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How to react to shallow water hydrodynamics: The larger benthic foraminifera solution

Antonino Briguglio* and Johann Hohenegger

Institut für Paläontologie, Universität Wien, Geozentrum, Althanstrasse 14, 1090 Vienna, Austria

Abstract

Symbiont-bearing larger benthic foraminifera inhabit the photic zone to provide their endosymbiotic algae with light. Because of the hydrodynamic conditions of shallow water environments, tests of larger foraminifera can be entrained and transported by water motion. To resist water motion, these foraminifera have to build a test able to avoid transport or have to develop special mechanisms to attach themselves to substrate or to hide their test below sediment grains. For those species which resist transport by the construction of hydrodynamic convenient shapes, the calculation of hydrodynamic parameters of their test defines the energetic input they can resist and therefore the scenario where they can live in. Measuring the density, size and shape of every test, combined with experimental data, helps to define the best mathematical approach for the settling velocity and Reynolds number of every shell. The comparison between water motion at the sediment-water interface and the specimen-specific settling velocity helps to calculate the water depths at which, for a certain test type, transport, deposition and accumulation may occur. The results obtained for the investigated taxa show that the mathematical approach gives reliable results and can discriminate the hydrodynamic behaviour of different shapes. Furthermore, the study of the settling velocities, calculated for all the investigated taxa, shows that several species are capable to resist water motion and therefore they appear to be functionally adapted to the hydrodynamic condition of its specific environment.

The same study is not recommended on species which resist water motion by adopting hiding or anchoring strategies to avoid the effect of water motion.

Keywords

Shell morphology; Transport; Tests distribution; Settling velocity; Shape entropy

1 Introduction

Habitats of larger benthic foraminifera (LBF) are determined by a set of environmental gradients. The main factors influencing the distribution of LBF are temperature, light intensity, water movement, substrate, and food (Hallock et al., 1991; Hohenegger, 2004). Distribution, abundance and ‘bauplan’ (construction plan) diversity (sensu Hohenegger, 2009) of living foraminifera reflect the variation and concurrence of these environmental

*Corresponding author. Fax: +43 142779535. antonino.briguglio@univie.ac.at (A. Briguglio).

factors. Accordingly, changes in ecological factors, such as global warming, ocean acidification, or sea level changes, are reflected and recorded in the fossil distribution of larger foraminifera (Pechoux, 1995; Hohenegger, 1996).

To occupy and flourish in a niche, a species must be adapted to the range of physical conditions in the environment and must be able to accumulate the trophic resources necessary to produce new generations at least as fast as predators, disease and physical factors reduce their numbers (Hallock et al., 1991). Concerning symbiont bearing LBF, morphology is the basic adaptive characteristic. Foraminifera have to provide enough light to the symbionts and must resist transport at the same time; these requirements induce them to build very complicated but adaptive test morphologies following distinct bauplans (Hohenegger, 2009). Depending on nutrient availability, presence of competitors and other adverse environmental factors, the ecological optimum for LBF will occur at that water depth where light intensity satisfies the symbiont's demand and where the foraminiferal shell resist entrainment due to its weight or attachment mechanisms.

These connections between test morphology and environment make LBF powerful palaeoenvironmental indicators, particularly in estimating palaeodepth, because water motion and light both decline exponentially with depth (Hallock, 1979).

Because LBF inhabit shallow waters, the hydrodynamic conditions they are subjected to may be very strong and transport or suspension might affect the living and empty tests distributions. Therefore a hydrodynamic study connecting energetic scenario and hydrodynamic parameters of LBF tests can reveal specific strategies adopted by these organisms to react to such extreme environments.

Under weak hydrodynamic conditions, tests with a large surface/volume-ratio (e.g., *Cycloclypeus*) are best adapted, whereas under strong hydrodynamic conditions the simplest way to resist transport in movable substrates like gravel and coarse sand is to develop high density or thick lenticular tests (e.g., *Archaias*, *Nummulites*) (Hohenegger et al., 1999; Yordanova and Hohenegger, 2002). Such shape differentiation favours also the symbiont's requirements: i.e., larger disc-shaped tests (with a larger light-exposed surface) may live in deeper water with low light penetration, whilst shallower specimens, with higher light availability, may need a smaller light-exposed surface (Hallock et al., 1991). This allows the depth distribution boundaries of living LBF to be calculated based on the light dependence of their symbionts, and their capability to resist to water motion by hydrodynamically convenient test shapes or anchoring mechanisms. Some species, exposed to extremely high water energy or adapted to reef crest environments (e.g., Calcarinids), possess spines and strong glue for fixation (Röttger and Krüger, 1990) which enables anchoring between filamentous algae. Post mortem distribution, however, follows completely different rules. After reproduction or death, anchoring and fixing mechanisms decay and all tests are at the mercy of water motion: they can be detached from the substrate and thus redistributed.

Evidence for transport is often found in bad test preservation; i.e., abrasion, destruction, or huge accumulations are considered as evidence for transport, deposition and accumulation processes. Concerning test abrasion, Beavington-Penney (2004) using recent LBF

demonstrates that mechanical test destruction is rare even during long-distance transport. Thus, mechanical abrasion or break-off of tests is only indicative of transport in very specific conditions and may reflect high-energy events (e.g., tsunamis, long-time rewashing within the breaking zone or entrainment by strong currents). Consequently, optimally preserved tests (*sensu* Yordanova and Hohenegger, 2002) may also have been affected by transport and cannot *a priori* be considered as *in situ* material.

Although transport and deposition of both living and dead tests significantly influence the distribution of LBF tests, very few studies have considered the importance of such modifications, particularly from a hydrodynamic point of view.

Some authors, mainly sedimentologists, provided mathematical solutions to approximate the hydrodynamic behaviour of sand particles moved by waves and currents. Some of these equations are well known (Airy, 1841; Soulsby, 1997; Wiberg and Sherwood, 2008) and others have been very recently published in an extensive study of Le Roux et al. (2010). Other authors studied the distribution of living foraminifera using various approaches: morphocoenoclines (Hohenegger, 2004), character combination (Hohenegger, 2006) and presence/absence data (Pechoux, 1995; Renema, 2002; Hohenegger, 2005; Rasser et al., 2005). The first study on nummulitid hydrodynamics was published by Jorry et al. (2006), subsequently expanded by Yordanova and Hohenegger (2007) to other species using an enhanced statistic approach. The high diversity of LBF test shapes leads to different hydrodynamic answers (Jorry et al., 2006) within the same energetic scenario, and these different hydrodynamic responses can be calculated for every test. As proposed by Beavington-Penney et al. (2005), a good parameter to calculate LBF variations along the palaeoenvironmental gradient is the diameter/thickness ratio. Such a calculation, sometimes used in recent publications (e.g., Adabi et al., 2008), gives some general results but approximate the LBF shape too vaguely and does not take LBF size and density into account, which are the most important parameters to evaluate the test distribution. In nummulitids, density may vary within the same genus (Jorry et al., 2006) and within the same species due to different growth stages (Yordanova and Hohenegger, 2007). More accurate calculations (Jorry et al., 2006; Yordanova and Hohenegger, 2007; Briguglio and Hohenegger, 2009), which consider shape entropy, nominal diameter and many other shape- or size-independent parameters, allow comparison between different environments and give much better results, without being very time consuming or depending on complex mathematical algorithms.

The present study uses the calculation of these parameters to yield precise values on foraminifera transportability and their capability to resist water motion, considering the differences in depth distribution between living specimens and optimally preserved tests. Such comparisons once measured and tested in recent environments, can be very useful for the fossil record. This paper explains how each test reacts to a hydrodynamic regime, at what depth the test may be transported, until what depth the test is transported under the same input, and how important the taxonomically significant geometric differences of LBF in this energy scenario are. In fact, the geometrical and structural characters, most useful in LBF palaeontology for taxonomy and ecology, are now the basis to quantify the response to hydrodynamics. However, the distribution of LBF within an environment cannot be

explained using hydrodynamics only. Nevertheless, this approach revealed and can still reveal interesting answers about the functional morphology of this complex and diverse group of organisms.

1.1 Transportability and the role of bottom orbital velocity

Wind-generated waves induce – in sufficiently shallow water (sensu Soulsby, 1997) – orbital motion within the water column to a depth roughly equal to half the wavelength of the source waves. When the water depth is less than half the wavelength, this wave-induced orbital motion affects particles laying on the sea floor. Depending on the material (i.e., density) and on the form (i.e., size and shape) of such particles, they can be entrained, moved or kept in suspension. Wave-generated water motion interacts with the sea floor to influence surface waves through frictional dissipation of wave energy. This influences the sea floor through mobilisation of bed sediment by wave-motion-induced bed shear stress (Wiberg and Sherwood, 2008). Theoretical relationships between low-amplitude monochromatic waves and near-bed water motion were derived during the late 1960s and then extended and improved to encompass an ever broader wave spectrum and environmental conditions. Many coastal problems require the calculation of wave-generated oscillatory (orbital) velocities at the sea-bed for applications such as sediment transport, suspension and mobility and many websites share java applets to easily calculate bottom velocities (and many others values) by surface wave parameters (e.g., <http://www.coastal.udel.edu/faculty/rad/>; http://woodshole.er.usgs.gov/staffpages/csherwood/sedx_equations/sedxinfo.html) and some publications include detailed and complete Microsoft Excel spreadsheets for a user-friendly sea wave parameters calculation (Le Roux et al., 2010).

During the last decade the bottom orbital velocity (BOV) periodic function has attracted more and more attention by marine scientists, as well as coastal and marine engineers (e.g., Cookman and Flemings, 2001; Li and Amos, 2001; Schutten et al., 2004).

Sediment suspension and subsequent transport occur only if some conditions are contemporarily satisfied. The BOV can only keep tests in suspension and move them vertically; without any other energy input, the particle will remain in the same environment or at the same depth. Once a secondary, orthogonal (i.e., in the horizontal plane) energy input is available (e.g., currents), the particle, if already kept in suspension by BOV, can be moved in the flow direction. When directional flow is present and orbital velocity is too weak to keep particles in suspension (e.g., in deeper water), transport may occur as traction or saltation depending on turbulence effects and near-bed friction laws. Because BOV varies with depth, there will be for every test a depth range in shallower environments where this test can be kept in suspension and can be transported. Below this depth range, the BOV is no more able to keep the test in suspension. At the water depth where suspension does not occur anymore, the equilibrium between orbital bottom velocity and test settling velocity is reached. For LBF without special attachment mechanisms or hiding strategies this depth represents an optimal condition where the foraminifer obtains a maximum amount of light possible without being transported.

The mathematical quantification of orthogonal secondary water energy inputs (i.e., currents or streams) becomes thus unimportant for transportability. Accordingly, current parameters are not considered in the equations presented here, although they are primarily responsible for transport distance and direction.

The transportability of LBF is given by the combination of many parameters, including test density, size and shape and – concerning the energy scenario – sea bottom morphology, sedimentology and wave-induced orbital bottom velocity. The major factor within the following calculation is the bottom orbital velocity vs. settling velocity ratio, which determines the transport – deposition boundary. Even if the calculation of the BOV is not the most modern one and some more advanced and comprehensive methods have been presented (e.g., Le Roux et al., 2010), the method proposed here is largely sufficient as a first approximation.

BOV can be calculated from surface-wave parameters using different equations. Water movement and, therefore, the resulting forces can be resolved at each point into vertical and horizontal components. Depending on the application and due to the vector character of velocity, all possible near bed velocities may be calculated to any direction and according to the linear wave theory known as the Airy wave theory (Airy, 1841) both in horizontal and in vertical direction as follows:

$$u = (\pi H / T) \{ \cosh [k(z_0 + h)] / \sinh(kh) \} \cos(kx - \omega t) \quad (1)$$

for the horizontal orbital velocity, and

$$w = (\pi H / t) \{ \sinh [k(z_0 + h)] / \sinh(kh) \} \sin(kx - \omega t) \quad (2)$$

for the vertical orbital velocity, where H is wave height, T is wave period, h is water depth, k is wave number, $\sinh$ and $\cosh$ are the hyperbolic sine and cosine, z_0 is the depth where the orbital velocity must be calculated, ω is the radian frequency $2\pi/t$, x is the coordinate in the direction of wave propagation, and t is the time (Fig. 1).

Because the highest values are reached for horizontal and vertical velocity, in both cases the periodic functions sine and cosine are equal to one. In fact the horizontal component of orbital velocity reaches its maximum when $\cos(kx - \omega t) = 1$ and, vertically, (i.e., $\pi/2$), the vertical component reaches its maximum when $\sin(kx - \omega t) = 1$.

Considering orbital velocity at the sea bottom, it induces the condition $z_0 = -h$ in both Eqs. (1) and (2).

In Eq. (2), at the given condition, $\cosh[k(z_0 + h)] = 1$. In Eq. (3), at the same condition $z_0 = -h$, the value $\sinh[k(z_0 + h)] = 0$. This means that at the sea bottom, the horizontal velocity is always calculable but the vertical component goes to zero. However, it increases rapidly from the condition $z_0 + h > 0$ because of the divergent (i.e., nonperiodic) character of the $\sinh(r)$ function.

Because of this inconvenience, several solutions have been proposed to quantify the vertical component of the orbital velocity at near-bed depth.

In linear wave theory, the equations for calculating the two components of bottom velocity differ for deep and shallow water, because friction with the bottom sediment plays a significant role in shallow water. According to several authors (Komar, 1998; Schutten et al., 2004), the formula for the deep-water approximation may be used for near bed vertical velocity providing a good fit with field observations. The vertical component of the orbital velocity for deep-water waves is:

$$w = (\pi H/T) \exp(kz) \sin(kx - \omega t). \quad (3)$$

For common waves of height around 1 m and of short period (i.e., $5 < T < 10$ s) there is almost no difference between horizontal and vertical component. Below 30 m water depth, they act, quantitatively, very similarly to the sediment (Fig. 2).

That is why in many studies on near bed orbital velocity only Eq. (1) is used (Soulsby, 1997; Cookman and Flemings, 2001; Wiberg and Sherwood, 2008) to quantify the energy input at the sea-floor; the use of the mere vertical component for near bed orbital velocity is thus no longer suggested.

However, in this work, the near bed orbital velocity was calculated using Eq. (1) modified after applying the conditions $z_0 = -h$ and $\cos(kx - \omega t) = 1$. The used equation is as follows:

$$U_w = H\pi/T \sinh(kh) \quad (4)$$

This formula is the best-suited one for small-amplitude wave theory, which assumes the bed to be frictionless (Soulsby, 1997; Wiberg and Sherwood, 2008). Orbital velocities, calculated using this theory, agree well with observed oscillatory flows under monochromatic waves. Note, however, that wind-generated waves are not monochromatic, and bed friction as well as sea bottom granulometry must be considered for the transport of sediment particles lying on the bottom. Nevertheless, for small-amplitude wind-generated waves, the approximation using H is still very accurate (Wiberg and Sherwood, 2008) and the calculation of bed friction can be omitted when studying long-distance transport of optimally preserved specimens (i.e., considering neither rolling nor saltation).

Fig. 3 shows down to what depth such velocities affect the sea bottom depending on surface wave parameters.

Using this formula for surface-wave parameters is not as easy and fast as it seems. Surface-wave parameters are normally expressed as H , T and h (because they are dependant of each other). The calculation of k is more complicated. The wave number k represents the number of oscillations made by a given wave within its distance unit and it is proportional to the reciprocal of the wavelength (L). The procedure presented here to calculate L is the main procedure used in the Java applets linked above and published by Hunt (1979) (therefore

called as “Hunt’s Method”), then in the following years widely corrected and improved (Soulsby, 1987, 1997; Komar, 1998; Wiberg and Sherwood, 2008).

The radian frequency is given by:

$$\omega = 2\pi/T. \quad (5)$$

The two dimensionless variables, calculated from the dispersion equation

$$\omega^2 = gk \tanh(kh), \quad (6)$$

are expressed as $x = \omega^2 h/g$ and $y = kh$.

The Hunt’s formula, used as follows, is an approximation for $y(x)$:

$$y = (x^2 + Bx)^{1/2}$$

where B is a constant calculated as:

$$B = 1 / (1 + x (0.66667 + x (0.16084 + x (0.02174 + x (0.00654 + x (0.00171 + x (0.00039 + x (0.00011)))))))$$

(7)

This is computationally fast because it avoids calculations of $\tanh(y)$ Eq. (6). The relative error in y is less than 10^{-5} for all x . The relative error in U_w is $<0.02\%$ for all x .

The calculation of the wave number is therefore given by:

$$k = y/h, \quad (8)$$

following the wavelength as

$$L = 2\pi/k. \quad (9)$$

To keep a particle in suspension and make it transportable, the water energy input must exceed the energy that pushes the particle to the bottom due to gravity. Such energy can be calculated as settling or sinking velocity. Some sedimentologists and palaeontologists have already recognised the importance of settling velocity for the study of particle transport and distribution on slopes and ramps. In recent years, mathematical equations allowed the calculation of settling velocities without empirical measurements. Concerning LBF, calculated settling velocities as well as experimental data are already published. Their

importance as a powerful tool in understanding the distribution of tests in shallow water environments has been already demonstrated (e.g., Beavington-Penney et al., 2005; Jorjy et al., 2006; Yordanova and Hohenegger, 2007; Briguglio and Hohenegger, 2009). However, the quantitative equation between water motion and LBF distribution remains, so far, unknown.

Concerning LBF shapes, high diversity in test geometry and bauplan (reflected in the high number of taxa, then duplicated due to the generation's dimorphism) may lead to the same high diversity in hydrodynamic behaviours. At the species level, the intraspecific variability within the same generation of LBF (e.g., agamonts) leads to a spectrum of settling velocities which may differ significantly from species to species (Yordanova and Hohenegger, 2007, Fig. 5). Such differences are reflected in the response of every taxon to the hydrodynamic conditions.

Correlating water depth with settling velocity of a given test and the orbital velocity (Fig. 4A), suspension will occur at those water depths where settling velocity is lower than orbital velocity, whereas deposition will occur when settling velocity is higher than orbital velocity. Due to the diversity of specimens belonging to the same species, the calculation of settling velocity for all the tests will give a range of settling velocities (Fig. 4B). The tests with higher settling velocity will be deposited in shallower environment than specimens with lower settling velocity. Accumulations of tests can be expected in deeper environments.

If a particle's settling velocity is lower than the orbital velocity, then this particle will be kept in suspension and, if a secondary force is present, will be transported. Consequently, the same particle may be unaffected in deeper water, where its settling velocity will exceed bottom orbital velocity. Concerning a single LBF specimen, its settling velocity value allows the definition of the water depth where, under given orbital bottom velocity conditions, the shell is not transportable and where the maximum light intensity is available for its symbionts: this depth might represent the ecological optimum for the organism.

The validity of this model is here tested. If LBF resist water motion during life time with the construction of hydrodynamic convenient tests, the majority of the living tests are to be expected just within the deposition area (Fig. 4B). Consequently, the depth distribution of empty tests, which represent the remain of former foraminifers associations can be expected in deeper environment as they might have experienced stronger water inputs.

Besides the specific behaviour of foraminiferal tests in fluids, slope morphology represents another important factor influencing transport: the steeper the slope, the more intensive the lateral transport of larger tests to greater water depths (Hohenegger and Yordanova, 2001).

2 Material and methods

Specimens were collected from the slope west of Sesoko Jima, a small island west of the Motobu-Peninsula, Okinawa, Japan. Two transects were chosen northwest of Sesoko Jima, one in the northern part of the slope and one in the southern part. Sampling was conducted in June and July 1996, and completed before the first typhoon occurrence. Thus, samples are

composed of non-transported living foraminifers. Additional data about these two transects are reported in Hohenegger et al. (1999).

The distribution of living specimens along the investigated transects is published in Hohenegger (2000), whereas the empty test distribution is reported in Yordanova and Hohenegger (2002). In the latter, the empty specimens were studied and sorted based on their preservation grade into optimally, well and poorly preserved tests (*sensu* Yordanova and Hohenegger, 2002).

The present study considers the distributions of living specimens and the distribution of optimally preserved empty tests. The distribution of living tests defines the depth limits of the habitats whereas the distribution of the optimally preserved ones defines the depth distributions under differing weather conditions averaged for a time interval of a few years (Yordanova and Hohenegger, 2002). Differences in tests distributions between living and empty tests should show the effects of hydrodynamics on the investigated taxa.

Several geometric and physic variables were measured (i.e., largest, intermediate and shortest diameter, equatorial surface, axial surface and density), and the list of equations published by Briguglio and Hohenegger (2009) was applied to calculate the theoretical hydrodynamic behaviour of nummulitids tests. Such mathematically obtained results were compared with experimental results using a settling tube (Yordanova and Hohenegger, 2007) (Fig. 5).

Four different formulas were used to calculate the settling velocity of a particle depending on its shape.

The first formula calculated settling velocity, termed “settling velocity of an equivalent sphere” (*sensu* Le Roux, 1997a)

$$W_s = W_d / \left(\rho_f^2 / (\mu g (\rho_s - \rho_f)) \right)^{1/3} \quad (10)$$

where W_d is the dimensionless sphere settling velocity (Jorjy et al., 2006), calculated as in Briguglio and Hohenegger (2009), ρ_f is the density of the fluid (seawater), ρ_s is the density of the test, μ is the dynamic viscosity of the fluid (seawater) and g is the gravity constant. This parameter is a shape-independent value and can be correctly used for comparisons involving other foraminifera having the same volume.

The second formula calculates settling velocity by considering the shape entropy, thus reducing the former formula values significantly.

$$W_e = W_s [(H_r - 0.5833) / 0.4167] \quad (11)$$

The deviation from sphericity H_r was calculated with the equation proposed by Hofmann (1994), widely used for ellipsoidal grains (Le Roux, 1997a, 2005), then for nummulitids (Jorjy et al., 2006; Briguglio and Hohenegger, 2009).

The shape entropy equation is based on the geometry of an ellipsoid and can be calculated with

$$H_r = [(p_l \ln p_l) + (p_i \ln p_i) + (p_s \ln p_s)] / 1.0986 \quad (12)$$

where p_l , p_i and p_s , are the proportions of the major (L), intermediate (I) and minor axes (S) of the ellipsoid

$$\begin{aligned} p_i &= I / (L + I + S) \\ p_l &= L / (L + I + S) \\ p_s &= S / (L + I + S) \end{aligned}$$

The third formula used was proposed by Allen (1984) for bivalve shells:

$$v^2 = 2gV(p_s - p_f) / C_d p_f A \quad (13)$$

where V is the volume, C_d is the drag coefficient and A is the area of the shell/test facing the water during sinking, which was calculated as reported in Briguglio and Hohenegger (2009).

The following formula was used to calculate the Reynolds number to quantify the particle's buoyancy

$$Re = p_f D_n v / \mu_f \quad (14)$$

where D_n is the True Nominal Diameter proposed by Le Roux (1997a) and v is the particle's settling velocity. The Reynolds number provides information on test buoyancy. Its calculation considers test settling velocity, drag coefficient and density; therefore the correctness of these values, by correlation with the experimental ones, is an additional proof of the rigour of the proposed equation sequence (Fig. 5).

For comparison with the daily and constant energy input at the sea bottom, the best-fitted settling velocity for every species was used. This comparison reveals how and how much the water motion (under normal fair weather conditions) may or may not influence test distribution. According to Hohenegger (personal observation, 1999), to get a good representation of the environment under fair weather conditions, the wave parameters in Eq. (4) could be: $T = 9$ s and $H = 1$ m (Fig. 3).

The obtained function may be represented as an exponential function $y = a \exp^{bx}$ where x is depth, a is the velocity at the depth 0 m and b is very close to 0.

For settling velocity, on all investigates species the statistical limits $\bar{x} \pm 1.96 s$ including 95% of all cases were calculated.

3 Results

The hydrodynamic behaviour of nummulitids obtained by the mathematical approach fits very well with the results obtained by experiments using a settling tube (Yordanova and Hohenegger, 2007). Up to the settling velocity and to the Reynolds numbers (Fig. 5), calculations are consistent with experimental results, both in smaller and in larger specimens. In Fig. 5, comparisons between the two methods are shown. For every taxon, the three settling velocities W_s (10), W_e (11) and v (square root of 13) were used to check which one fits the experimental data best.

In fact, depending on the specimen's shape entropy (Eq. 12), one of the three calculated settling velocities fits best. Considering the shape entropy parameter, the most accurate equation for calculating the settling velocity of specimens with $H_f > 0.95$ (i.e., well-rounded tests like *Palaeonummulites venosus*) is Eq. (10), which assumes the falling object is spherical. The most accurate settling velocity equation for specimens with $H_f < 0.85$ (i.e., disc-like test such as *Cyloclypeus carpenteri*) is Eq. (13), where the volume/half-surface ratio significantly reduces the sinking effect. For specimens with $0.85 < H_f < 0.95$ (i.e., plate-like tests or not rounded tests) the best mathematical calculation, which correlates well with the experimental data, is Eq. (11). Here, shape entropy becomes important strongly reducing the settling velocity of a sphere.

The combination of the energy scenario (i.e., the orbital velocity calculated with Eq. 4) with the hydrodynamic behaviour of every single test (i.e., the settling velocity as a results of the calculated size shape and density) provides the key to evaluate the depth transport distribution along the transect. As already stated, to permit transport, together with the necessary orbital velocity, a secondary force must be available: it is here the case due to the influence of tidal currents and downwelling by the Kuroshiyo Current strengthened by dominant summer winds from the south (Hohenegger et al., 1999). It means that the sampling area can be considered as an appropriate location to investigate and quantify hydrodynamics. The two transects, with different morphologies but with almost the same diversity in foraminifera may allow quantification of the influence of slope morphology on living foraminifera distribution and transport, deposition and accumulation of empty shells due to water dynamics.

The hydrodynamic equilibrium conditions allow estimating the water depth where a shell, with its hydrodynamic parameters, may be transported or deposited, i.e., the transport–deposition boundary.

In Fig. 6 the bathymetric profiles of the two transects are reported with their relative BOV function. Since BOV is a function of water depth, it follows the profile morphology in both transects.

In Figs. 7–9 the main results of this work are displayed. Figures show the depth distribution of the investigated species on the two studied transects. Living and optimally preserved tests are displayed. Due to different sample sizes, normalisation of test abundance to a standard weight of 500 g sediment was necessary to enable comparison between sites. On the upper part of each graph the BOV function is reported as a thick black line as it was reported in

Fig. 6. The light coloured grey area represents the species specific settling velocity range. At the intersection between settling velocity and BOV, which represents the depth where the tests start resisting water motion, a dark grey area has been displayed. Dotted lines correlate this dark grey area with the real depth distribution of the tests. A continuous line indicates the depth distribution of optimally preserved empty tests whereas a light grey area shows the depth distribution of the living tests.

For the non-anchoring or non-hiding taxa investigated, the distribution of living individuals matches always the settling velocity vs. fair weather BOV equilibrium along both transects. Optimally preserved tests show in many cases depth transport due to different hydrodynamic conditions.

In the following section the living and empty test distributions along the transects according to their hydrodynamic behaviour are discussed for the investigated species.

3.1 Hydrodynamic behaviour of the investigated taxa

3.1.1 *P. venosus* (Fichtel and Moll) (Fig. 7)—This species is restricted to sandy bottoms in both transects and lives in the uppermost sand layer. Within the nummulitidae, *P. venosus* is the species with the highest settling velocities. This allows individuals to live in shallower water being transported only by very strong energetic input. If the tests are entrained together with the surrounding sand grains and put into suspension, the rounded test, characterised by a high settling velocity, makes the foraminifer sink faster than the smaller carbonate grains and in the case of burial, its peculiar lenticular shape is favourable for relatively quickly climbing up through the sediment again (Hohenegger et al., 1999).

The settling velocities of the investigated specimens of *P. venosus* are between 13 and 4 cm/s which correspond to water depths between 35 and 65 m. The highest abundance of *P. venosus* specimens is located exactly at these depths. It means that the tests built by *P. venosus* at the water depth where they live may resist water motion without being transported out of their habitat. Optimally preserved tests are displayed at the same depths on both transects, testifying once more the capability for this species to resist water motion. In the southern transect, more exposed to the open sea and to the action of the Kuroshio current (see Fig. 2 in Hohenegger et al., 1999), depth transport occurs for empty tests which have probably experienced stronger current actions.

3.1.2 *C. carpenteri* Brady (Fig. 7)—This species lives on sandy substrates in the medium euphotic zone. The ecological optimum, visible by the highest living specimen number per unit area, is present at a water depth between 45 and 68 m. This depth range is defined also by the range of the calculated settling velocity between 11 and 1.7 cm/s. Between these two boundaries defined by settling velocity and BOV the maximum abundance of living specimens is located.

In the northern transect this water depth is characterised by a very flat profile, on which *C. carpenteri* is well represented and, because at that water depth the equilibrium between settling velocity and BOV is reached, shells are not transported. In the southern transect, the water depths at which *C. carpenteri* is abundant are perfectly comparable to the northern

transect but the topography becomes important. At this water depth, the profile is steeper and the optimum for *C. carpenteri* is reached in a much smaller area; any small variation of water motion intensity can have easily transported empty specimens downslope. Similarly to *P. venosus*, on the southern transect, the optimally preserved tests show depth transport due to both transect morphology and the stronger effect of the Kuroshio current.

3.1.3 Operculina ammonoides (Gronovius) including O. complanata (Defrance) (Fig. 8)

—This species frequently inhabits fine-grained bottoms of lagoons behind patch reefs; it is abundant on sand, and has similar frequencies on soft bottoms and firm substrates along the slope of the northern transect (Hohenegger et al., 1999). This species avoids the reef edge and is rare in the uppermost 10 m of the slope. It prefers lower-energy environments with medium light intensities. Settlement in shallower waters is restricted to firm substrates with well-structured surfaces, where the individuals resist hydrodynamic forces by hiding within small grooves and holes (Hohenegger et al., 1999). Abundance is higher on sandy than on hard substrates in both transects.

Settling velocity values for these species are comprehended between 8 and 2 cm/s. On both transects, the majority of the living tests have been observed at the water depth limited by similar BOV. The hiding strategy of these species allows several specimens to live in very shallow water without being affected by water motions as is clearly visible in both transects. Depth estimation by using the hydrodynamic boundary between transport and deposition areas can be not very precise for such a species. In fact, they start to be common outside the calculated areas. As already discussed for *C. carpenteri* and *P. venosus*, optimally preserved specimens accumulate in deeper environments.

3.1.4 Planostegina operculinoides Hofker (Fig. 8)

—It lives on sandy bottoms in the deepest parts of the euphotic zone (Hohenegger and Yordanova, 2001). *P. operculinoides* has a very broad spectrum of settling velocities (from 0.9 to 6 cm/s) resulting from very different shape entropies. This characteristic is an advantage permitting the taxon to live in different environments under different energetic conditions. The estimated water depth where this species can resist water motion is located between 50 and 90 m, where living tests are abundant. As this species can live in very deep environments where water motion does not play any role also for stronger weather conditions, living tests accumulate after death in great quantity. Rarely, *P. operculinoides* occupies niches in very shallow water environments, where it hides itself between sand grains to avoid water motion.

3.1.5 Heterostegina depressa d'Orbigny (Fig. 9)

—This species hides itself in small holes in carbonate rocks or between the thalli of macro-algae. Because of its hiding peculiarity, *H. depressa* may live in very shallow environments such as reef edges without being affected by water motion, which drastically reduces in rock crevices and on a vegetated sea bottom. That is why a high abundance of individuals of both living individuals and optimally preserved tests occurs in very shallow areas. If hidden in holes or between algae, water motion can transport neither living nor dead individuals. The use of the settling velocity analysis for such taxa which adopt hiding strategies may produce unrealistic results as displayed in Fig. 9. The very large settling velocity range of *H. depressa*, comprehended

between 0.8 and 7 cm/s, does not fit with its ecological optimum which is definitely outside the estimated water depth range.

4 Discussions

The comparison between wave orbital velocity and settling velocity for a particle is not new in coastal engineering and marine geology, but it is for palaeontologists. The hydrodynamic equilibrium concept and the study of transportability to determine the shell's functional morphology are also new in palaeontology. Such an approach is proposed here with reference to a few species of LBF, but it can be expanded to the different families in both the recent and fossil record as the physical laws acting on the hydrodynamic distributions can be considered to be the same at present-day and in the past. The measurements of density, shape and size and the successive calculations give interesting results and help to accurately interpret the hydrodynamically induced depth distribution of tests and can give some insights in the palaeobiology of organisms. Even if shape, size and density can be considered as the main parameters to determine the hydrodynamics, they still need some attention by scientists.

Concerning LBF, the density issue remains open. It can be measured in recent specimens, but no fixed values are known for fossil forms. In recent nummulitids, the density ranges between 1.1 and 1.9 g/cm³ (Yordanova and Hohenegger, 2007) but values are mostly concentrated, for adult specimens, at 1.4 g/cm³. Other approximations for density in fossil specimens yield slightly higher values. According to Jorjy et al. (2006), the apparent density value of fossil *Nummulites* ranges from 1.4 to 2.61 g/cm³, but for water-filled specimens the range drops to 1.7 and 1.9 g/cm³; an average value of 1.8 g/cm³ was used for predicting hydrodynamics of the fossil *Nummulites globulus* (Briguglio and Hohenegger, 2009). Using X-ray computed tomography, a value of 1.75 g/cm³ was calculated for *P. venosus* and of 1.46 g/cm³ for *O. ammonoides* (Briguglio et al., 2011). This does not consider the surface microporosity, which decreases values by 10–20% to 1.2–1.4 g/cm³. However, although a fixed value (or a species-specific range including growth stages) is not yet available for fossil species, the used data are consistent with the calculated hydrodynamic scenario.

Size and shape, beside density, play a fundamental role in the overall calculation and drive the sequence of equations. For LBF transportability, the main deviation from classical particle sorting involves the shape. Particle shape is an even more complex subject than density or size; during the last decades different shapes indices have been proposed. Flatness index (Wentworth, 1922), oblate–prolate indices (Dobkins and Folk, 1970), disc-rod index and rod index (Illenberger, 1991), several measures of sphericity (Wadell, 1932; Rubey, 1933; Krumbein, 1941; McNown and Malaika, 1950; Aschenbrenner, 1956; Janke, 1966; Hofmann, 1994) are only the most cited and used indices within a much longer list (Le Roux, 2005). Some of these shape indices help to determine the settling velocity of non-spherical particles (Komar and Reimers, 1978; Baba and Komar, 1981a,b), which are very useful for nummulitid tests. Le Roux (1996, 1997b) demonstrated that the Hofmann (1994) shape entropy H_r gives the best results for ellipsoidal grains, and thus can be considered as well suited for nummulitids (Briguglio and Hohenegger, 2009).

The importance of modelling shape to contrast water motion has often been taken into account in the study of nummulitids hydrodynamics and of functional test morphology; but a quantification of how the shape must vary or how intense water input must be to transport a test to a certain water depth, is so far unknown. Some methods to evaluate the distribution of tests along a transect or a geologic profile consider the calculation of the diameter/thickness ratio as the main parameter for test shape hydrodynamics (Beavington-Penney et al., 2005). But the calculation of the hydrodynamics of nummulitids is much more complicated and can give much more insight for a single species. The calculation of the diameter/thickness ratio is only an approximation and does not take into account density (which may significantly vary between species and changes during growth) and size. The mathematical procedure used here (extensively published in Briguglio and Hohenegger, 2009) is very simple and can be reproduced without using advanced mathematics programmes.

The shape effects determined here finally solve the problems inherent to the subjective and not useful morphological definitions such as “disc-like”, “plate-like”, “lens-shaped”, “egg-shaped”, “globular” and “elongate” test form. Shape entropy and its calculation is a powerful parameter to differentiate test forms and to compare forms that are apparently different, but which may have a similar hydrodynamic behaviour. In fact, it is very common in both recent and fossil environments to find, within the same assemblage, very different test shapes possessing similar shape entropy. The shape entropy ranges outlined here lead to different settling velocity calculations and thus to different depth ranges where the test is no longer transportable any more. This methodology could lead to more detailed and exact interpretations of depositional environments, especially in the case of monospecific associations, such as the nummulite banks. Such banks are mainly composed of almost monospecific assemblages with a relative high abundance of B-forms (Arni, 1965; Papazzoni, 2008). It remains unclear whether this facies represents biological accumulation and thus shows nummulitids in living positions, or whether it represents the result of sorting and displacement due to turbulence and comparable settling velocities.

The habitat of high shape entropy tests (e.g., *P. venosus*) is characteristic of a high-energy scenario, but, as in the study area discussed here, such an environment also contains tests with low shape entropy. Such tests have a very low settling velocity and can be transported very easily by water motion. To avoid that, some species have developed particular transport resistance methods such as hiding (*P. operculinoides* or *H. depressa*) or anchoring (*Amphistegina bicirculata* Larsen). For palaeoenvironmental reconstructions, high shape entropy tests will possibly remain as potential fossils in the same habitat because of their settling velocity, and are thus more useful for palaeodepth calculations. The use of settling velocity for low shape entropy tests in a high energy scenario can lead to misinterpretations but can be pivotal to support ecological adaptations (e.g., anchoring or hiding strategies, or infaunal lifestyle). Such differences in shape may help to differentiate autochthonous from allochthonous sediments solely by analysing the shape entropy of tests.

Nevertheless, LBF shapes are the final result of many factors acting together. On one hand, larger foraminifera, because of their symbiontbearing character, have to build tests with a high surface/volume ratio to get enough light to obtain a positive net rate in photosynthesis. On the other hand, as demonstrated here, the resulting shell must somehow resist transport

either with hydrodynamically convenient shape or with alternative strategies such as anchoring, hiding, or density increase. Such coexistence of strong light dependence and bauplan intelligence causes foraminifera to live within a strictly delimited water depth range characterised by BOV always lower than the tests settling velocity. The investigated taxa which do not possess any hiding or fixing strategies fit to this rule. Additionally, LBF ecological optimum depth, defined by the largest number of individuals and always located within the settling velocities range, occupies for every species the depths just below the boundary with the transport area. It is convenient for a cell to live where not only transport is avoided but also where the maximum light penetration is available, i.e., at the depth just below the transport deposition boundary. If the species is not hiding or has not developed any anchoring system, the evaluation of water depth by comparison between settling velocity and BOV is quite precise even if the equations proposed do not consider the transect morphology.

The deeper boundary, obtained by the lowest settling velocity of all the tests belonging to the same species, determines the water depth where the wave-induced BOV does not play any role in suspending tests anymore. Suspension, at the given energy condition, is unreliable for all investigated tests. The deep tail of the species-specific distribution curve must depend on other factors as the endosymbiont's need for light, but probably not on the hydrodynamics. Therefore, the lower hydrodynamic boundary should be considered as the specific water depth where accumulation of all tests may occur.

All species studied here appear to be adapted to species-specific water depths resisting water motion in various ways: by hiding themselves amongst the sand grains (*H. depressa*) or by constructing hydrodynamic convenient tests shapes. The cells of the investigated specimens can live and reach reproduction without being transported out of their habitat if the energetic conditions are typical for fair weather as we have supposed and calculated. By varying the weather conditions and increasing the time span of exposition of tests to water movement, the distributions of empty tests with non-optimal preservation are, for every species, moved significantly downslope (Yordanova and Hohenegger, 2002).

The example of *H. depressa* is very important as it shows how the strategies to resist water motion are not always related to shape morphologies but can be connected to other factors. Therefore, the hydrodynamic study on test shape for such species gives unrealistic results and should be avoided.

5 Conclusion

The hydrodynamic approach used here to estimate the transport deposition boundary and to evaluate shell functionality gives interesting results and may be useful for palaeoenvironmental and palaeohydrodynamic reconstructions. The requested measurements are easy to obtain and already known in the literature, the proposed calculation can be carried out by any calculator and even if equations must be considered only as a mere approximation of the real hydrodynamic behaviour of the shells, it is evident that they are consistent with the values obtained experimentally. When corresponding to the correct Reynolds number, the equations are rigorous and mirror the experimental results and

diversity of parameters such as given by the study of shape, density and size, allowing their use in a very broad spectrum of applied tasks. Even if such a calculation requires more data than the mere diameter/thickness ratio, it allows much more detailed palaeoenvironmental reconstructions and hypotheses concerning the energy scenario of microfossil in shallow water environments.

Comparing the depth distributions of living individuals and empty tests helps to interpret the transport, deposition, and reworking of sediments. Different transport intensities between species along the same transect reflect variable test buoyancies caused by differences in test shape and settling velocity.

In the present study, the shell functionality is evaluated by its resistance to water motion and thus by its capability not to be transported out of its habitat, at least during the lifetime of the individual. Once the energy input by water motion at the seafloor has been defined and the settling velocity has been calculated for every test, the results show that tests are characterised by settling velocities comparable to the orbital velocity found at the water depth where the ecological optimum occurs. The settling velocity of a shell can be considered the main hydrodynamic parameter, because it depends on shape, size and density. It may also be considered as the key parameter to predict the water depth where the same shell can live and resist to water motion, which is very useful in the fossil record. For some studied taxa, it seems that the test geometry and the relative entropy are in good correlation to species specific water depth and let the foraminifer survive within its ecological optimum without being transported away, at least during fair weather conditions as supported by the depth distribution of optimally preserved tests. Such evidence underlines the potentiality of the use of bottom orbital velocity for palaeontological analyses to the much broader spectrum of the fossil nummulitids which have been subdivided in many hundreds of species, all of which possess a specific geometry that provided different entropy and settling velocity and thus different water depths.

Summarising, this study shows a correlation between shell morphology, ecological optimum, water depth and wave induced bottom orbital velocity. Such correlations may be useful to characterise monospecific assemblages or highly diverse associations, broadly deposited during Palaeocene and Eocene periods.

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Fig.1.

Wave generated orbital velocity geometry and parameters. Modified after Komar, 1998.

Fig. 2. Horizontal (u) and vertical (w) orbital bottom velocities calculated with Eqs. (1) and (3), respectively.

Fig. 3. Bottom orbital velocity calculated with Eq. (4) at different T and H conditions. The dotted line represents the energy condition used in the present work.

Fig. 4.

Settling and orbital velocity versus water depth. The solid line represents the orbital velocity function related to the water depth. The intersection between settling velocity of a single specimen and bottom orbital velocity marks the suspension–deposition boundary (A). Accumulation of tests may occur at water depth where bottom orbital velocity is always lower than the settling velocity of the tests (B).

Fig. 5.

Comparison between real and calculated settling velocities on the left and amongst real and calculated Reynolds numbers on the right. To allow linear comparisons of different tests sizes without taking into account shapes difference, the True Nominal Diameter (Wadell, 1932) has been used as size parameter on the x-axes. It is calculated with the formula $TND = 2(3V/4\pi)^{1/3}$ where V represents the volume of the test.

Fig. 6. Grey areas show the bathymetric profile of the investigated transects. The solid line represents the orbital bottom velocity at the given condition ($T = 9$ s and $H = 1$ m).

Fig. 7. Depth distribution of living and optimally preserved tests of *P. venosus* and *C. carpenteri* on the two transects. Living tests distribution (dark grey area) and optimally preserved tests distribution (solid line) are displayed below the bathymetric profiles. A light grey area indicates the settling velocity range of the investigated species and, at the intersection with the orbital velocity a dark grey area represents the calculated depth where living foraminifera resist transport.

Fig. 8.

Depth distribution of living and optimally preserved tests of *O. ammonoides* and *P. operculinoides* on the two transects. Living tests distribution (dark grey area) and optimally preserved tests distribution (solid line) are displayed below the bathymetric profiles. A light grey area indicates the settling velocity range of the investigated species and, at the intersection with the orbital velocity a dark grey area represents the calculated depth where living foraminifera resist transport.

Fig. 9. Depth distribution of living and optimally preserved tests of *H. depressa* on the two transects. Living tests distribution (dark grey area) and optimally preserved tests distribution (solid line) are displayed below the bathymetric profiles. A light grey area indicates the settling velocity range of the investigated species and, at the intersection with the orbital velocity a dark grey area represents the calculated depth where living foraminifera resist transport.