Quantitative Estimates of Time-Averaging in Brachiopod Shell Accumulations from a Holocene Tropical Shelf (SW Brazil)

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Abstract

Time-averaging, the mixing of fossils of different ages within a single bed, defines the limit of temporal resolution of the fossil record. Quantitative estimates of this resolution threshold have not been acquired for any group other than mollusks. This study provides the first quantitative estimates of time-averaging for brachiopods, extending our understanding of intrinsic, or group specific controls on this process. Estimates were obtained by direct dating of individual terebratulid brachiopod shells *Bouchardia rosea* (Mawe) collected from modern surficial shelly accumulations in the Southeast Brazilian Bight (SW Atlantic).

Using amino acid racemization dating calibrated with radiocarbon, 82 individual brachiopod shells, collected from four nearshore localities, were dated. The shells vary in age from modern to 3000 years, standard deviation = 680 years. The age distribution is significantly right-skewed (K_3=2.48). At 50-year resolution, the temporal completeness is 75% for the last 1000 years and declines to 20% completeness for 1000-2000 yr. BP. Preservational quality (taphonomy) of modern (<50 yr.) shells is statistically indistinguishable from that of older shells, demonstrating that shell taphonomy is not a good predictor of within-assemblage relative age. These results conform to previously published results for mollusks.

Therefore, brachiopods can show considerable time-averaging and this time-averaging can be on a scale similar to aragonitic mollusks despite the apparent lack of robustness of calcitic brachiopod shells. This suggests that the brachiopod fossil record can be notably time-averaged, but estimates of this mixing cannot be reliably deciphered from the taphonomic condition of shells.

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Dedication

There was an old crow
Who sat upon a clod
That’s the end of my song
That’s odd
-anonymous

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for the exposure to science from nursery school through high school whether I wanted it or not.

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Chapter 1: Introduction

Single fossiliferous horizons (e.g., shell beds) represent the finest level of resolution available for sampling in the fossil record. As such, it is incumbent upon us to recognize the time periods represented within fossil shell beds for fine scale studies such as community (alpha) diversity, within species morphological variation, and paleoecological patterns or stable isotopes. Yet, the temporal resolution of these beds is not obvious in many cases, and varies between environments, communities and species (e.g., Kidwell and Bosence, 1991, Kowalewski, 1997). This study provides the first analysis of the temporal resolution of articulate brachiopod accumulations or fossil shell beds in the making.

The processes that cause the mixing of fossils of different ages before their entry into the fossil record were collectively termed time-averaging by Walker and Bambach (1971). Since then, numerous studies have been performed to quantitatively estimate the temporal scale of, and variation in age structure between, modern accumulations of mollusks. Dating of individual shells of aragonitic mollusks (mostly venerid bivalves), collected from surficial and sub-fossil assemblages has revealed that shelly benthic macro-invertebrates may show time-averaging on a scale of 10^2-10^4 years (Table 1.1). However, no estimates exist for other macro-invertebrates common in the fossil record. Brachiopods are one of the most ubiquitous fossil groups in the Paleozoic marine fossil record, yet few rigorous studies regarding the rate of shell destruction and scale of time-averaging exist. And many authors have been cautious to extrapolate time-averaging data from mollusks to other organisms such as brachiopods (Kidwell 1993, 1998, Kidwell and Flessa 1995, Behrsenmeyer 2000).

We estimate time-averaging in brachiopod accumulations by direct dating of individual shells collected from modern surficial deposits. Previous work has indicated that amino acid racemization dating, calibrated with radiocarbon ages, can be used to date mollusks and foraminifera to ~50 years (Wehmiller, 1977, 1982; Miller and Hare, 1980; Hearty, 1987; Miller et al., 1987; Goodfriend, 1987, 1991). This method allows high-resolution dating of a large number of shells. Our approach follows methods previously used to quantify the time-averaging of mollusk assemblages (Goodfriend 1989, Flessa et al. 1993,

Table 1.1. Estimates of Time-Averaging in the Marine Realm[1].

Study[2]	Organisms	Environment[3]	Study Area	Time-averaging
ANDERSON ET AL., 1997	Mollusks	Nearshore	Gulf of Mexico, USA	$>10^3$ years
FLESSA, 1998	Mollusks	Nearshore	North Sea, Germany	$>10^3$ years
FLESSA ET AL., 1993	Mollusks	Intertidal	Gulf of Calif., Mexico	$>10^3$ years
GOODFRIEND & STANLEY, 1996	Mollusks	Deltaic	Nile Delta, Egypt	$>10^3$ years
KOWALEWSKI ET AL., 1998	Mollusks	Intertidal	Gulf of Calif., Mexico	10^2 - 10^3 years
MARTIN ET AL., 1996	Mollusks, forams	Intertidal	Gulf of Calif., Mexico	$>10^3$ years
MELDAHL ET AL., 1997	Mollusks	Nearshore	Gulf of Calif., Mexico	10^2 - 10^3 years
WEHMILLER ET AL., 1995	Mollusks	Nearshore	Atlantic Coast, USA	$>10^4$ years

[1] For examples of studies on time-averaging in terrestrial and freshwater mollusks see COHEN et al. (1987), GOODFRIEND & MITTERER (1993) and GOODFRIEND & GOULD (1996).

[2] This list is restricted to case studies that are based on direct dating of individual shells. Studies based on literature compilations (e.g., FLESSA & KOWALEWSKI, 1994) or uncalibrated amino acid dates (e.g., POWELL & DAVIS, 1990) are excluded here (the excluded studies also focus on mollusks).

[3] The term "nearshore" denotes studies that include various shallow subtidal and intertidal environments, whereas the term "intertidal" is used here for studies that focus on environments above low tide line (intertidal and/or supratidal zones).

Flessa and Kowalewski,1994, Wehmiller et al. 1995, Goodfriend et al. 1996, Martin et al.1996, Meldahl et al. 1997, Kowalewski et al. 1998, 2000) and makes our study comparable with previous work. These dates, combined with scoring of observed taphonomic condition, provide the first analysis of the taphonomic clock in articulate brachiopods, or the extent to which the state of preservation of brachiopod shells is a function of time.

Articulate brachiopods appear to be highly susceptible to fragmentation and dissolution according to both laboratory experiments (Collins, 1986, Daley 1993) and field observations (Caulet, 1972, Mundlos, 1978, Stewart, 1981, Benigni, 1987, Emig 1990, Gaspard, 1996). Rapid destruction or dissolution would cause shells to be removed from accumulations quickly, leading to abbreviated scales of time-averaging. Kidwell & Boscence (1991) agreed that “the inherent and highly specific susceptibility of those shells to post-mortem destruction or modification," is a major control on time-averaging. Yet, quantitative analysis of the age structure of articulate brachiopod accumulations has not been performed to test whether the difference in shell mineralogy and microstructure is sufficient to alter patterns of time-averaging from those displayed by mollusks.

The brachiopod assemblages analyzed in this study are suitable as an analog for tropical shell beds such as the brachiopod-rich Paleozoic shell beds of North America and Europe. Articulate brachiopods are abundant in our study area, off the coast of Brazil in the Southern Atlantic, north of the Tropic of Capricorn. While modern calcitic brachiopods have been well-documented in waters around South Africa, Australia and South America (Zezina, 1980, Cooper, 1981, Foster, 1989, Dawson, 1990, Hiller, 1990), this abundant population of brachiopods is uniquely tropical. Kowalewski (et al., submitted) have described large populations of articulate brachiopods at this latitude in the cold upwelling waters of the shelf break. This study, though, focuses on the shallow coastal populations that are present in warm water (>20°C). The study species, the terebratulid *Bouchardia rosea*, shares shell mineralogy and microstructure with a lineage of articulate brachiopods extending back through the Middle Devonian (Muir-Wood et al. 1965, Williams 1997) which allows us to apply our results to the fossil record.

Moreover, temporally mixed accumulations will contain records of average environmental conditions and can make death assemblages comparable to repeated biological surveys over a period of hundreds to thousands of years. (Martin, 1999, see also, e.g.; Kidwell and Bosence 1991, Kidwell and Flessa 1995). Therefore, a modern time-averaged assemblage provides a range of common values, and averages out extreme values caused by short-term fluctuations that may be useful in understanding the Holocene history of nearshore environments as well as a populations sensitivity to small-scale environmental change (Kowalewski et al., 2000).

Chapter 2: Study Area, Materials & Sampling Methods

The study area (Figure 2.1) is located in the Ubatuba Bay area (23°26'S and 45°02'W) on the inner shelf off northwest coast of the state of São Paulo, Brazil. This area is isolated from inland drainage by the coastal mountains designated as the Mata Atlantica ecological region. The region encompasses Rio de Janiero, Espirito Santos and São Paulo, and represents the industrial center of South America and the most heavily populated area (>25 million inhabitants) in the Southern Hemisphere. The sampled area falls within the South Brazilian Bight Marine Province. This province is characterized by a tropical humid climate and water masses dominated by the South Brazil Current, a warm west-boundary current flowing from the equatorial zone. The inner shelf of Ubatuba Bay is located above the thermocline and dominated by the Coastal Water (Campos et al 1995, 2000) which is warm (>20°C), fully saline (>36.4‰) and thoroughly oxygenated.

Figure 2.1. Map of Study Area (pdf, 82 KB)

The study area is one of pocket bays delineated by promontories made of igneous and metamorphic rocks. The total area of the bay is about 8 km^2 , and the width at the entrance of about 4.5 km. Four small rivers (Indaia, Grande, Lagoa and Acarau) flow into the bay. The average water depth in the bay is about 9.3 m. The following annual mean values have been reported for bay waters: temperature 23.8°C, salinity 33.2 ‰, dissolved oxygen 5.11 mg/l. The substrate is medium-grained mixed siliciclastic/carbonate with considerable terrestrial organic input. The surficial sediments are rich in shell material including diverse mollusks and rhynchonelliform (terebratulid) brachiopods overwhelmingly dominated by the endemic form *Bouchardia rosea.*

The species chosen for this study, the terebratulid brachiopod, *Bouchardia rosea* (Mawe) has a fossil record extending back to the Cretaceous in the Southern Continents (Mancenido et al. 1988). *B. rosea* is a member of a brachiopod class extending back through the middle Devonian (Muir-Wood, et al. 1965). *B. rosea* is a small (<30 mm) brachiopod with a low Mg-calcite punctate shell, a brachidium with a simple calcareous loop, and a strong hinge structure. As in most terebratulides, *B. rosea* has a thin primary shell layer, a thick secondary shell layer with a fibrous fabric and no tertiary shell layer. A fibrous fabric is invariably characteristic of the secondary shell of extant rhynchonellides and terebratulides and was already well developed in Paleozoic members of these groups, such as the Devonian *Mutationella* and the Ordovician *Rostricellula*, respectively (Williams, 1997). It is also the standard fabric for all spire-bearing brachiopods, pentamerides, and most orthides (Williams, 1968). *B. rosea* is a sessile epifaunal benthic organism that selectively inhabits substrates with carbonate concentrations ranging from 40 to 70%. (Simoes et al. in prep., Kowalewski et al., submitted). *B. rosea* does not need to attach to the substrate but perhaps uses its pedicle in a ratchet fashion to stay at the sediment water interface (Richardson, 1981, Brunton, 1996).

The shell samples were collected in conjunction with an ongoing project of the marine ecology group of the State University of São Paulo. The study sites included four sub-tidal sites within the general area of Ubatuba Bay including Ubatumirim (localities 1 & 2), Ilha das Couves (locality 3) and Ubatuba Bay (locality 4) (Figure 2.1). These localities ranged in depth from 4.6 to 25 meters and were collected using a Van Veen grab sampler (1/40m^2). This method samples the topmost sediments within 10 cm of the surface. The samples represent modern surficial unconsolidated deposits of the shallow shelf. The temperature, salinity and organic content of the bottom water at collection were taken for each sample (Table 2.1). The sites varied in their proximity to shore and location within the bays. Locality 1 is within a pocket bay, while Locality 2 is at the bay's mouth. Locality 3 is on the landward side of a coastal island and Locality 4 is in a distant inlet of the main bay (see Figure 2.1).

For each of the 4 sampling localities specimens were collected. A total of ~20 specimens were randomly selected from bulk samples (Table 2.1), using numerical assignments for shells and a random number generator. Specimens smaller than 1 cm in length were excluded due to insufficient material for amino acid and radiocarbon analyses.

Table 2.1. Summary of the Environmental Variables and Sampling Information for the Four Localities Sampled.

	Locality 1 Ubatumirim	Locality 2 Ubatumirim	Locality 3 Ilha das Couves	Locality 4 Ubatuba Bay
Water depth (m)	5.7-6	22.8	15.8-16.8	9.2-10
Distance from shore (km)	0.5	2	2.5	0.3
Temperature (°C)		20.4+2.6	23.7	23.8+2.9
Salinity (‰)		35.5+1.1	33	34.3+2
% Organic Carbon		0.8+0.3		7.8+2.8
Location	23º 21' S 44º 54' W	23º 24' S 44º 54' W	23º 25' S 44º 51' W	23º 27' S 45º 02' W
Random sample selected for dating	19	20	21	22
Total sample size	19	153	29	731

Specimens were digitally imaged and measured for length and width by an electronic digital caliper with a precision of +/- 0.1mm. Each shell was then categorized into presence/absence grades in terms of the ten following taphonomic characteristics: (1) disarticulation, (2) fragmentation, (3) edge completeness, (4) removal of gloss, (5) interior surface alteration, (6) exterior surface alteration, (7) invisibility of muscle scars, (8) bioerosion, (9) interior encrustation, and (10) exterior encrustation. The summation of all values provided a total taphonomic grade used to evaluate the overall degree of shell alteration (see Fürsich & Flessa, 1987, 1991). The raw data are presented in Appendix A.

Chapter 3: Dating by Epimerization of L-isoleucine to D-alloisoleucine.

To obtain ages of individual shells we used amino acid racemization rates, which have been used as a dating tool throughout the Cenozoic. We analyzed for the organic amino acid isoleucine (I) and its inorganic epimer, alloisoleucine (A). This ratio (A/I) has been used for time periods covering the Holocene and the Pleistocene (Wehmiller, 1977, 1982; Miller and Hare, 1980; Hearty, 1987; Miller et al., 1987; Goodfriend, 1987, 1991) and has been shown to be more precise for the last 350 years than ^{14}C dating (Goodfriend, 1992).

All shells used for amino acid racemization and radiocarbon analyses were cleaned by a combination of ultrasonication, mechanical cleaning using dental tips on a motorized tool, and etching with dilute HCl (see Goodfriend, 1987, 1991 for details of procedures). Shell fragments (20-80 mg in weight) were analyzed for isoleucine epimerization and amino acid composition by High Performance Liquid Chromatography (HPLC) using post-column derivatization with o-phthaldialdehyde (OPA) (Hare and Mitterer 1985), following 20 hr hydrolysis in 6N HCl at 100°C and desalting with HF. Peak areas were integrated using Waters Millennium 2.00 software. A/I values were calculated from peak area ratios, calibrated against a standard A/I mixture (with A/I = 0.30), prepared by Glenn Goodfriend, George Washington University. Analytical errors typically average 4.5% of the A/I value. This error increases with time, with more recent shells producing smaller error and older shells greater error.

Variation within the shell. Studies of relatively larger shells of bivalves (Goodfriend et al., 1997) indicate substantial variation in amino acid epimerization rates among the shell layers and positions of shell sampled. In the initial analysis, we evaluated *B. rosea* shells for intrashell variability in racemization rates. The primary shell layer in *Bouchardia rosea* is very thin, ~10 µm, therefore we were unable to isolate this layer for separate sampling. We focused instead on the secondary fibrous layer by removing the outer primary layer (previous studies have shown that the outer layer has a lower concentration of organic material; Williams, 1997).

Three shells were sampled at six locations within the shell to evaluate intrashell variability (see Fig. 3.1; Table 3.1). Our data suggest that variation within the shell is about 10% or twice the analytical error. In addition, our data indicate no systematic variation due to position. In order to minimize the variation due to intrashell variability we have sampled each specimen consistently from the same area (secondary layer of the anterior part of the valve).

Figure 3.1. Images of Interior of Brachial and Pedicle Valves (pdf, 133 KB)

Table 3.1. Results from A/I Analysis for Intrashell Variability

specimen	position						mean	std dev
	a	b	c	d	e	f		
BB-2	0.0090	0.0085	0.0082	0.0081	0.0086	0.0075	0.0083	6.20%
CB-1	0.039	0.040	0.046	0.046	0.042	0.051	0.044	10%
AA-3	0.038	0.031	0.038	0.028	0.036	0.040	0.035	13%

Calibration with Radiocarbon Dates. The rate of epimerization of L-isoleucine to D-alloisoleucine is directly dependent on temperature and varies among organisms. In order to determine the rate of epimerization, the amino acid ratios must be calibrated against an independent estimate of absolute age. Because all our sites represent subtidal settings from the same bay with water temperatures varying among sites by less than 2°C and because all specimens belong to a single species, a single calibration of racemization rates should be sufficient. After analyzing ~30 specimens for A/I ratios, we submitted 5 specimens covering a broad range of A/I ratios for radiocarbon analysis at NOSAMS Lab (Woods Hole) where ^{14}C was measured by Accelerator Mass Spectrometry. (see http://www.nosams.whoi.edu/nosams.html for details of the procedure they use).

The five ^{14}C-dated specimens were reprepared and reanalyzed for A/I ratio at least once, the exact number of repreps depending on the quantity of the available shell material: the specimen AA-8 was reprepared twic, BB-15 5 times and the other three shells once (see Appendix A). The arithmetic mean of all repreps for one specimen was used as the A/I value for the calibration against radiocarbon estimates. Error estimates for radiocarbon (see Figure 3.2) are based on information provided by NOSAMS.

Figure 3.2. Calibration Curve of Uncorrected Radiocarbon Age vs. A/I Ratio (pdf, 25 KB)

The five specimens dated show a significant positive correlation of A/I values with apparent ^{14}C age ($r^2=0.925$, $F=37.13$, $p=0.009$). The results show that A/I ratios are an excellent predictor of radiocarbon age with the slope of the regression line: ^{14}C age=15980*A/I ratio.

Because marine radiocarbon ages are subject to a reservoir effect due to the upwelling of older residence bottom waters, the calibration against apparent ^{14}C age, according to the above equation, overestimates the actual shell age (e.g., a shell that is 100 years old will have an apparent age of 100 + reservoir effect). In order to quantify the reservoir effect in Ubatuba Bay, 2 live collected specimens were analyzed to measure epimerization induced by sample preparation procedures. A/I values for live-collected specimens are not zero because the hydrolysis procedure causes racemization, a constant value among shells of the same species. The average A/I value of the live collected specimens (0.0056) was then used as the zero age ratio. The resultant calibration; age=15980*(A/I ratio-0.0056), was used to convert all A/I values to age in years. See Appendix A for A/I values and corresponding age estimates.

Regressing A/I value for live-collected specimens against apparent ^{14}C age produces an estimate of the local reservoir effect. The predicted value of 510 years is reasonable given that the reservoir effect fluctuates from a couple hundred years to over 1000 years and low-latitude worldwide ocean values are typically between 300 and 500 years. (Bowman 1990, Stuiver 1998).

Given the excellent agreement between A/I ratio and apparent radiocarbon age, and the reservoir estimate's consistency with expected values, the calibrated A/I values should provide reliable and reasonably precise estimates of shell age.

Chapter 4: Results

Age Structure. A total of 82 specimens from four localities were dated. When all localities are pooled, shells range in age from modern to 3100 yr BP. The median shell age is 300 years, the modal age-class is 0-50 yr BP and the standard deviation is 680 years (Table 4.1). These values vary significantly among localities, with an age range of 377 yr (loc 1) at the least time averaged site and 3134 yr (loc 4) at the most time-averaged site. The standard deviation varies from 131 years (loc 1) to 1081 years (loc 4).

Figure 4.1. Age Distribution of Brachiopod Shells (pdf, 94 KB)

The pooled distribution shows pronounced right-skewness reflecting the fact that shells become increasingly less frequent in older age classes (see Fig. 4.1). The decreasing frequency of shells appears to follow an exponential (hollow) curve and shows a significant log-linear fit (r^2 value of 0.743, $p < 0.05$). Significant departures can be observed for age classes 250-300 yr BP and 300-350 yr BP. Using a method described by Meldahl (et al. 1997), we obtain a half-life estimate of 144 years.

Table 4.1. Summary Statistics of Temporal Resolution by Locality

	Locality 1 Ubatumirim	Locality 2 Ubatumirim	Locality 3 Ilha das Couves	Locality 4 Ubatuba Bay	Pooled
Sample size	19	20	21	22	82
Range (yrs)	359	531	2000	3134	3134
Standard deviation (yrs)	129	149	633	1078	680
Mean shell age (yrs)	176	303	583	683	460
Median (yrs)	135	357	454	215	288
Min shell age (yrs)	0	69	0	0	0
Max shell age (yrs)	359	600	2000	3134	3134
Skewness	0.03	-0.33	1.22	1.36	2.48
Kurtosis	-1.55	-0.61	0.38	0.32	5.86
Observed completeness	87.5%	81.8%	35.0%	22.2%	38.1%
Expected at 100% completeness (w 95%)	92.0% .75-1	85.0% .636-1	41.2% .325-475	29.9% .254-333	72.9% .651-.81
Probability of 100% completeness	0.553	0.165	0.105	0.001	0.001

For pooled data, at 50-year resolution, the observed completeness of the record over the time-series of shells at 50-year resolution is 38% (ie. 38% of 50-year time-intervals contain shells) (See Table 4.1). We assumed a uniform distribution of shells in each age class, equal numbers of 3000-year-old shells to modern shells and simulated 1000 samplings of 82 shells. The expected completeness for a uniform time-series is 73%. The observed completeness of our record is significantly lower ($p<0.05$).

The age structure and completeness vary among localities. Two of the localities (loc 1 & 2) do not show right-skewness and display two modal age classes (Figure 4.2) unlike localities 3 and 4. Localities 1 and 2 have over 80% observed completeness while 3 and 4 have 35% and 22%, respectively. Assuming a uniform distribution and simulating sampling 1000 times, Locality 1 is indistinguishable from a uniform distribution while Locality 4 is significantly different ($p<0.05$). Localities 2 and 3 fall somewhere in the middle. These results indicate a strong similarity between Localities 1 and 2 within the Bay of Ubatumirim, whereas widely separated Localities 3 and 4 resemble each other.

Figure 4.2. Age Distribution by Locality (pdf, 100 KB)

Taphonomy. The dated shells vary over a wide spectrum of preservation states with total taphonomic score ranging from 2 to 10. However the plot of total taphonomic score versus age does not reveal any clear correlation between age and preservation ($r^2 = 0.019$, $p = 0.22$) (Figure 4.3). The plot suggests that within only decades shells achieve the full range of observed taphonomic conditions. The frequency of well preserved shells decreases slightly over time; shells older than 1500 years have a range of 3-10 and over 2000 years old range from 5-10.

Figure 4.3. Plot of Taphonomic Score vs. Age (pdf, 7 KB)

Figure 4.4. Comparative Taphograms (pdf, 7 KB)

We separated those shells younger than 50 years (n=17) from older shells (n=65), artificially creating one sample set of very recent shells and one sample of time-averaged shells. The two samples show no significant difference in taphonomic pattern (Figure 4.4): the two resulting taphograms do not differ significantly in shape (D=0.12; p=0.99; Kolmogorov-Smirnov) or average state of preservation (medians 6.6 and 7.1; p=0.42 Wilcoxon test).

Chapter 5: Discussion

The results indicate that brachiopod shell accumulations from a modern tropical shelf undergo time-averaging on the scale of hundreds to thousands of years. This estimate provides insights both into the taphonomy and time-averaging of brachiopod shell accumulations as well as the nature of taphonomic processes and the temporal resolution of the fossil record in general.

Taphonomy and Time-Averaging in Brachiopod Shell Accumulations.

The results are unexpected given the widely stated fragility of brachiopod shells relative to mollusks. Emig (1991) observes that the rapid alteration of organic matter within the secondary shell layer of terebratulid brachiopods, followed by weakening and fragmentation of the shell structure leads to the reduction of the shell to microfibers within 6-7 months. In an experimental laboratory study, Daley (1993) shows that rapid weakening (within months) in the hinge area facilitates fragmentation of the shell even before disarticulation is achieved. This fragility should result in high rates of shell destruction and consequently it has been suggested that time-averaging in fossil brachiopods might be only on the scale of tens to hundreds of years (Kidwell, 1998). Despite this fragility of brachiopod shells, we found that many shells in surficial accumulations are hundreds or even thousands of years old.

Levels of time-averaging documented here for modern brachiopod accumulations from a shallow tropical shelf suggest that brachiopod shell beds found in the fossil record may represent deposits affected by extensive temporal mixing. Consequently, they may not be suitable for reconstructing population dynamics, community structure, and other short-term aspects of brachiopod ecology. Moreover, brachiopod diversity, shell morphometrics, and geochemical signatures extracted from shell beds may represent records time-averaged on centennial to millennial scales.

Our study may overestimate time-averaging in Paleozoic shell beds, given that the scale of time-averaging may have increased through the Phanerozoic (Kidwell, 1990, 1998; Kidwell and Brenchley, 1996; Kowalewski, 1996; Kowalewski and Bambach, in press). On the other hand, our estimates of time-averaging may be too conservative considering that surficial assemblages may still undergo further mixing before their final incorporation in the fossil record. Note that, following post-glacial transgression, the sea level in the region has not changed notably through the late Holocene: <1 m during the last 3 kyr (Angulo et al., 1999; Lessa et al., 2000; Baker et al., 2001). Thus, the sampled brachiopod accumulations have been forming in a context of high and relatively stable sea level. The results provide the best analog for shell bed types (see Carter et al., 1991; Kidwell, 1991, 1993) associated with maximum flooding surfaces and highstand deposits.

Brachiopod shells dated in this study show no correlation between age and taphonomic condition. Modern accumulations show the same taphonomic pattern that time-averaged accumulations of 3000 years do (Figure 4.4). Therefore, the apparent condition of a fossil brachiopod shell should not be used to assess the duration of its pre-burial history relative to other shells within an assemblage. And the variation in taphonomic conditions of fossil brachiopod assemblages need not reflect the duration of time-averaging. There is no taphonomic clock.

Brachiopods vs. Mollusks. In addition, the conceptual model that intrinsic characteristics of an organism define its preservational potential and time-averaging (Kidwell and Bosence, 1991, Kowalewski, 1997) may be overly complex. We observe a range of time-averaging in brachiopods that falls well within the range observed for mollusks despite differences in shell mineralogy and microstructure (Figure 5.1).

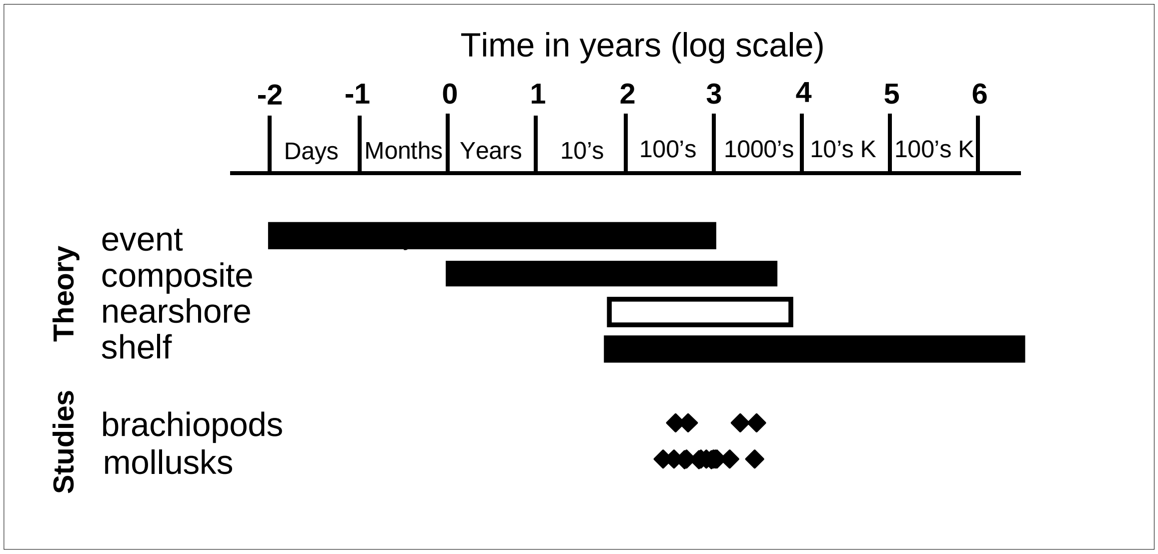

Figure 5.1. Years of Time-Averaging per assemblages (log scale), Marine invertebrates adapted from Kidwell & Behrensmeyer, 1993.

The processes of time-averaging produce startlingly contradictory observations. Shells are rapidly destroyed yet survive for thousands of years. More fragile brachiopod shells survive as long as more robust mollusk shells. Taphonomic condition, intuitively only worsening through time, shows no correlation with age of shells. Driscoll (1970), in an early tethering experiment, explored the importance of environmental processes between death and final burial. He tethered 84 valves from 3 species (*Mercenaria mercenaria*, *Argopecten i irradians* and *Mya arenaria*) in a shallow, low energy environment. Within 3 years he was able to recover only 25-50% of valves and, of those, up to 100%, for *M. arenaria*, were substantially altered by boring organisms, abrasion and chemical dissolution demonstrating the rapid and selective destruction of mollusk shells. He concluded that buried shells survived and that preservational selection was based on shell properties (surface area per unit weight) that effect how rapidly a shell is buried. Consequently we arrive at another contradiction. The more rapidly a shell is buried the greater the likelihood that the shell will be preserved over long periods of time allowing greater range in time-averaging (see also Flessa et al., 1993, Martin et al., 1996). Yet, the more rapidly shells are buried, the less time is available for mixing those shells with younger generations shortening the scale of time-averaging. But as Driscoll concludes, burial and preservation are dependent on more than sedimentation rate. Studies have shown that bioturbation, resuspension of sediment, and settling of shells provides for rapid shallow burial of shells while not burying them so deeply as not to be susceptible to reworking. Clifton (1971) observed 50% burial by a thin sediment coating of empty pelecypod valves off St. John in the U.S. Virgin Islands within 40 days. SSETI has observed 1-2 cm of burial of empty mollusk shells at a variety of water depths and soft substrates within two years (Parsons-Hubbard et al., 1999) even when net sedimentation rates were only 0.01-0.06 cm/yr. Clearly, *B. rosea* of our study are rapidly buried because surficial modern shells can show the greatest level of alteration measured. Exposure leads to rapid destruction.

In fact, the temporal window of taphonomic alteration is vanishingly small (days to years) in relation to the scale of time-averaging (hundreds to thousands of years). Therefore, taphonomic condition must be based on a complex function of the frequency of reworking, the length of exhumation and the rate and type of taphonomic processes at the depth of exhumation, i.e. surface vs. various depths within the taphonomically active zone (TAZ of Davies et al., 1989). From the point of view of the fossil record, taphospace, or the range of possible taphonomic conditions, is time-independent.

Time-averaging and taphonomic pathways seem to apply, not only to mollusks but may be universal for shelly benthos. We are unable to demonstrate differences in nearshore time-averaging based on intrinsic characteristics of an organism’s hard parts. The next step is to test even more fragile fossils, for example echinoids, crab claws, to look for a threshold of fragility beyond which time-averaging patterns differ.

<u>Implications for Conservation Biology, Historical Ecology and Holocene Research</u>. The high-resolution dating method of this study provides a three thousand year history of the living population of *B. rosea* in the nearshore waters of Saõ Paulo, Brazil. It is a region of the South Atlantic that has been affected by changing ocean circulation patterns through the Cenozoic and by changing human inputs over the past thousand years. Therefore, the time-averaging in modern assemblages allows for the preservation of information useful in the study of short-term ecological change.

Our results show that a single species of brachiopod (constant shell mineralogy, microstructure, etc.) can vary in time-averaging; hundreds of years (Localities 1 & 2) and thousands of years (Localities 3 & 4), across seemingly uniform depositional sites (Figure 5.2). Such variations indicate environmental effects, perhaps local variation in sedimentation rate, type and rate of taphonomic processes or local variation in marine productivity. Meldahl et al. (1997) attributed variation in local age structures to sedimentation rate and frequency of reworking. Unlike their study, though, our data shows no consistent pattern between range of time-averaging and locality depth, distance from shore or proximity to river outlets. The absence of depth vs. scale of time-averaging correlation discourages depth dependent interpretations such as bioturbation, wave action and even storm reworking. The processes of time-averaging do not seem to be causing the local variations in time-averaging.

Figure 5.2. Diagram of locality sites and results (pdf, 182 KB)

The underlying control on time-averaging, then, is the living population that forms an assemblage over time. Kowalewski et al. (2000) use calculations of the density of bivalve beach ridges at the mouth of the Colorado Delta in concert with quantitative estimates of the age structure of the assemblage to arrive at a minimum value for the size of the living population in the area over the past thousand years. These calculations provided a robust means of analyzing deviations over time in the living population, notably the near elimination of bivalve populations in the past hundred years due to decreased fresh water inputs caused by dams. Assuming variation in input of new shells, a conservative evaluation of our data suggests a couple of temporal questions. One is the abbreviated scale of time-averaging in the two localities within Ubatumirim Bay. A second is the apparent absence of shells for an interval within the past 500 years. In Mancenido & Griffin's 1988 study (also Sandy, 1991) of the paleoceanography of the genus *Bouchardia* (*B. rosea* is the only living species), the authors document its northward migration. In the Paleocene *Bouchardia* were found in Antarctic waters. As ocean currents changed with the initiation of the circum-Antarctic current, *Bouchardia* moved progressively up the coast, presumably following ideal ocean temperatures. Modern *Bouchardia* are common in the cold waters of the shelf break off the coast of Brazil (Kowalewski et al. 2000) and have not been found south of Uruguay (Dall

1920, Zezina 1970). Variation in size of coastal populations of *B. rosea* may be due to sporadic colonization of coastal waters from the shelf break and/or small but significant variations in the coastal environment effecting its habitability by *B. rosea*.

The marine ecology program at Sao Paulo State University is exploring recent environmental change in Ubatuba Bay and its effects on crustaceans. One factor they are studying is heightened productivity due to urban run-off (Tommasi, 1970, Mantellatto and Fransozo 1999). Time-averaged brachiopod shell assemblages offer complementary long-term records of this coastal marine environment for the sub-fossil record.

Chapter 6: Conclusions

Articulate brachiopod assemblages on a shallow coastal shelf in Brazil show time averaging on the scale of 10^2-10^3 years. The scale and the structure of the age distribution show marked similarities to those obtained for mollusk assemblages in previous studies of shallow coastal environments elsewhere. In addition, brachiopods show the full range of taphonomic grades at relatively young ages (by 50 years) and maintain this range throughout the sampled time interval. This indicates that in depositional environments over prolonged periods of time, articulate brachiopods can withstand or be protected from circumstances that have been observed to destroy or alter them rapidly.

These results support arguments that ‘sufficiently durable shells’ will show time-averaging primarily controlled by extrinsic variables such as sedimentation rate or influx of new shell material. While this idea has grown out of work done on several genera of mollusks, this study provides the first data documenting that pervasive time-averaging affects not only mollusks, but other shelly benthos as well.

REFERENCES

ANDERSON, L.C., GUPTA, B.K., and BYRNES, M.R., 1997, Reduced seasonality of Holocene climate and pervasive mixing of Holocene marine section: Northeastern Gulf of Mexico shelf: *Geology* **25:** 127-130.

ANGULO, R.J., GIANNINI, P.C.F., SUGUIO, K., and PESSENDA, L.C.R., 1999, Relative sea-level changes in the last 5500 years in southern Brazil (Laguna-Imbituba region, Santa Catarina State) based on vermetid ^{14}C ages: *Marine Geology* **159**: 323-339.

BAKER, R.G.V., HAWORTH, R.J., and FLOOD, P.G., 2001, Warmer or cooler late Holocene marine palaeoenvironments? Interpreting Southeast Australian and Brazilian sea-level changes using fixed biological indicators and their δ^{18}O composition: *Palaeogeography, Palaeoclimatology, Palaeoecology* **168:** 249-272.

BEHRENSMEYER, A.K., KIDWELL, S.M., and GASTALDO, R.A., 2000, Taphonomy and paleobiology: *Paleobiology (supplement)* **26:** 103-147.

BENIGNI, C., 1987, Shell microstructure of Mediterranean terebratulids from Pliocene to Recent and its diagnostic significance. *Bolletino del Museo regionale de Scienza naturale de Torino* **15:** 211-217.

BOWMAN, S., 1990, *Radiocarbon Dating:* University of California Press, Berkeley, 64p.

BRUNTON, C.H.C., 1996, The Functional morphology of the Recent Brachiopod *Bouchardia rosea*: *Acta Zoologica* **77:** 233-240.

CAMPOS, E.J.D., GONÇLAVES, J.E., and IKEDA, Y., 1995, Water mass characteristics and geostrophic circulation in the South Brazil Bight: Summer of 1991: *Journal of Geophysical Research* **100:** 18537-18550.

CAMPOS, E.J.D., VELHOT, D., and DA SILVERIRA, I.C.A., 2000, Shelf break upwelling driven by Brazil Current cyclonic meanders: *Geophysical Research Letter* **27:** 751-754.

CARTER, R.M., ABBOTT, S.T., FULTHORPE, T., CRAIG, S., HAYWICK, D.W., and HENDERSON, R.A., 1991, Application of global sea-level and sequence-stratigraphic models in Southern Hemisphere Neogene strata from New Zealand. *In* MACDONALD, D.I.M., (ed.), *Sedimentation, tectonics and eustasy; sea-level changes at active margins: Special Publication of the International Association of Sedimentologists* **12:** 41-65.

CAULET, J.P., 1972, Les sediments organogenes du precontinent algerien. *Memoires du Museum National d'Histoire naturelle, Paris* **25:** 1-295.

CLIFTON, H.E., 1971, Orientation of empty pelecypod shells and shell fragments in quiet water. *Jornal of Sedimentary Petrology* **41:** 671-682.

COLLINS, M.J., 1986, Post mortality strength loss in shells of the Recent articulate brachiopod *Terebratulina retusa* (L.) from the West coast of Scotland. In, Racheboeug, P.R. and C.C. Emig (eds), Les brachiopodes fossiles et actuels. *Biostratigraphie du Paleozoique* **4**: 209-218.

COOPER, G.A., 1981, Brachiopods from the southern Indian Ocean: *Smithson. Contr. Paleobiol.* **43:** 1-93.

DALEY, G.M., 1993, Passive deterioration of shelly material: A study of the recent eastern pacific articulate brachiopod *Terebratulia transversa* Sowerby: *Palaios* **8:** 226-232.

DALL, W.H., 1920, Annotated list of the Recent Brachiopoda in the collection of the United States National Museum, with descriptions of thirty-three new forms: *Proceedings of the U.S. National Museum* **57**(2314): 261-377.

DAVIES, D.J., POWELL, E.N. AND STANTON R.J.JR., 1989, Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast. *Palaeogeography, Palaeoclimatology, Palaeoecology* **72:** 317-352.

DAWSON, E.W., 1990, The living brachiopod fauna of New Zealand: a systematic reference list: *Occas. Publs Hutton Fdn* **2**.

DRISCOLL, E.G., 1970, Selective bivalve shell destruction in marine environments, a field study: *Journal of Sedimentary Petrology* **40:** 898-905.

EMIG, C.C., 1990, Examples of post-mortem alteration in recent brachiopod shells and (paleo)ecological consequences: *Marine Biology* **104:** 233-238.

FLESSA, K.W., 1998, Well-traveled cockles: Shell transport during the Holocene transgression of the southern North Sea: *Geology* **26:** 187-190.

FLESSA, K.W., and KOWALEWSKI, M., 1994, Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature: *Lethaia* **27:** 153-165.

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* **19:** 266-286.

FOSTER, M.W., 1989, Brachiopods from the extreme South Pacific and adjacent waters: *Journal of Paleontology* **63:** 268-301.

FÜRSICH, F.T., and FLESSA, K.W., 1987, Taphonomy of tidal flat molluscs in the northern Gulf of California; paleoenvironmental analysis despite the perils of preservation: *Palaios* **2:** 543-559.

FÜRSICH, F.T., and FLESSA, K.W., 1991, The origin and interpretation of Bahia la Choya (northern Gulf of California) taphocoenoses; implications for paleoenvironmental analysis: Zitteliana **18:** 165-169.

GASPARD, D., 1996, Taphonomy of some Cretaceous and Recent Brachiopods, In Copper, P. and J. Jin (eds), *Brachiopods; Proceedings of the Third Internation Brachiopod Congress*: 95-102.

GOODFRIEND, G.A., 1987, Chronostratigraphic studies of sediments in the Negev Desert, using amino acid epimerization analysis of land snail shells: *Quaternary Research* **28:** 374-392.

GOODFRIEND, G.A., 1989, Complementary use of amino acid epimerization and radiocarbon analysis for dating mixed-age fossil assemblages: *Radiocarbon* **31:** 1041-1047.

GOODFRIEND, G.A., 1991, Patterns of racemization and epimerization of amino acids in land snail shells over the course of the Holocene: *Geochimica et Cosmochimica Acta* **55:** 293-302.

GOODFRIEND, G.A., 1992, Rapid racemization of aspartic acid in mollusk shells and potential for dating over recent centuries: *Nature* **357**: 399-401.

GOODFRIEND, G.A., and GOULD, S.J., 1996, Paleontology and chronology of an evolutionary transition by hybridization in the Bahamian land snail *Cerion*: *Science* **274**: 1894-1897.

GOODFRIEND, G.A., and MITTERER, R.M., 1993, A 45,000-yr record of a tropical lowland biota: the land snail fauna from cave sediments at Coco Ree, Jamaica: *Geological Society of America Bulletin* **105**: 18-29.

GOODFRIEND, G.A., and STANLEY, D.J., 1996, Reworking and discontinuities in Holocene sedimentation in the Nile Delta: documentation from amino acid racemization and stable isotopes in mollusk shells: *Marine Geology* **129**: 271-283.

GOODFRIEND, G.A., BRIGHAM-GRETTE, J., and MILLER, G.H., 1996, Enhanced age resolution of the marine Quaternary record in the Arctic using aspartic acid racemization dating of bivalve shells: *Quaternary Research* **45**: 176-187.

GOODFRIEND, G.A., FLESSA, K.W., and HARE, P.H., 1997, Variation in amino acid epimerization rates and amino acid composition among shell layers in the bivalve *Chione* from the Gulf of California: *Geochimica et Cosmochimica Acta* **61:** 1487-1493.

HARE, P.E., and MITTERER, R.M., 1985, Laboratory simulations of amino-acid diagenesis in fossils: *Carnegie Institution of Washington Yearbook* **64:** 223-232.

HEARTY, P.J., 1987, New data on the Pleistocene of Mallorca: *Quaternary Science Reviews* **6:** 245-257.

HILLER, N., 1990, The southern African Recent brachiopod fauna: *in* MACKINNON, D.I., LEE, D.E., CAMPBELL, J.D., (eds), *Brachiopods through time*, Second International Brachiopod Congress, New Zealand: 439-445.

KIDWELL, S.M., 1990, Phanerozoic evolution of macroinvertebrate shell accumulations: preliminary data from the Jurassic of Great Britain. Pp. 309-327, *in* MILLER, W.M.III, (ed.), *Paleocommunity Temporal Dynamics*, Paleontological Society Special Publication **5**.

KIDWELL, S.M., 1991, The stratigraphy of shell concentrations. Pp. 211-290, *in* ALLISON, P.A., and BRIGGS, D.E.G., (eds.), *Taphonomy: Releasing the Data Locked in the Fossil Record*, Plenum Press, New York.

KIDWELL, S.M., 1993, Patterns of time-averaging in the shallow marine fossil record. Pp. 275-300, *in* KIDWELL, S.M., and BEHRENSMEYER, A.K., (eds.), *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology* **6**, Paleontological Society, Knoxville, Kentucky.

KIDWELL, S.M., 1998, Time-averaging in the marine fossil record: overview of strategies and uncertainties: *Geobios* **30:** 977-995.

KIDWELL, S.M., and BEHRENSMEYER. A.K., eds., 1993, *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology* **6**, Paleontological Society, Knoxville, Kentucky.

KIDWELL, S.M., and BOSENCE, D.W.J., 1991, Taphonomy and time-averaging of marine shelly faunas. *In* ALLISON, P.A., and BRIGGS, D.E.G., (eds.), *Taphonomy: Releasing Data Locked in the Fossil Record*: *Topics in Geobiology* **9:** 115-209, Plenum Press, New York.

KIDWELL, S.M., and BRENCHLEY, P.J., 1996, Evolution of the fossil record: thickness trends in marine skeletal accumulations and their implications: IN JABLONSKI D., ERWIN D.H. AND LIPPS, J.H. (eds), *Evolutionary Paleobiology*, 209-336.

KIDWELL, S.M., and FLESSA, K.W., 1995, The quality of the fossil record: populations, species, and communities: *Annual Reviews of Ecology and Systematics* **26:** 269-299.

KOWALEWSKI, M., 1996, Time-averaging, over-completeness and the geological record: *Journal of Geology* **104:** 317-326.

KOWALEWSKI, M., 1997, The reciprocal taphonomic model: *Lethaia* **30:** 86-88.

KOWALEWSKI, M., and BAMBACH, R.K., in press, The limits of paleontological resolution. *In* HARRIS, P.J., and GEARY, D.H., (eds.), *High resolution approaches in paleontology: Topics in Geobiology Series:* Kluwer Academic/Plenum, New York.

KOWALEWSKI, M., GOODFRIEND, G.A., and FLESSA, K.W., 1998, The high-resolution estimates of temporal mixing in shell beds: the evils and virtues of time-averaging: *Paleobiology* **24:** 287-304.

KOWALEWSKI, M., AVILA SERRANO, G.E., FLESSA, K.W., and GOODFRIEND, G.A., 2000A, A dead delta's former productivity: Two trillion shells at the mouth of the Colorado River: *Geology* **28:** 1059-1062.

KOWALEWSKI, M., SIMÕES, M.G., CARROLL, M., and RODLAND, D.L., 2000B, Distribution of articulate brachiopods across a modern low-latitude shelf from the western South Atlantic: *Geological Society of America Abstracts with Programs* **32:** A96.

KOWALEWSKI, M., SIMÕES, M.G., CARROLL, M., and RODLAND, D.L., submitted, Abundant articulated brachiopods in low-latitude upwelling zones: *Geology*.

LESSA, G.C., ANGULO, R.J., GIANNINI, P.C., AND ARAUJO, A.D., 2000, Stratigraphy and Holocene evolution of a regressive barrier in South Brazil: Marine Geology 165: 87-108.

MANCENIDO, M. AND GRIFFIN, M., 1988, Distribution and palaeoenvironmental significance of the Genus *Bouchardia* (Brachiopoda, Terebratellidina): Its bearing on the Cenozoic evolution of the South Atlantic: Revista Brasileira de Geociencias 18(2): 201-211.

MANTELATTO, F.L.M., and FRANSOZO, A., 1999, Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo State, Brazil: *Revista Brasileira de Biologia* **59:** 23-31.

MARTIN, R.E., 1999. *Taphonomy: A Process Approach:* Cambridge University Press, Cambridge, 508 p.

MARTIN, R., WEHMILLER, J.F., HARRIS, M.S., and LIDDEL, W.D., 1996, Comparative taphonomy of bivalves and foraminifera from Holocene tidal flat sediments, Bahia la Choya, Sonora, Mexico (northern Gulf of California): taphonomic grades and temporal resolution: *Paleobiology* **22:** 80-90.

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* **23:** 207-229.

MILLER, B.B., and HARE, P.E., 1980, Amino acid geochronology: integrity of the carbonate matrix and potential of molluscan fossils. Pp. 415-443, *in* HARE, P.E., et al. (eds.), *Biogeochemistry of Amino Acids:* Wiley, New York.

MILLER, B.B., MCCOY, W.D., and BLEUER, N.K., 1987, Stratigraphic potential of amino acid ratios in Pleistocene terrestrial gastropods: an example from West-Central Indiana: *Boreas* **16:** 133-138.

MUIR-WOOD, H.M; STEHLI, F.G; ELLIOTT, G.F; HATAI, K., 1965, Terebratulida. In *Treatise on invertebrate paleontology--Pt. H, Brachiopoda* **2:** H728-H857.

MUNDLOS, 1978, Terebratulid shell beds. *Neues Jahrbuch, geologishe-palaontologische Abhandlung* **157:** 45-47.

PARSONS-HUBBARD, K.M.; CALLENDER, W.R.; POWELL, E.N.; BRETT, C.E.; WALKER, S.E.; RAYMOND, A.L.; STAFF, G.M., 1999, Rates of burial and disturbance of experimentally-deployed molluscs; implications for preservation potential. *Palaios* **14:** 337-351.

POWELL, E.N., and DAVIS, D.J., 1990, When is an ‘old’ shell really old?: *Journal of Geology* **98:** 823-844.

RICHARDSON, 1981, Brachiopods and pedicles. *Paleobiology* **7:** 87-95.

SANDY, M.R., 1991, Cretaceous brachiopods from James Ross Island, Antarctic Peninsula, and their paleobiogeographic affinities. *Journal of Paleontology* **65:** 396-411.

SIMÕES, M.G., KOWALEWSKI, M., MELLO, L.H., RODLAND, D.L., and CARROLL, M., 2000, Present-day terebratulid brachiopods from the southern Brazilian shelf: Paleontological and biogeographic implications: *Geological Society of America Abstracts with Programs* **32:** A14.

STEWART, I.R., 1981, Population structure of articulate brachiopod species from soft and hard substrates. *New Zealand Journal of Zoology* **8:** 197-207.

STUIVER, M., REIMER, P.J., and BRAZIUNAS, T.F., 1998, High-precision radiocarbon age calibration for terrestrial and marine samples: *Radiocarbon* **40:** 1127-1151.

TOMMASI, L.R., 1970A, Sobre o braquiópode *Bouchardia rosea* (Mawe, 1823): *Boletim do Instituto Oceanográfico* **19:** 33-42.

WALKER, K.R., and BAMBACH, R.K., 1971, The significance of fossil assemblages from fine-grained sediments: time-averaged communities: *Geological Society of America Abstracts with Program* **3:** 783-784.

WEHMILLER, J.F., 1977, Amino acid studies of the Del Mer, California, midden site: apparent rate constants, ground temperature models, and chronological implications: *Earth Planet Science Letters* **37:** 184-196.

WEHMILLER, J.F., 1982, A review of amino acid racemization studies in Quaternary mollusks: stratigraphic and chronologic applications in coastal and interglacial sites, Pacific and Atlantic coasts, United States, United Kingdom, Baffin Island and tropical islands: *Quaternary Science Reviews* **1:** 83-120.

WEHMILLER, J.F., York, L.L., and Bart, M.L., 1995, Amino-acid racemization geochronology of reworked Quaternary mollusks on U.S. Atlantic coast beaches. implications for chronostratigraphy, taphonomy, and coastal sediment transport: *Marine Geology* **124:** 303-337.

WILLIAMS, A., 1965, Treatise on invertebrate paleontology. Part H. Brachiopoda **1-2**.

WILLIAMS, A., AND MANY, 1997, Treatise on invertebrate paleontology. Part H. Brachiopoda; Revised, **1**

ZEZINA, O.N., 1970, Brachiopod distribution in the Recent Ocean with reference to problems of zoogeographic zoning: *Paleontological Journal* **4:**147-160.

ZEZINA, O.N., 1980, On the composition, distribution and some biological features of cold water brachiopods in the Southern Hemisphere: In KUZNETSOV, A.P., (ed.), *Ekologicheskiye issledovaniya shel'fa,* Moscow: P.P. Shirshov Institute of Oceanology:9-35.

Appendix A: Data

The data collected in this study. A/I ratio is the ratio of D-Alloisoleucine/L-Isoleucine calculated at the lab of G. Goodfriend. The radiocarbon values (C-14) obtained at NOSAMS. The calibrated age of the shell obtained using the equation 'Age=(A/I-0.005855)*15978' (see Figure 3 and Calibration section for details). Repreparation indicates those shells from which multiple samples were taken for analysis of intrashell variability and for calibration purposes (the number indicates how many samples were reprepared). See Table 3.1 for A/I values of repreparations. The final column provides total taphonomic score for individual shells (see Methods section for details).

Locality	ID#	Reprep	A/I ratio	c-14	Calibrated Age (BP)	Total Taphonomic Score
1	AB-1		0.00472		0	7
1	AB-2		0.00589		1	8
1	AB-3		0.0102		69	9
1	AB-4		0.0236		284	10
1	AB-5		0.00875		46	9
1	AB-6		0.0227		269	6
1	AB-7		0.0143		135	5
1	AB-8		0.0256		315	5
1	AB-9		0.0224		264	6
1	AB-10		0.0283		359	9
1	AB-11		0.0267		333	9
1	AB-12		0.0119		97	8
1	AB-13		0.0128		111	7
1	AB-14		0.0173		183	8
1	AB-15		0.014		130	8
1	AB-16		0.00556		0	6
1	AB-17		0.0264		328	6
1	AB-18		0.0222		261	6
1	AB-19		0.00542		0	8
2	689		0.0319		416	7
2	691		0.0434		600	10
2	708		0.0277		349	7
2	711		0.0157		157	9
2	723		0.0316		411	8
2	727		0.0318		415	6
2	AA-1		0.0102		69	4
2	AA-2		0.0152		149	8
2	AA-3	6	0.0351	898	467	8
2	AA-4		0.0103		71	9
2	AA-5		0.028		354	9
2	AA-6		0.0132		117	9
2	AA-7		0.0111		84	9
2	AA-8	3	0.0286	880	363	8
2	AA-9		0.0319		416	8
2	AA-10		0.0284		360	6
2	AA-11		0.0288		367	6
2	AA-12		0.0273		343	3

Locality	ID#	Reprep	A/I ratio	c-14	Calibrated Age (BP)	Total Taphonomic Score
2	AA-13		0.0287		365	8
2	AA-14		0.0245		298	5
3	669		0.0241		292	5
3	670		0.0413		566	4
3	672		0.0497		701	5
3	675		0.00933		56	4
3	676		0.0126		108	5
3	677		0.0108		79	3
3	679		0.0975		1464	3
3	681		0.0165		170	9
3	CB-1	6	0.044083		611	7
3	CB-2		0.00884		48	7
3	CB-3		0.0343		454	5
3	CB-4		0.131		2000	7
3	CB-5		0.0454		632	7
3	CB-6		0.00598		2	9
3	CB-7		0.0075		26	10
3	CB-8		0.0117		93	8
3	CB-9	2	0.1037	2500	1563	9
3	CB-10		0.0352		469	3
3	CB-11		0.00322		0	5
3	CB-12		0.0548		782	6
3	CB-13		0.123		1872	8
4	301		0.137		2095	9
4	376		0.202		3134	10
4	442		0.0272		341	6
4	543		0.149		2287	5
4	546		0.197		3054	9
4	594		0.0115		90	9
4	BB-1		0.00566		0	5
4	BB-2	6	0.00832		39	3
4	BB-3		0.00548		0	7
4	BB-4		0.00756		27	6
4	BB-5		0.0048		0	8
4	BB-6		0.0437		605	10
4	BB-7		0.00535		0	8
4	BB-8		0.0145		138	9
4	BB-9		0.00544		0	5
4	BB-10		0.00461		0	2
4	BB-11		0.00922		54	8
4	BB-12		0.0297		381	8
4	BB-13		0.0241		292	9
4	BB-14	2	0.161	2790	2479	8
4	BB-15	2	0.0614	1250	887	6
4	BB-16		0.0431		595	8

Appendix B: Author's Role in Research

I went on dredging trips to collect samples and was involved in the sampling but all our samples were attained on trips I was not on.

Once samples were collected I measured specimens, photographed them and evaluated them for taphonomy based on an evaluation scheme determined by Me, Michal Kowalewski, Marcello Simoes and David Rodland.

I then took specimens to George Washington University where I cleaned, prepared and analyzed the shells for A/I ratio under the supervision of Glenn Goodfriend. He advised me in the methods, protocol for the HPLC and in the processing of the chromatograms which yielded A/I ratios.

I cleaned specimens sent to NOSAMS for radio-carbon analysis. They performed all subsequent protocols as follows: (http://www.nosams.whoi.edu/nosams.html);

I then performed analysis of data using Excel, Deltagraph and SAS 8.0.1

Remaining specimens are housed in the Department of Geological Sciences of Virginia Polytechnic Institute and State University under the supervision of Dr. Michal Kowalewski.

Curriculum Vitae
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EDUCATION

M.S. in Geology (expected Spring 2001), Department of Geology, Virginia Tech, Blacksburg, Virginia
ADVISOR: Michal Kowalewski
THESIS: Quantitative Estimates of Time-Averaging in Brachiopod ShellAccumulations from a Holocene Tropical Shelf (SW Brazil)

B.A. in Liberal Arts *cum laude*, 1996, Gallatin School of Individualised Study, New York University, New York, New York
ADVISOR: Steven Hutkins
UNDERGRADUATE DEFENSE: The Meaning of Service

EMPLOYMENT

08.1999 – Present: Teaching Assistant - Department of Geological Sciences, Virginia Tech, Blacksburg, Virginia
05.2000 - 08.2000: Research Assistant - Department of Geological Sciences, Virginia Tech, Blacksburg,Virginia
05.1999 – 08.1999: Summer Research Assistant - Center for Science and Math Education, Purchase, New York
08.1997-08.1998: Grant Writer (Americorps*VISTA)- Down East Resource Conservation and Development, Cherryfield, Maine

CURRENT RESEARCH INTEREST

1. Geochemical analysis of Quaternary marine assemblages to evaluate temporal resolution and to reconstruct climatic and ecologic changes.
2. Paleontological approaches to questions of human development and dispersion.
3. The role of pathogens and endosymbiosis in paleoecology.

TEACHING EXPERIENCE

Teaching Assistanship

1. Historical Geology (GEOL 1024), Department of Geology, Virginia Tech (Instructor: Michal Kowalewski)
2. Physical Geology (GEOL 1004), Department of Geology, Virginia Tech (Instructor: varied)
3. Resources Geology (GEOL 1104), Department of Geosciences, Virginia Tech (Instructor: J. Craig)

GRANTS

1. Graduate Student Assembly, Virginia Tech, Travel Grant.; $300; October, 2000.
2. Paleontological Society Student Grant; $500, June 2001.
3. Geological Society of America Student Grant; $2000, June 2001.

PRESENTATIONS AT PROFESSIONAL MEETINGS

1.June 2001 – Berkeley, California: North American Paleontological Conference: “Quantitative estimates of time-averaging in articulate brachiopod accumulations from a Holocene tropical shelf (Southern Brazil)".

2.November 2000 - Reno, Nevada: Geological Society of America National Meeting: "Quantitative estimates of time-averaging in articulate brachiopod accumulations from a Holocene tropical shelf (Southern Brazil)".

3. March 2000 - Blacksburg, Virginia: 5th Annual Geological Sciences Student Research Symposium: "Amino Acid Dating of Brachiopods".

PUBLICATIONS

Peer-Review Articles

1. KOWALEWSKI, M., SIMOES, M.G., CARROLL,M., and RODLAND,D.L., (submitted), Discovery of abundant articulate braciopods in low-lattitude upqelling zones: submitted to Science, January 2001, 8 pages + 4 figures.

2. CARROLL, M., KOWALEWSKI, M., SIMÕES, M.G., GOODFRIEND, G.A., (in preparation), Quantitative estimates of time-averaging in articulate brachiopod accumulations from a Holocene tropical shelf (Southern Brazil).

Abstracts

1. CARROLL, M., KOWALEWSKI, M., SIMÕES, M.G., GOODFRIEND, G.A., (2000) Quantitative estimates of time-averaging in articulate brachiopod accumulations from a Holocene tropical shelf (Southern Brazil). Geological Society of America Abstracts with Programs, v. 32, A13-A14.

2. KOWALEWSKI, M., SIMÕES, M.G., CARROLL, M., and RODLAND, D.L., (2000) Distribution of articulate brachiopods across a modern low-latitude shelf from the western South Atlantic. Geological Society of America Abstracts with Programs, v. 32, A96.

3. SIMÕES, M.G., KOWALEWSKI, M., MELLO, L.H., RODLAND, D.L., and CARROLL, M., (2000) Present-day terebratulid brachiopods from the southern Brazilian shelf: Paleontological and biogeographic implications. Geological Society of America Abstracts with Programs, v. 32, A14.