., Thompson, K.H., Hardbattle, M.I.J., Kemp, A., Woodroffe, S.A. and Wright, M.R., 2005, The development of a modern foraminiferal data set for sea-level reconstructions, Wakatobi Marine National Park, Southeast Sulawesi, Indonesia: Journal of Foraminiferal Research, v. 35, p. 1-14.

Hippensteel, S.P. and Martin, R.E., 1999, Foraminifera as an indicator of overwash deposits, Barrier Island sediment supply, and Barrier Island evolution: Folly Island, South Carolina: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 115-125.

Hippensteel, S.P., Martin, R.E., Nikitina, D. and Pizzuto, J.E., 2000, The formation of Holocene marsh foraminiferal assemblages, middle Atlantic coast , USA: implications for Holocene sea-level change: Journal of Foraminiferal Research, v. 30, p. 272-293.

Hippensteel, S.P., Martin, R.E., Nikitina, D. and Pizzuto, J.E., 2002, Interannual variation of marsh foraminiferal assemblages (Bombay Hook National Wildlife Refuge, Smyrna, DE): Do foraminiferal assemblages have a memory?: Journal of Foraminiferal Research, v. 32, p. 97-109.

Jennings, A.E. and Nelson, A.R., 1992, Foraminiferal assemblage zones in Oregon tidal marshes – relation to marsh floral zones and sea-level: Journal of Foraminiferal Research, v. 22, p. 13-29.

868 Jonasson, K.E. and Patterson, R.T., 1992, Preservation potential of salt marsh foraminifera
869 from the Fraser River delta, British Columbia: Micropaleontology, v. 38, p. 289-301.

870

871 Jorissen, F.J. and Wittling, I., 1999, Ecological evidence from live-dead comparisons of
872 benthic foraminiferal faunas off Cape Blanc (Northwest Africa): Palaeogeography,
873 Palaeoclimatology, Palaeoecology, v. 149, p. 151-170.

874

875 Jorissen, F.J., de Stigter, H.C. and Widmark, J.G.V., 1995, A conceptual model explaining
876 benthic foraminiferal microhabitats: Marine Micropaleontology, v. 26, p. 3-15.

877

878 Kidwell, S.M., 1985, Palaeobiological and sedimentological implications of fossil
879 concentrations: Nature, v. 318, p. 457-460.

880

881 Kidwell, S.M., 1986, Models for fossil concentrations: paleobiologic implications:
882 Paleobiology, v. 12, p. 6-24.

883

884 Leorri, E. and Martin, R.E., 2009, The input of foraminiferal infaunal populations to sub-
885 fossil assemblages along an elevational gradient in a salt marsh: application to sea-level
886 studies in the mid-Atlantic coast of North America: Hydrobiologia, v. 625, p. 69-81.

887

888 Leorri, E., Gehrels, W. R., Horton, B.P., Fatelad, F. and Cearretae, A., 2010, Distribution of
889 foraminifera in salt marshes along the Atlantic coast of SW Europe: Tools to reconstruct past
890 sea-level variations: Quaternary International, v. 221, p. 104-115.

891

892 Licari, L. and Mackensen, A., 2005, Benthic foraminifera off West Africa (1 degrees N to 32
893 degrees S): do live assemblages from the topmost sediment reliably record environmental
894 variability?: Marine Micropaleontology, v. 55, p. 205-233.

895

896 Licari, L., Schumacher, S., Wenzhöffer, F., Zabel, M. and Mackensen, A., 2003,
897 Communities and microhabitats of living benthic foraminifera from the tropical east Atlantic:
898 impact of different productivity regimes: Journal of Foraminiferal Research, v. 33, p. 10-31.

899

Loubere, P., 1989, Bioturbation and sedimentation-rate control of benthic microfossil taxon abundances in surface sediments – a theoretical approach to the analysis of species microhabitats: Marine Micropaleontology, v. 14, p. 317-325.

Loubere, P. and Gary, A., 1990, Taphonomic process and species microhabitats in the living to fossil assemblage transition of deeper water benthic foraminifera: Palaios, v. 5, p. 375-381.

Loubere, P., Gary, A. and Lagoe, M., 1993, Generation of the benthic foraminiferal assemblage: theory and preliminary data: Marine Micropaleontology, v. 20, p. 165-181.

Martin, R.E., 1999, Taphonomy: a process approach: Cambridge University Press, Cambridge, 508 p.

Martin, R.E., Wehmiller, J.F., Harris, M.S. and Liddell, W.D., 1996, Comparative taphonomy of bivalves and foraminifera from Holocene tidal flat sediments, Bahia la Choya, Sonora, Mexico (northern Gulf of California): Paleobiology, v. 22, p. 80-90.

Matera, N.J. and Lee, J.J., 1972, Environmental factors affecting standing crop of foraminifera in sublittoral and psammolittoral communities of a Long-Island salt marsh: Marine Biology, v. 14, p. 89-103.

Meldahl, K.H., Flessa, K.W. and Cutler, A.H., 1997, Time-averaging and post-mortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments: Paleobiology, v. 23, p. 207-229.

Moodley, L., van der Zwaan, G.J., Rutten, G.M.W., Boom, R.C.E. and Kempers, A.J., 1998, Subsurface activity of benthic foraminifera in relation to porewater oxygen content: laboratory experiments: Marine Micropaleontology, v. 34, p. 91-106.

Morvan, J., Debenay, J-P., Jorissen, F., Redois, F., Bénéteau, E., Delplancke, M and Amato, A-S., 2006, Patchiness and life cycle of intertidal foraminifera: implication for environmental and palaeoenvironmental interpretation: Marine Micropaleontology, v. 61, p. 131-154.

933 Murray, J.W., 1983, Population dynamics of benthic foraminifera: results from the Exe
934 Estuary, England: Journal of Foraminiferal Research, v. 13, p. 1-12.

935

936 Murray, J.W., 1989, Syndepositional dissolution of calcareous foraminifera in modern
937 shallow-water sediments: Marine Micropaleontology, v. 15, p. 117-121.

938

939 Murray, J.W., 1991, Ecology and palaeoecology of benthic foraminifera: Longman Scientific
940 and Technical, Harlow, England, 397 p.

941

942 Murray, J.W. and Alve, E., 1999, Natural dissolution of modern shallow water benthic
943 foraminifera: taphonomic affects on the palaeoecological record: Palaeogeography,
944 Palaeoclimatology, Palaeoecology, v. 146, p. 195-209.

945

946 Murray, J.W. and Alve, E., 2000, Major aspects of foraminiferal variability (standing crop
947 and biomass) on a monthly scale in an intertidal zone: Journal of Foraminiferal Research, v.
948 30, p. 177-191.

949

950 Olszewski, T.D, 1999, Taking advantage of time-averaging: Paleobiology, v. 25, p. 226-238

951

952 Olszewski, T.D, 2004, Modeling the influence of taphonomic destruction, reworking, and
953 burial on time-averaging in fossil accumulations: Palaios, v. 19, p. 39-50.

954

955 Osaki, S., Sugihara, S., Momoshima, N. and Maeda, Y., 1997, Biodiffusion of 7Be and
956 210Pb in intertidal estuarine sediment: Journal of Environmental Radioactivity, v. 37, p. 55-
957 71.

958

959 Ozarko, D.L., Patterson, R.T. and Williams, H.F.L., 1997, Marsh foraminifera from
960 Nanaimo, British Columbia: infaunal habitat and taphonomic implications: Journal of
961 Foraminiferal Research, v. 27, p. 51-68.

962

963 Patterson, R.T., 1990, Intertidal benthic foraminiferal biofacies on the Fraser River Delta,
964 British Columbia: modern distribution and palaeoecological importance: Micropaleontology
965 v. 36, p. 229–244.

966

967 Patterson, R.T., Guilbault, J-P. and Clague, J.J., 1999, Taphonomy of tidal marsh
968 foraminifera: implications of surface sample thickness for high-resolution sea-level studies:
969 Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 199-211.

970

971 Powell, E.N., 1992, A model for death assemblage formation: can sediment shelliness be
972 explained?: Journal of Marine Research, v. 50, p. 229-265.

973

974 Powell, E.N., Hu, X., Cai, W-J., Ashton-Alcox, K.A., Parsons-Hubbard, K.M and Walker,
975 S.E., 2012, Geochemical controls on carbonate shell taphonomy in northern Gulf of Mexico
976 continental shelf and slope sediments: Palaios, v. 27, p. 571-584.

977

978 Saffert, H. and Thomas, E., 1998, Living foraminifera and total populations in salt marsh peat
979 cores: Kelsey Marsh (Clinton, CT) and The Great Marshes (Barnstaple, MA): Marine
980 Micropaleontology, v. 33, p. 175-202.

981

982 Schink, D.R. and Guinasso, N.L., 1977, Effects of bioturbation on sediment-seawater
983 interaction: Marine Geology, v. 23, p. 133-154.

984

985 Scott, D.B. and Medioli, F.S., 1978, Vertical zonations of marsh foraminifera as accurate
986 indicators of former sea-levels: Nature, v. 272, p. 528-531.

987

988 Scott, D.B. and Medioli, F.S., 1980, Living vs. total populations: their relative usefulness in
989 paleoecology: Journal of Paleontology, v. 54, p. 814-831.

990

991 Scott, D.B. and Leckie, R.M., 1990, Foraminiferal zonation of Great Sippewissett salt-marsh:
992 Journal of Foraminiferal Research, v. 20, p. 248-266.

993

Smoak, J.M. and Patchineelam, S.R., 1999, Sediment mixing and accumulation in a mangrove ecosystem: evidence from 210Pb, 234Th and 7Be: Mangroves and Salt Marshes, v. 3, p. 17-27.

Tobin, R, Scott, D.B., Collins, E.S. and Medioli, F.S., 2005, Infaunal benthic foraminifera in some North American marshes and their influence on fossil assemblages: Journal of Foraminiferal Research, v. 35, p. 130-147.

Tomašových, A., Fürsich, F.T. and Olszewski, T.D., 2006, Modelling shelliness and alteration in shell beds: variation in hardpart input and burial rates leads to opposing predictions: Paleobiology, v. 32, p. 278-298.

Vance, D.J., Culver, S.J., Corbett, D.R. and Buzas, M.A., 2006, Foraminifera in the Albemarle estuarine system, North Carolina: distribution and recent environmental change: Journal of Foraminiferal Research, v. 36, p. 15-33.

Wang, P. and Chappell, J., 2001, Foraminifera as Holocene environmental indicators in the South Alligator River, Northern Australia: Quaternary International, v. 83-85, p. 47-62.

Widdows, J., Blauw, A., Heip, C.H.R., Herman, P.M.J., Lucas, C.H., Middleburg, J.J., Schmidt, S., Brinsley, M.D., Twisk, F. and Verbeek, H., 2004, Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands: Marine Ecology Progress Series, v. 274, p. 41-56.

Woodroffe, S.A., Horton, B.P., Larcombe, P. and Whittaker, J.E., 2005, Intertidal mangrove foraminifera from the central Great Barrier Reef shelf, Australia: implications for sea-level reconstruction: Journal of Foraminiferal Research, v. 35, p. 259-270.