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Left-Right Phenomena Among Bivalve Shells: Examples from the Georgia Coast.*)

With 10 Text-Figures and 2 Tables.

ROBERT W. FREY & STEPHEN W. HENDERSON.

Abstract.

[FREY, R. W. & HENDERSON, S. W. (1987): Left-right phenomena among bivalve shells: examples from the Georgia coast. — Senckenbergiana marit., 19 (3/4): 223-247, 10 figs., 2 tabs.; Frankfurt a. M.]

Distributions of left and right valves of the trigonal bivalve *Donax variabilis* and the orbicular bivalve *Abra aequalis* were evaluated with respect to prevailing patterns of sediment transport and shell accumulation in a beach/tidal inlet/longshore channel/nearshore shelf system.

Intertidal shell deposits were governed principally by longshore drift, which varied because of wave refraction around nearshore shoals. During nonstorm conditions, left valves of *D. variabilis* preferentially moved southward and right valves northward, most being deposited in beach reentrants. *A. aequalis* valves were sorted primarily on the nearshore shelf and more right than left valves were delivered to the beach; further sorting occurred within beach reentrants.

A tropical storm then flushed most shells from the beach, leaving the greatest accumulations midway between origins of southward and northward longshore drift. Left valves of *A. aequalis* practically disappeared, and left:right valve ratios for *D. variabilis* increased markedly along the southern half of the beach.

During nonstorm conditions at subaqueous sites, shells accumulated chiefly at the seaward end of the longshore channel, an ebb-tidal effect, and secondarily within the tidal inlet, a flood-tidal effect; valves were relatively rare on the nearshore shelf. Left valves of *A. aequalis* and right valves of *D. variabilis* predominated in the longshore channel, and left valves of *D. variabilis* and right valves of *A. aequalis* predominated inside the tidal inlet.

Kurzfassung.

[FREY, R. W. & HENDERSON, S. W. (1987): Links-Rechts-Verhältnisse bei Muschelklappen: Beispiele an der Küste von Georgia. — Senckenbergiana marit., 19 (3/4): 223-247, 10 Abb., 2 Tab.; Frankfurt a. M.]

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Untersucht wurde die Verteilung von linken und rechten Klappen der dreieckförmigen Muschel *Donax variabilis* und der runden Muschel *Abra aequalis* im Hinblick auf Aussagen über Sedimenttransport und Schillanreicherungen in einem Düneninsel-System mit Baljen, Strand, strandparallelen Vorstrandrinnen und küstennahem Schelfbereich.

Die Schillablagerungen in den eulitoralen Bereichen werden bestimmt durch Küstenlängsströmungen, die im Bereich der vorgelagerten Sandplaten durch Brandungseinwirkung abgewandelt werden. Bei sturmfreien Wetterlagen wurden die linken Klappen von *D. variabilis* überwiegend nach S, die rechten nach N verfrachtet; die Hauptmengen wurden in flachen Strandeinbuchtungen abgelagert. *A. aequalis* wurde vor allem im küstennahen Schelfbereich sortiert; von dort wurden mehr rechte als linke Klappen zum Strand verfrachtet. Ein weiterer wichtiger Sortierungsbereich waren die Strandeinbuchtungen.

Im weiteren Untersuchungszeitraum wurden die meisten Schalen bei einem tropischen Wirbelsturm vom Strand weggespült und zum größten Teil im Bereich zwischen den Ausgangspunkten des N-wärtigen un des S-wärtigen Küstenlängsstromes abgelagert. Dabei verschwanden die linken Klappen von *A. aequalis* fast vollständig, während in der Südhälfte des Strandbereiches das links:rechts-Verhältnis der *D. variabilis*-Klappen deutlich anstieg.

Im Unterwasserbereich wurden die Schalen bei sturmfreien Wetterlagen unter Ebbstromwirkung hauptsächlich im Mündungsbereich der strandparallelen Vorstrandrinne, daneben auch unter Flutstromwirkung innerhalb der Balje abgelagert. Auf dem küstennahen Schelf waren Muschelklappen relativ selten. In der Vorstrandrinne überwogen linke Klappen von *A. aequalis* und rechte Klappen von *D. variabilis.* In der Balje überwogen linke Klappen von *D. variabilis* und rechte Klappen von *A. aequalis.*

Contents.

Introduction.

Up until a decade or so ago, discussions on disarticulation and displacement of valves in shell assemblages were much in vogue (e.g., Boucot 1953; Fagerstrom 1964; Lawrence 1968; Seilacher 1973; see Salazar-Jiménez et al. 1982: 565-567). A component process, termed the "left-right phenomenon" (Lever 1958), is the spatial sorting and separation of left and right valves. The phenomenon was noticed early in the study of shell assemblages (e.g., Richter 1922, 1924) and occurs even among brachiopods (Boucot et al. 1958). Left:right valve ratios continue to be utilized occasionally in analyses of ancient shell accumulations (Fürsich & Heinberg 1983), although this approach generally is undersubscribed today.

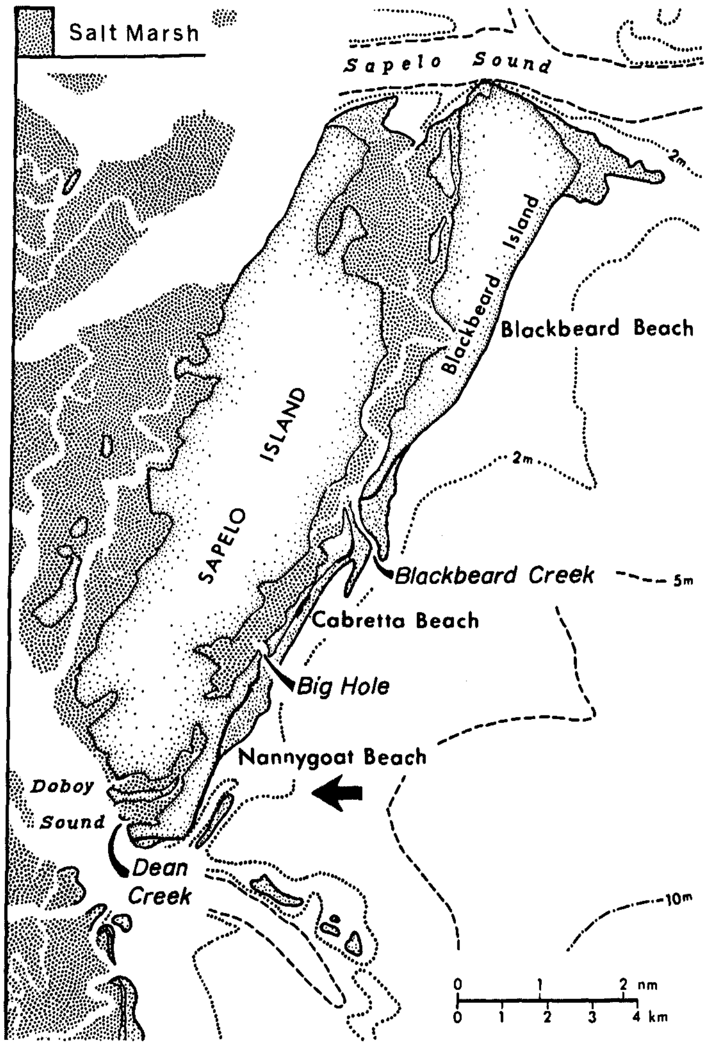

Fig. 1. Index map of study area (large arrow), Sapelo Island, Georgia, U. S. A. — Intertidal samples were taken from Nannygoat Beach; subaqueous samples were taken along the trend of the longshore channel between Nannygoat Beach and the adjacent shoals.

Abb. 1. Das Untersuchungsgebiet auf der Düneninsel Sapelo Island, Georgia, U. S. A. — Die Proben aus dem Gezeitenbereich wurden im Inselabschnitt Nannygoat Beach genommen, die Unterwasserproben in der strandparallelen Vorstrandrinne und auf den angrenzenden Sandplaten.

Studies of present-day shell sorting and transport or burial phenomena have been conducted mainly either on beaches (e.g., VAN DER MEULEN 1947-48; MARTIN-KAYE 1951; LEVER 1958; LEVER et al. 1961; KORNICKER et al. 1963; NAGLE 1964; LEVER & THIJSSEN 1968; BEHRENS & WATSON 1969; LAWRENCE 1979; FREY 1987) or within flumes (e.g., TRUSHEIM 1931; MENARD & BOUCOT 1951; JOHNSON 1957; BOUCOT et al. 1958; KORNICKER & ARMSTRONG 1959; KELLING & WILLIAMS 1967; MIDDLETON 1967; BRENCHLEY & NEWALL 1970). Each of these investigations has approached the various problems somewhat differently, and the respective conclusions vary accordingly.

We became interested in a local depositional system that seems to include both of the above types of experimental sites: the Sapelo Island beach and, immediately adjacent to it, a subtidal longshore channel system (Fig. 1), which constitutes a natural flume. Our main objective was to evaluate the environmental distribution of left and right valves of two common species — the donacid *Donax variabilis* and the semelid *Abra aequalis* — with respect to associated bivalve assemblages and prevalent patterns of sediment transport. This approach, involving the entire depositional system, should have greater application in the rock record (KIDWELL & JABLONSKI 1983) than many of the site-specific or process-specific approaches used previously.

The Local Setting.

Because of a broad, gently dipping continental shelf, coastal waters within the Georgia Bight are dominated by tides rather than by waves (HUBBARD et al. 1979). Ebb-tidal effects predominate over flood-tidal effects. A large system of shoals and channels thus extends seaward from sound or estuary entrances (OERTEL 1985), and adjacent beach segments are partly protected from open-ocean waves. The entire coast is classified as a mesotidal, low- to moderate-energy zone. Mean tidal range is about 2.4 m; storm tidal ranges may exceed 3.4 m.

Beach slopes typically are less than 2°, and sediments consist principally of fine-grained, angular, well-sorted quartz sand (HOWARD & FREY 1980). Protected low-energy beaches, such as those along tidal inlets, generally are narrower and steeper than higher energy beaches fronted by the sea. Characteristic beach shell accumulations were described by DÖRJES et al. (1986).

Although at least six distinctive sediment types comprise local inlet-shoal subfacies here (OERTEL 1973a, 1985), subtidal sediments encountered during the present study consisted predominantly of fine-grained sand. Muddy, fine- to medium-grained sands also were present within the channel (cf. HOWARD & REINECK 1972; OERTEL 1973b; MAYOU & HOWARD 1975). Characteristic shell accumulations were described by FREY & PINET (1978) and HENDERSON & FREY (1986).

Methods and Approaches.

Donax variabilis (Fig. 2A) was selected for study because much already is known about both its natural history (LEBER 1982; MIKKELSEN 1981, 1985) and the accumulation and intertidal orientation of this truncate small valve (WOBBER 1967; BEHRENS & WATSON 1969; MILLER & KOOSER 1982). *Abra aequalis* (Fig. 2B),

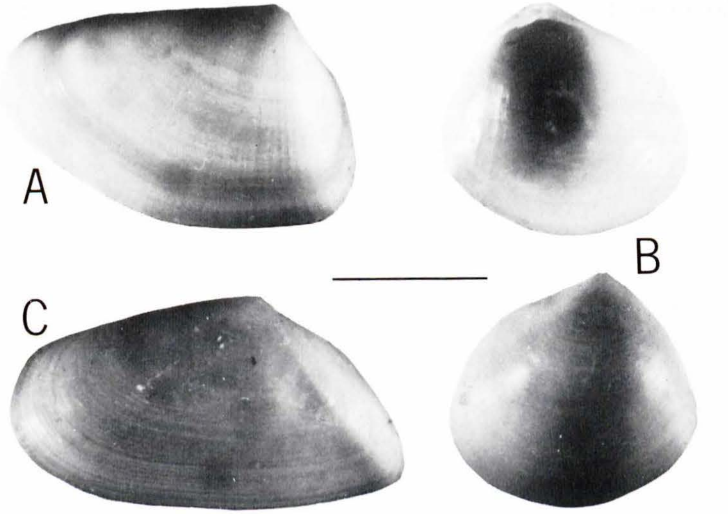

Fig. 2. Examples of bivalves used in the study of left-right valve sorting, Sapelo Island, Georgia. — A. *Donax variabilis*, left valve. — B. *Abra aequalis*, right valve, interior and exterior views. — C. *Tellina versicolor*, left valve. — Bar scale = 1 cm.

Abb. 2. Die untersuchten Muschelarten. Sapelo Island, Georgia. — A. *Donax variabilis*, linke Klappe. — B. *Abra aequalis*, rechte Klappe, innen und außen. — C. *Tellina versicolor*, linke Klappe. — Maßstab 1 cm.

somewhat comparable in size, was selected because of its orbicular shape (ABBOTT 1974). Limited observations also were made on valves of *Tellina versicolor* (Fig. 2C). Shells of these species are considerably less abundant than those of the small mactrid *Mulinia lateralis* (DÖRJES et al. 1986; HENDERSON & FREY 1986); yet its valves exhibit considerably more phenotypic variation, thus complicating any analysis of valve sorting.

Beach samples were obtained from 55 1-m^2 quadrats, each spaced 100 m apart along the wrack line (previous high-tide line) of Nannygoat Beach, from within Doboy Sound to Big Hole Inlet (Fig. 3A). June samples (e.g., Figs. 4, 5) were judged to be typical of the long-term, low-energy conditions of summer (HOWARD et al. 1972; KURODA & MARLAND 1973), whereas July samples were taken immediately after a small tropical storm had passed. The latter did little obvious damage other than small-scale beach erosion (cf. DÖRJES et al. 1986: Pl. 2 figs. 4-6), but beach flotsam was altered appreciably.

Adjacent subtidal specimens were recovered by means of a Smith-McIntyre grab sampler. Bulk sediment samples (0.025 m^3) were taken at 8 stations, from the shallow flank of Doboy Sound, through the longshore channel, to the contiguous nearshore shelf off Nannygoat Beach (Fig. 3A). These samples, taken during the same field season as the beach samples, also were deemed to be representative of summer conditions.

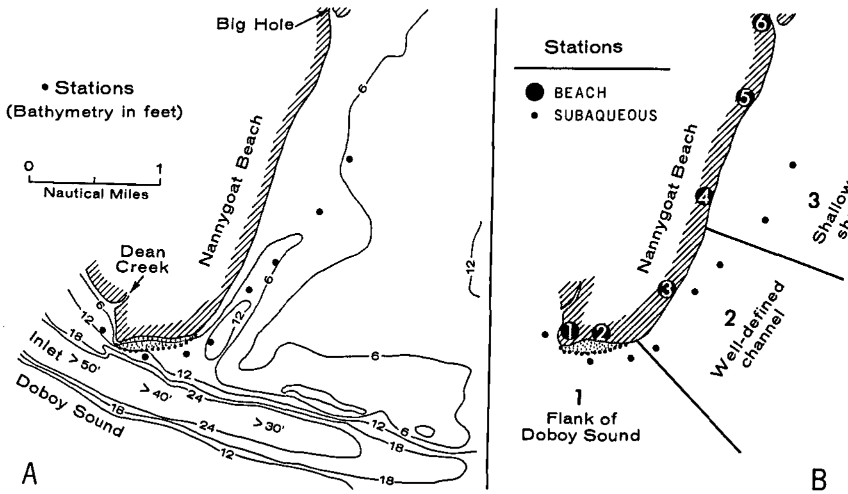

Fig. 3. Location and classification of sampling sites, Sapelo Island, Georgia. — A. Distribution of subaqueous stations, and the beach setting. Intertidal stations consisted of 55 1-m² quadrats, spaced 100 m apart, from Dean Creek to Big Hole Inlet, along the wrack line (last excursion of high tide). — B. Environmental classification of sites. The 8 subaqueous stations reduce to three areas: 1, the sound flank; 2, the longshore channel; and 3, the nearshore shelf. The 55 intertidal quadrats reduce to six areas: 1, the sound beach; 2, a beach above a tidal flat; 3, south beach; 4, middle beach; 5, north beach; and 6, an inlet beach (see text).

Abb. 3. Detailkarte und charakteristische Teilbereiche des Untersuchungsgebietes, Sapelo Island, Georgia. — A. Die Unterwasser-Topographie vor dem Südende der Insel und die Unterwasser-Probenpunkte. — B. Die charakteristischen Teilbereiche im Unterwasser- und Gezeitenbereich. Unterwasserbereich: 1, Randbereich der Balje; 2, strandparallele Vorstrandrinne; 3, küstennaher Schelfbereich. Gezeitenbereich: 1, Baljenstrand; 2, Strand oberhalb Wattfläche; 3-5, Strandbereiche; 6, Strand an einer küstenparallel ausmündenden Prielmündung.

Observed Valve Distributions.

Beach Samples.

Total samples for June (Tab. 1A) revealed a near balance between left and right valves of *Donax variabilis* (ratio = 1.05) but a substantial excess of right valves of *Abra aequalis* (0.53). In July, left valves were slightly excessive for *D. variabilis* (1.21) and right valves were markedly so for *A. aequalis* (0.08).

Although data on total samples are important in establishing local shell budgets, the subenvironmental distribution of valves is more instructive. Thus, the 55 beach stations were reduced to six characteristic sites (Fig. 3B): (1) Doboy Sound Inlet beach — a protected, low-energy beach segment well inside the sound mouth (5 quadrats), (2) tidal flat beach — a slightly embayed sound-mouth

Table 1. Summary characteristics of selected left:right bivalve samples, Nannygoat Beach, Sapelo Island, Georgia.

Tabelle 1. Die links:rechts-Verhältnisse ausgewählter Muschelklappenproben aus dem Strand- und Unterwasserbereich von Nannygoat Beach, Sapelo Island, Georgia.

Species	Total valves counted (left/right)	Mean density* of valves (left/right)	Mean left:right valve ratios
	A--Beach samples.		
Donax variabilis:			
June samples	566/539	10.3/9.8	1.05
July samples	151/125	2.7/2.3	1.21
Abra aequalis:			
June samples	70/133	1.3/2.4	0.53
July samples	5/ 59	0.1/1.1	0.08
	B--Subaqueous samples.		
Donax variabilis	309/303	38.6/37.9	1.02
Abra aequalis	98/ 93	12.3/11.6	1.05

*Per unit sample size (1 m^2 for Part A, 0.025 m^3 for Part B).

beach segment of low to moderate energy levels, slightly higher than and landward of the tidal flat described by HOWARD & DÖRJES (1972) (6 quadrats), (3) south beach — a very gently arcuate, mostly open-ocean beach segment, concave landward (12 quadrats), (4) middle beach — a nearly straight open-ocean beach segment (12 quadrats), (5) north beach — a gently arcuate open-ocean beach segment, concave seaward (14 quadrats), and (6) Big Hole Inlet beach — a protected, low-energy beach segment inside a sizeable tidal inlet, in the lee of a spit developed off the southern end of Cabretta Beach (Fig. 1) (6 quadrats).

During June, minimal numbers of valves of *Donax variabilis* were present on the two inlet beaches (Fig. 4A), and they were only slightly more abundant on south beach. Maxima occurred on tidal flat beach and, to a lesser extent, on north beach. Left valves exceeded right valves from Doboy Sound beach through south beach, but were subordinate to right valves from there through Big Hole Inlet beach. *Abra aequalis* (Fig. 5A) exhibited minima along the two inlet beaches and at south and middle beaches, and maxima at tidal flat beach and north beach, right valves being predominant throughout. Unlike valves of *D. variabilis*, those of *A. aequalis* were most abundant on north beach.

July samples, representing a change from normal low-energy conditions of summer to the aftermath of a small tropical storm, revealed appreciably fewer total valves present and a striking change in subenvironmental distributions. For

D. variabilis, the pronounced maxima at tidal flat beach and north beach were replaced by a lesser maximum on middle beach. Total numbers of valves otherwise were similar throughout Nannygoat Beach. As in June, however, left valves

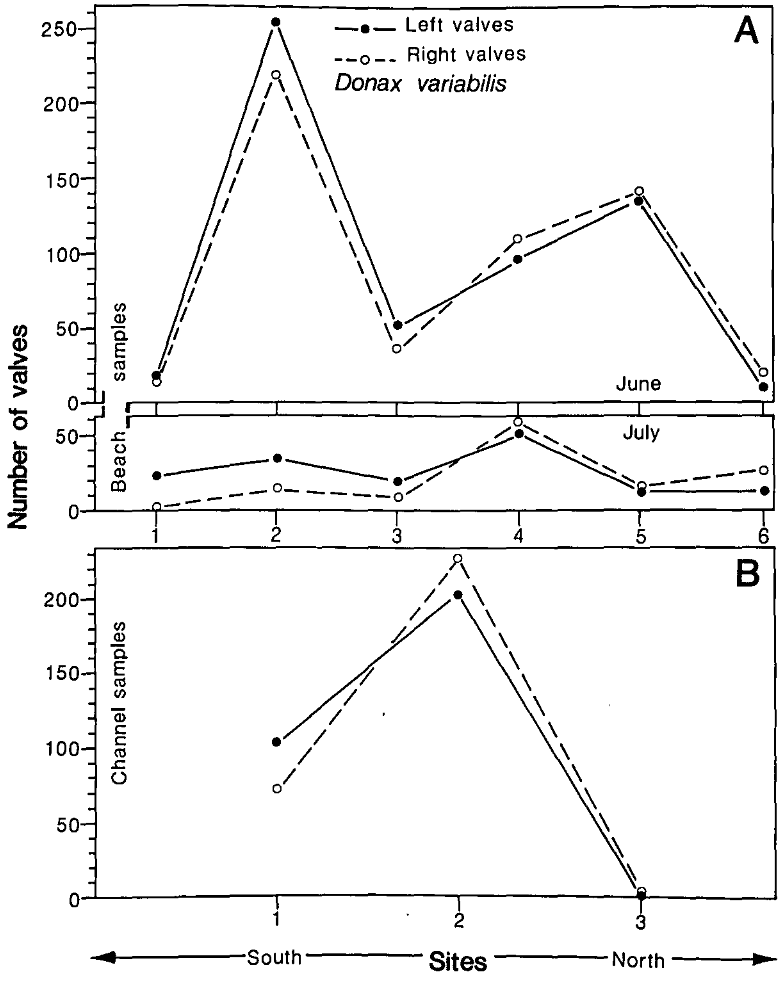

Fig. 4. Distribution of left and right valves of *Donax variabilis,* Sapelo Island, Georgia. — Compare with Fig. 3B and Tab. 1. — A. Intertidal samples. 1, Doboy Sound Inlet beach; 2, tidal flat beach; 3, south beach; 4, middle beach; 5, north beach; 6, Big Hole Inlet Beach. — B. Subaqueous samples. 1, Flank of Doboy Sound; 2, well-defined channel; 3, shallow shelf.

Abb. 4. Verteilung der linken und rechten Klappen von *Donax variabilis,* Sapelo Island, Georgia. — A. Gezeitenbereich: 1, Baljenstrand; 2, Strand oberhalb Wattfläche; 3, Strand, S; 4, Strand Mittelabschnitt; 5, Strand, N; 6, Strand an Prielmündung. — B. Unterwasserbereich: 1, Baljenrand; 2, strandparallele Vorstrandrinne; 3, küstennaher flacher Schelf.

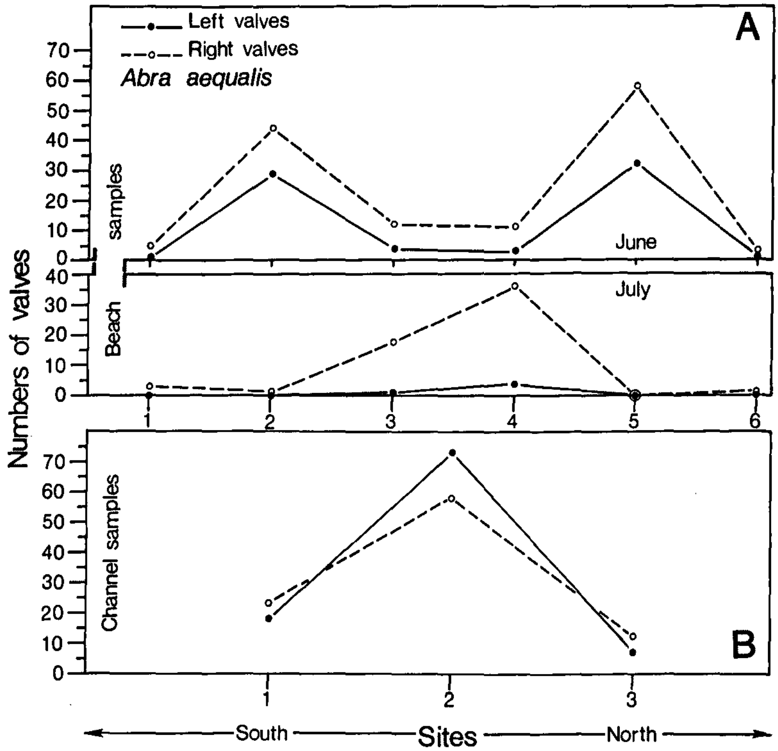

Fig. 5. Distribution of left and right valves of *Abra aequalis*, Sapelo Island, Georgia. — Compare with Fig. 3 and Tab. 1. Key to sites as in Fig. 4. — A. Intertidal samples. B. Subaqueous samples.

Abb. 5. Verteilung der linken und rechten Klappen von *Abra aequalis*, Sapelo Island, Georgia. — Stationen siehe Abb. 4.

predominated from Doboy Sound beach through south beach, and right valves from there to Big Hole Inlet beach. Valves of *A. aequalis* were rare along the two inlet beaches and on tidal flat and north beaches but were conspicuous on south and middle beaches. Right valves were predominant throughout, particularly on south and middle beaches.

Subaqueous Samples.

Total subaqueous samples (Tab. 1B) show a remarkably close match between left and right valves of both *Donax variabilis* (ratio = 1.02) and *Abra aequalis* (1.05). Within this inlet-shelf system, therefore, the detrital valve budget was balanced for these two species.

As with beach specimens, however, left and right valves exhibited considerable environmental differentiation. The 8 submarine stations were reduced to three characteristic sites (Fig. 3B): (1) the shallow flank of Doboy Sound, (2) the longshore channel, and (3) the adjacent nearshore shelf.

Valves of *D. variabilis* (Fig. 4B) were most abundant within the channel, were next most abundant in Doboy Sound, and were rare on the nearshore shelf. Left valves exceeded right valves in Doboy Sound but were subordinate to right valves within the channel and on the shelf. Trends in distribution of *A. aequalis* valves (Fig. 5B) were somewhat similar, except that left valves predominated within the longshore channel.

These results thus negate the contention of BEHRENS & WATSON (1969: 165) that left-right valve sorting is strictly an intertidal process. [Subaqueous shell sorting also was documented by FÜRSICH & HEINBERG (1983).]

Discussion and Perspective.

As outlined in literature cited previously (introduction), the most important biotic aspects of bivalve shell separation and sorting — aside from the mechanics of articulation — are valve size, mass, effective density, shape (including sphericity and intra- and intervalve symmetry), fragility, ornamentation, and investments by borers or encrusters. Extrinsic biotic factors, such as predation (CARTER 1974), also may be involved. Physical aspects, in addition to numerous hydrologic parameters, especially include bedload grain size, sediment cohesiveness, valve orientation, and — for intertidal shells — the degree of submersion. To this list, for reasons discussed subsequently, we would add the effect of valve crowding.

Many of these variables were standardized in the present study by the selection of (1) relatively simple, whole, essentially unaltered small valves of limited phenotypic range, (2) uniform sampling sites, e. g., the wrack line on Nannygoat Beach and collective subaqueous sites representing the shallow flank of Doboy Sound, the longshore channel, and the nearshore shelf, respectively, and (3) substrates of similar texture and fabric, especially on Nannygoat Beach but also to an appreciable extent among individual subaqueous sites. We thus conclude that the hydrologic regime and prevailing patterns of sediment transport and shell deposition are the most informative contexts in which to place this analysis of left-right valve sorting.

Hydrography and Sediment Transport.

Interactions between waves and tidal flow are complex within this mesotidal system (OERTEL 1972, 1973b, 1973c, 1974). Bedform configurations do not necessarily conform to patterns of grain transport. At shallow offshore sites, for example, transport routes generally correspond to directions of tidal flow whereas bedform characteristics are governed mainly by wave surges.

The foreshore of southern Nannygoat Beach exhibits three net components of water and sediment movement (OERTEL 1973c: 87-89): tidal currents, longshore currents, and local swash and rip currents. The first two involve relatively continuous flows of water, although tidal currents are bidirectional and are strongly influenced by the proximity of Doboy Sound and the longshore channel (Fig. 3A). Wave incidence is from the northeast — the waves having been refracted around the shoal system — thus establishing a southward longshore current. [For the coast as a whole, northward longshore currents predominate during summer, albeit at reduced energy levels relative to autumn and winter (HOWARD et al. 1972; KURODA & MARLAND 1973).]

In this system (OERTEL 1973c), the line of breakers forms a boundary between tidal currents within the longshore channel and wave-induced longshore currents on the foreshore. Interactions between the two prevailing currents are confined mainly to the breaker zone, although occasional stronger wave surges may transfer tidal water and sediments to the longshore current, and local rip currents may transfer longshore water and sediments to the tidal current. Wave-induced currents landward of the breaker line are very turbulent and temporarily carry appreciable quantities of sand and many small shells in suspension; tidal currents seaward of the breakers are considerably less turbulent and carry most sand and shells in traction. Ebb-tidal currents, which are substantial within the longshore channel (OERTEL & HOWARD 1972), flow in a direction opposite to that of the longshore current; flood-tidal currents parallel and augment the flow of longshore currents toward Doboy Sound.

Northward along Nannygoat Beach, as the longshore channel grades into the nearshore shelf, tidal currents gradually dissipate. This part of the beach thus is influenced mainly by breakers and wave-induced currents, including those originating in the shoreface (cf. NIEDORODA et al. 1985). As mentioned previously, longshore currents and sediments on such beach segments ordinarily move northward during summer. Farther north, however, these open-ocean beach segments give way to tidally influenced beaches along Big Hole Inlet — a smaller version of the system described above.

The tidal flat beach near the mouth of Doboy Sound (HOWARD & DÖRJES 1972) is a special case. During most of the tidal cycle this beach segment is shielded by inlet shoals, some of which are intertidal (OERTEL 1973c). At low stages of tide, waves break on these shoals before reaching shore. As high tide is approached and the shoals are submersed, waves pass over them and break at the shoreline. Therefore, only the upper part of this beach is "normal"; it grades directly into a low-energy tidal flat and is separated from the ocean by both the longshore channel and flanking shoals. During lower stages of tide, longshore drift is interrupted and the site is swept by shallow tidal currents.

Within the longshore channel (OERTEL & HOWARD 1972), bottom currents ordinarily ebb from the time of predicted high water to 1 to 2 hours after predicted low water; the duration of flood flow is comparably diminished. Ebb velocities also exceed flood velocities. Net sediment movement thus is mostly seaward, even though a small component of shelf sediment reenters the channel and moves landward during maximum flood flow.

Collectively, these intergradational hydrologic components govern both local depositional sites for shells and the character (e.g., "grain-size distribution") of individual assemblages. Left-right valve sorting is only one aspect of this overall process.

Patterns of Shell Transport and Deposition.

These beach specimens constitute part of a comprehensive study of total detrital mollusks there (FREY & DÖRJES in prep.). Total bivalve valves during June (Fig. 6A) were most abundant on north beach and tidal flat beach, because both sites involved reentrants, albeit slight, along the strand. Such embayments, characterized by refracted onshore waves and diffused swash currents (ROSS 1982: Fig. 9-21), enhance shell accumulation. This overall trend is mirrored rather closely by the orbicular valves of *Abra aequalis* (Fig. 5A). The truncate valves of *Donax variabilis* are similarly distributed, except that the maxima are reversed geographically (Fig. 4A). The disparity probably is related in part to the proximity of additional live individuals of *D. variabilis* on the upper tidal flat adjacent to this part of the beach (HOWARD & DÖRJES 1972). *A. aequalis* dwells farther offshore (DÖRJES 1972).

This trend also was generally true of *Tellina versicolor* (Tab. 2). Except for tidal flat beach, however, valves were too rare to depict major patterns of shell transport and deposition other than the near balance between total left and right valves (ratio = 0.98).

In contrast with the reentrants of north beach and tidal flat beach, the south beach site is slightly protrusive. The gentle seaward curvature acts as an apex or "headland", albeit subtle, which helps to focus wave-induced currents (ROSS 1982: Fig. 9-21), increase current velocities, and thereby reduce shell accumulations. This trend is even more pronounced for the small valves of *D. variabilis* and *A. aequalis* (Figs. 4A, 5A) than for the total assemblage (Fig. 6A).

Thus, of all sites involved, only middle beach consists of a relatively straight stretch of open-ocean shoreline. Moderate accumulations of shells there (Fig. 6A) were reflected in the number of *D. variabilis* valves (Fig. 4A); yet *A. aequalis* valves

Table 2. Wrack-line distribution of left and right valves of *Tellina versicolor*, Nannygoat Beach, during June. — Compare with Fig. 3B.

Tabelle 2. Gesamtzahlen und links:rechts-Verhältnisse der Klappen von *Tellina versicolor* im Spülsaum von Nannygoat Beach, Sapelo Island, Georgia. — Vgl. Abb. 3B.

Sampling site	Number of valves counted	Left:right valve ratio
1, Doboy Sound beach	7	0.40
2, tidal flat beach	53	1.12
3, south beach	12	0.71
4, middle beach	23	0.64
5, north beach	21	1.63
6, Big Hole Inlet beach	1	---
Total	117	0.98

remained sparse (Fig. 5A), apparently having been transported northward. The "spherical" shape of *A. aequalis* valves (= intercept sphericity of MENARD & BOUCOT 1951) facilitates their entrainment at current velocities lower than those required to move otherwise similar valves of other species.

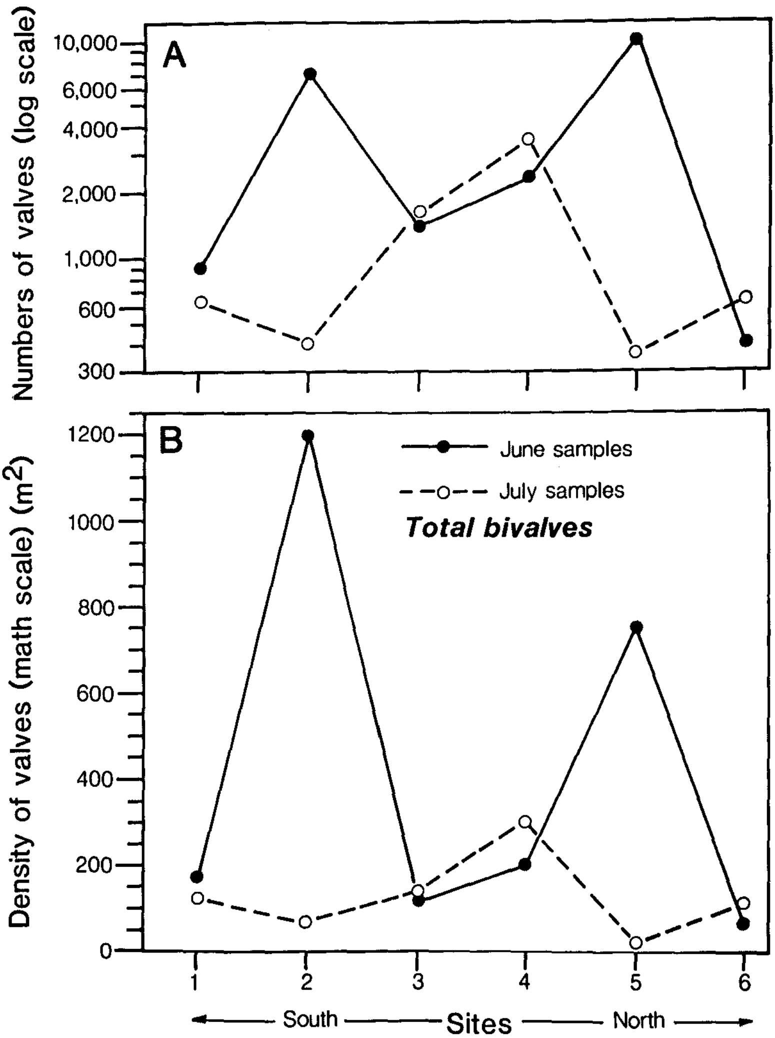

Fig. 6. Distribution of total bivalve valves, Nannygoat Beach, Sapelo Island, Georgia. — Individual valves were tallied as separate specimens. — A. Valve abundance. B. Valve density.

Abb. 6. Schillanreicherungen (gesamt) am Strand Nannygoat Beach, Sapelo Island, Georgia. — A. Gesamtzahl im Teilbereich. B. Dichte pro m².

Reduced shell accumulations on the two inlet beaches (Fig. 6A) evidently reflect the predominance of tidal currents over wave-induced currents in this protected setting. Ebb-tidal currents tend to return most shells delivered by the flood or by low-energy wave surges. Lag residues consist mainly of sparse larger shells. The few small shells remaining tend to be partly buried concave-down and therefore are more difficult to reentrain (cf. JOHNSON 1957).

During the tropical storm of July, virtually all of these trends were reversed (Fig. 6A). Maximum shell deposition occurred on relatively straight stretches of middle beach, the reentrants having been flushed of valves. However, valves of *D. variabilis* (Fig. 4A) remained more abundant throughout Nannygoat Beach than did those of *A. aequalis* (Fig. 5A).

The subtidal samples utilized here also are parts of a more comprehensive study of shell distributions within the longshore channel (HENDERSON & FREY 1986). That study established a nodal point at the deepest, soundward end of the channel (Station 4, Fig. 7), a hydrographic constriction. The corresponding jet effect causes substrate scour and shell flushing in the vicinity. Some shells, having been jetted past

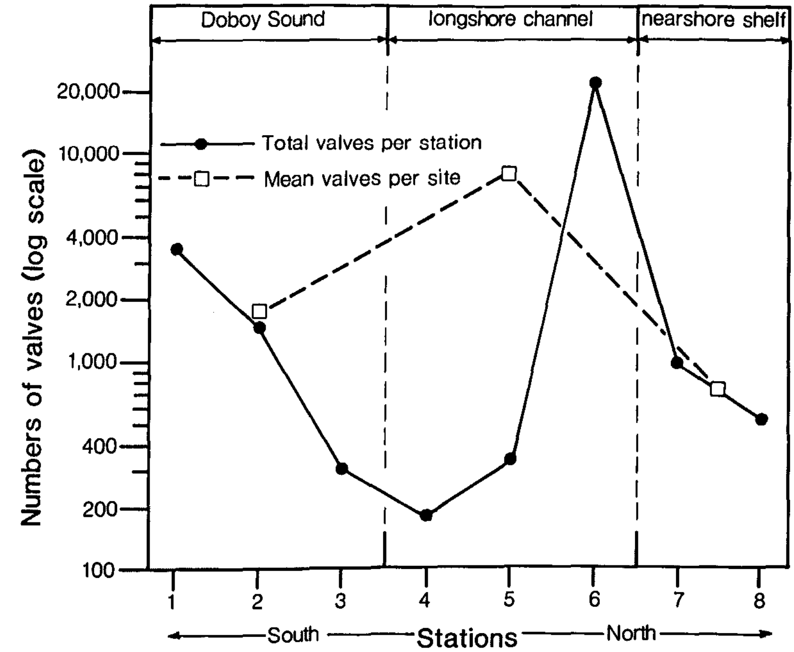

Fig. 7. Distribution of total bivalve valves, subaqueous samples, Sapelo Island, Georgia. — Compare with Fig. 3. — Individual valves were tallied as separate specimens. Each station was represented by a 0.025-m^3 sample.

Abb. 7. Schillanreicherungen (gesamt) im Unterwasserbereich von Sapelo Island, Georgia. — Probenmenge jeweils 0,025 m^3.

that point during flood tide, are transported soundward; most shells, however, are jetted seaward during ebb tide. Maximum shell accumulations at the seaward end of the channel (Station 6, Fig. 7) represent an equilibrium point between inlet-shoal tidal effects and nearshore shelf wave effects (HUBBARD et al. 1979: 1079).

Mean valves per site (Fig. 7) correspond closely to the general distributional patterns of *Donax variabilis* and *Abra aequalis* (Figs. 4B, 5B). However, the relative importance of *A. aequalis* is slightly less in Doboy Sound and substantially greater than that of *D. variabilis* on the shelf. This disparity probably is explained in part by the proximities of their respective life sites: shelf-related areas for *A. aequalis* and beach-related areas for *D. variabilis* (DÖRJES 1972).

Mechanisms for Valve Sorting.

As summarized by NAGLE (1964), whose study included Nannygoat Beach, the swash-zone separation of disarticulated left and right valves of equivalved species is linked not only to valve symmetry but also to the obliqueness of wave incidence and consequent directions of longshore drift. Left and right valves tend to be rotated or translated differently by backwash. The beak of one valve faces into the next impinging wave and the valve may be displaced by it; the beak of the opposite valve faces away from the wave and the valve tends to remain in place. Valves of large species are separated more efficiently than those of small species, because the latter are more easily entrained regardless of beak orientation (see also KORNICKER et al. 1963; LEVER & THIJSSEN 1968; BEHRENS & WATSON 1969; FREY 1987).

The trigonal shape of *Donax variabilis* imparts an additional aspect to its hydrodynamics. Both valves tend to orient with backwash so that the truncated posterior end comes to rest more or less parallel to shore (WOBBER 1967) and essentially faces the next swash. In that configuration, with northeasterly waves impinging on Nannygoat Beach (Fig. 8), the beak of the left valve is oriented up-drift and the valve tends to move down-drift; the beak of the right valve is oriented down-drift, but the valve tends to be less mobile. With southeasterly waves impinging on the beach, as is true of most Georgia beach segments during summer, the right valve is apt to drift farther northward than the left valve.

Shell-sorting mechanisms from subaqueous sites are considerably more difficult to reconstruct. To our knowledge, this process also has been omitted from consideration during previous flume experiments. Nevertheless, because azimuthal orientations of valves are important in the bidirectional beach system (swash/backwash), flume experiments involving the azimuthal aspect of valve transport (e. g., KELLING & WILLIAMS 1967; BRENCHLEY & NEWALL 1970) may yield important clues to the valve-sorting process in a bidirectional "natural flume" such as the longshore channel off Nannygoat Beach.

BRENCHLEY & NEWALL (1970) reported that on sand substrates, initial transport of bivalve valves is governed mainly by concavity orientations, angles between long axes and the direction of current flow, and bed roughness. Valves are most easily entrained and transported in concave-up position. The majority are deposited with long axes perpendicular to the current, as modified somewhat by valve shape and center of gravity. Since centers of gravity tend to be associated with the umbonal area, most valves exhibit an up-current orientation of umbones. In contrast,

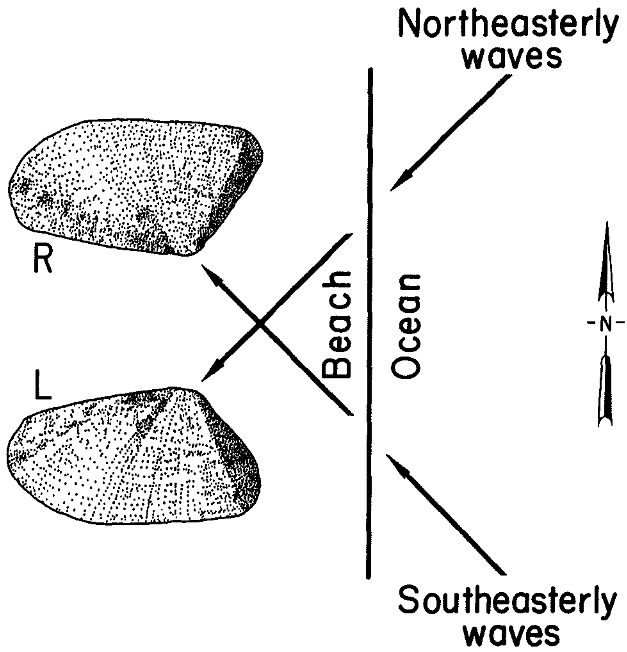

Fig. 8. Ideal orientation of *Donax variabilis* valves, Nannygoat Beach, Sapelo Island, Georgia. — Northeasterly waves tend to move left valves southward, whereas southeasterly waves tend to move right valves northward.

Abb. 8. Einregelung der Klappen von *Donax variabilis* am Strand von Nannygoat Beach, Sapelo Island, Georgia. — Wellen aus NE verfrachten die linken Klappen gegen S; Wellen aus SE verfrachten die rechten Klappen gegen N.

concave-down valves tend to be oriented but not entrained by currents, and very light shells such as *Cultellus* tend to tumble; the latter exhibit a final long-axis alignment parallel with current flow.

Because most bivalve valves evidently are deposited with long axes normal to current direction and with umbones facing up-drift (Brenchley & Newall 1970), beak orientations of left and right valves ideally should be in symmetrical (mirror) opposition. We thus suggest that in a bidirectional natural system, valves deposited by waning tidal currents are somewhat preconditioned for differential transport by the next reversed flow, via processes rather analogous to those operating on beaches (Nagle 1964).

However, valve separation and sorting may be related more closely to the concavity orientation of individual valves during transport than to initial alignments per se. The latter have relatively little effect on threshold velocities needed to entrain the valves (Brenchley & Newall 1970); yet concave-up valves tend to move freely with the current until impeded or flipped into a concave-down position, at which time transport usually ceases. The preconditioning mentioned above therefore may actually be expressed as an increased susceptibility of either left or right valves to impediment or flipping during a given reversal of tidal flow. Additional work obviously is needed.

Left:Right Valve Ratios.

During June, left:right valve ratios for beach specimens of *Donax variabilis* (Fig. 9A) followed trends that might have been predicted from knowledge of the hydrologic regime, characteristic depositional sites, and valve-sorting mechanisms. Refraction of waves around the inlet-shoal system resulted in northeasterly impingement; hence, more left valves than right valves were driven southward, from south beach through Doboy Sound beach. Most accumulated in the reentrant of tidal flat beach. As effects of the shoal system diminished northward, normal southeasterly waves impinged on the beach; thus, more right valves than left valves were driven northward, from middle beach through Big Hole Inlet beach. Most accumulated in the reentrant of north beach. The near balance between total left and right valves (Tab. 1A) indicates that most shells were sorted on the beach, not while en route to it.

In contrast, for *Abra aequalis,* the number of right valves delivered to the beach was nearly twice the number of left valves (Tab. 1A). Most valves thus were sorted on the nearshore shelf; the ratio of total valves there (0.58) was virtually identical to that of the beach (0.53) (Fig. 9B). This artifact was retained as valves were transported to shore. The main beach-sorting effect was the increased proportion of left valves accumulating in the reentrants of north beach and tidal flat beach.

Although comparatively rare, virtually equal numbers of left and right valves of *Tellina versicolor* were delivered to the beach, and relatively little sorting occurred within the largest shell population on tidal flat beach (Tab. 2). In fact, the mean left:right ratio for the southern half of the beach was 0.95 and for the northern half was 1.05. These small valves evidently are so easily entrained that sorting occurs only under very local circumstances.

The July storm, which reversed the sites of major shell accumulations (Fig. 6A), also caused a marked change in valve ratios. Left valves of *A. aequalis* virtually disappeared (Fig. 9B), and only sparse right valves of *D. variabilis* accumulated on the southern half of Nannygoat Beach (Fig. 9A). The latter distribution suggests that even though the previous pattern of southerly and northerly longshore drift was maintained, valve-transporting processes predominated over valve-sorting processes along the southern half of the beach, perhaps reflecting a "sling shot" effect of wave refraction around the shoals. The chief shell accumulations remained on middle beach, intermediate between the principal southward and northward longshore currents.

Although valve-sorting mechanisms for subaqueous samples remain speculative, the near balance between left and right valves of *Abra aequalis* and *Donax variabilis* (Tab. 1B) shows that the sorting occurred primarily within this overall system. [The total-shell assemblages also exhibited pronounced size-sorting and temporal and environmental mixing of valves (Henderson & Frey 1986).] Greater numbers of left valves of *A. aequalis* and right valves of *D. variabilis* accumulated at the seaward

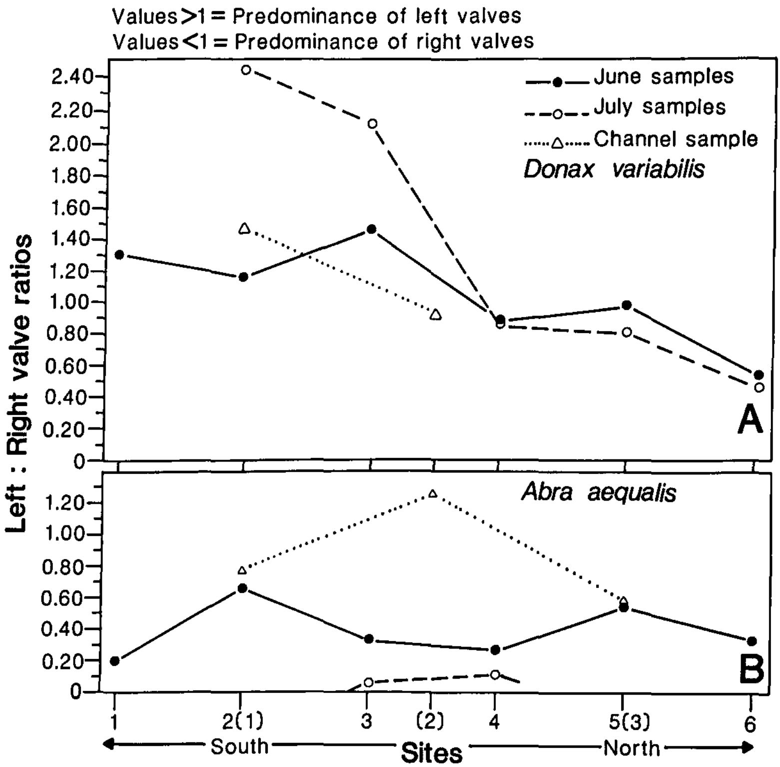

Fig. 9. Valve ratios per sampling site, Sapelo Island, Georgia. — On lower ordinate, numbers for subaqueous sites are in parentheses. — A. *Donax variabilis*: July right valves rare at intertidal Site 1; all valves rare at subaqueous Site 3. — B. *Abra aequalis*.

Abb. 9. Links:rechts-Verhältnisse von Muschelklappen im Untersuchungsgebiet von Sapelo Island, Georgia. — Die Unterwasserteilbereiche sind gekennzeichnet durch Zahlen in Klammern. — A. *Donax variabilis*. B. *Abra aequalis*.

end of the longshore channel (Fig. 9), and greater numbers of right valves of *A. aequalis* accumulated in Doboy Sound and on the nearshore shelf. Left valves of *D. variabilis* predominated in Doboy Sound, but all valves were rare on the shelf.

Valve Crowding.

Although valves are comparatively sparse at most wrack-line sites on Nannygoat Beach, local valve densities are sufficiently great that shells are in contact with one another. At places lower on the beach, especially on the lowermost foreshore and along landward flanks of runnels, actual windrows of shells may be present (Dörjes et al. 1986). There, normal processes of valve sorting are ineffectual and left:right ratios vary markedly within short distances.

In demonstration of this phenomenon, 5 1-m^2 quadrats placed 1 m apart were sampled along a transect parallel to shore, at a lower foreshore site which appeared uniform throughout (DÖRJES et al. 1986). Valves of three species of comparable size were tallied: *Donax variabilis*, *Mulinia lateralis*, and *Tellina versicolor*. Mean density of total mollusk valves at these 5 sites was 694/m^2. Resulting local variations were profound (Fig. 10), especially for *D. variabilis* and *T. versicolor*. Nevertheless, valve-

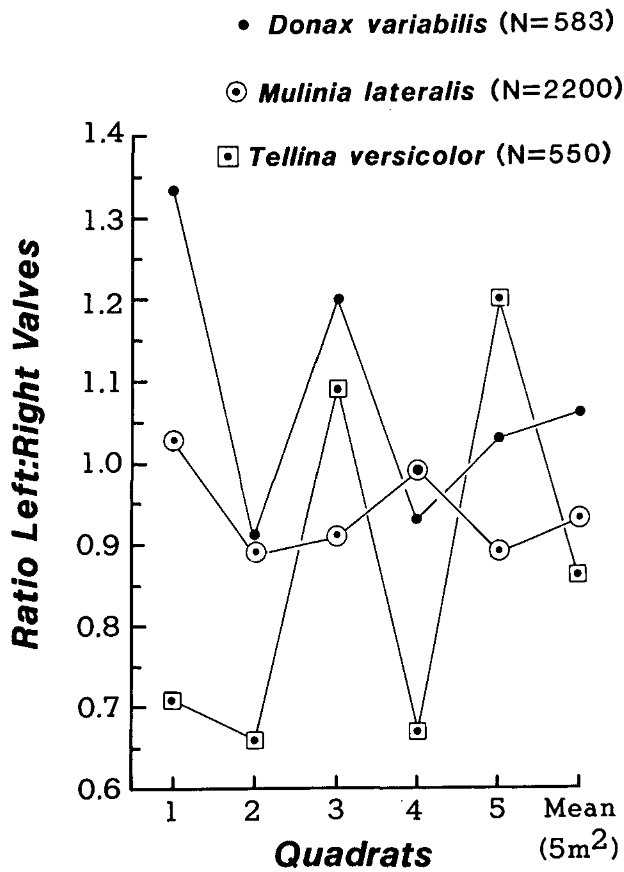

Fig. 10. Left:right valve ratios for selected bivalve species, lowermost foreshore, Nannygoat Beach, Sapelo Island, Georgia. — Quadrats were spaced 1 m apart along a transect parallel to shore. — Adapted from DÖRJES et al. (1986).

Abb. 10. Verhältnis von rechten und linken Schalenklappen bedeutender Muschelarten im untersten Strandbereich der Düneninsel Sapelo Island, Georgia. — Die Entnahmequadrate wurden küstenparallel angelegt. Ihre Entfernung voneinander betrug 5 m.

sorting processes already had begun to operate there, as indicated by a slight net excess of left valves for *D. variabilis* and similar net excesses of right valves for *M. lateralis* and *T. versicolor.*

Over a period of time, as swash currents push such shells landward, valve density gradually decreases and sorting mechanisms become correspondingly more efficient. In most instances the process seems to have been completed by the time that the valves reach the wrack line; further movements of, and accrued distances between, left and right valves are mostly a function of weak longshore currents near the upper extent of the swash zone. Where the supply of shells is excessive, however, the sorting process may remain incomplete even at the wrack line.

Among wrack-line beach sites (Fig. 6B) total bivalve density during June was appreciable only on tidal flat beach and north beach, the sites of greatest shell accumulation (Fig. 6A). However, unlike trends among total valve accumulations, mean density was greater on tidal flat beach than on north beach. At these two sites, therefore, total density was sufficient to interfere with valve-sorting processes in the upper part of the swash zone. Valve densities elsewhere were comparatively insignificant, in this context. During July, valve densities were insufficient to interfere with valve sorting.

Possible effects of valve crowding are more difficult to assess among subaqueous sites (Fig. 7), the samples having been mixed by the grab. Sediment peels and X-ray radiographs of undisturbed box cores (HOWARD & REINECK 1972; MAYOU & HOWARD 1975; SALAZAR-JIMÉNEZ et al. 1982) reveal a diversity of shell distributions and bedding styles among subsurface layers. However, most shell concentrations observed in these cores seem to be the result of storm-wave erosion and subsequent reburial. Elsewhere the valves are sufficiently sparse that surficial shell-sorting processes probably would not have been retarded appreciably. Nevertheless, extreme concentrations of shells at the seaward end of the longshore channel (Station 6, Fig. 7), and to some extent at the landward flank of Doboy Sound (Station 1, Fig. 7), suggest densities sufficient to retard valve-sorting processes during normal nonstorm conditions.

As mentioned previously, tidal currents are more important there than are wave-induced currents; these respective shell concentrations (Fig. 7) mainly represent deposition from waning tidal currents and lack of reentrainment by the next reversed flow (HENDERSON & FREY 1986). In that sense, valve ratios observed at these sites (Figs. 4B, 5B) probably represent the "final dumping ground" for valves that were sorted mainly while en route to those sites.

Summary and Conclusions.

Beach shell concentrations were related primarily to patterns of longshore drift. During normal low-energy conditions of summer the northern half of the beach was subject to northward drift, in response to impingement of southeasterly waves; the southern half experienced southward drift, because wave refraction around inlet shoals caused the impingement of northeasterly waves. Shell concentrations were greatest in slight reentrants along the strand, which functioned as sediment traps for valves. Accumulations were reduced at slight protrusions along the shoreline, which tended to be bypassed by shells, and were negligible along tidal inlet beach segments, where ebb-tidal currents predominated over longshore currents and tended to flush the beach of shells.

Nearly equal numbers of left and right trigonal valves of *D. variabilis* were delivered to the wrack line, and valves remained in that ratio near the middle of the beach. However, southward drift along the southern half of the beach transported more left than right valves, and northward drift along the northern half transported more right than left valves. In contrast, orbicular valves of *A. aequalis* were sorted mainly on the nearshore shelf, and disproportionately large numbers of right valves were delivered to the beach. The primary effect of sorting there was slightly greater accumulations of left valves in beach reentrants. Thus, in addition to shell-sorting mechanisms, local valve budgets also were related to the proximity of bivalve life sites: beach-related habitats for *D. variabilis* and shelf-related habitats for *A. aequalis.*

During a small tropical storm, most of the above trends were reversed. Although previous patterns of southerly and northerly drift remained, higher energy waves and wave-induced currents tended to deplete shell accumulations there; the greatest concentrations remained along a straight shoreline segment near the central part of the beach, an area intermediate in position between the main northward and southward longshore currents. Within this regime, left valves of *A. aequalis* virtually disappeared from the beach. *D. variabilis* exhibited a slight net deficit in right valves, and left:right valve ratios were substantially increased along the southern part of the beach.

Among subtidal sites, the greatest shell concentrations occurred at the seaward end of the longshore channel, an equilibrium point between coastal tides (especially the ebb) and shelf wave effects. Accumulations were next most important well within the sound, reflecting a flood-tidal component of shell transport, and were comparatively sparse on the nearshore shelf, where normal tidal currents are ineffectual.

Subaqueous valve-sorting mechanisms remain poorly known, yet substantial sorting occurred within this sound/longshore channel/shelf system. Virtually equal numbers of left and right valves of both species were present, overall, but left valves of *A. aequalis* and right valves of *D. variabilis* predominated in the channel and right valves of *A. aequalis* and left valves of *D. variabilis* predominated in the sound. Right valves of *A. aequalis* also predominated on the shelf; but valves of *D. variabilis* were rare there because of the distality of life sites of this essentially nearshore species.

All these results demonstrate the complexities involved in left-right valve sorting. Relatively few common denominators or "universal parameters" are discernible, other than those related to specific sedimentological and hydrological processes. Paralic fossil assemblages and shell budgets therefore must be evaluated primarily in terms of the local depositional setting. Nevertheless, such analyses can yield valuable information on depositional conditions and shell distributional patterns, and they deserve more attention from taphonomists than they have received to date. Major variables to be evaluated in such studies include (1) proximities of bivalve life sites, (2) valve symmetry, ornamentation, and condition, (3) distances and processes of shoreward or within-channel transport, (4) channel and beach configurations, and (5) interactions between waves and tidal currents, particularly as they relate to prevailing patterns of refraction, tidal flow, and longshore drift.

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References.

ABBOTT, R. T. (1974): American Seashells. — 2nd Edn., 663 pp.; New York (Van Nostrand Reinhold).

BEHRENS, E. W. & WATSON, R. L. (1969): Differential sorting of pelecypod valves in the swash zone. — J. Sed. Petrol., **39**: 159-165.

BOUCOT, A. J. (1953): Life and death assemblages among fossils. — Amer. J. Sci., **251**: 25-40.

BOUCOT, A. J. & BRACE, W. & DE MAR, R. (1958): Distribution of brachiopod and pelecypod shells by currents. — J. Sed. Petrol., **28**: 321-332.

BRENCHLEY, P. J. & NEWALL, G. (1970): Flume experiments on the orientation and transport of models and shell valves. — Palaeogeogr. Palaeoclimatol. Palaeoecol., **7**: 185-220.

CARTER, R. W. G. (1974): Feeding sea birds as a factor in lamellibranch valve sorting patterns. — J. Sed. Petrol., **44**: 689-692.

DÖRJES, J. (1972): Georgia coastal region, Sapelo Island, U. S. A.: sedimentology and biology. VII. Distribution and zonation of macrobenthic animals. — Senckenbergiana marit., **4**: 183-216.

DÖRJES, J. & FREY, R. W. & HOWARD, J. D. (1986): Origins of, and mechanisms for, mollusk shell accumulations on Georgia beaches. — Senckenbergiana marit., **18**: 1-43.

FAGERSTROM, J. A. (1964): Fossil communities in paleoecology: their recognition and significance. — Bull. Geol. Soc. Amer., **75**: 1197-1216.

FREY, R. W. (1987): Distribution of ark shells (Bivalvia: *Anadara*), Cabretta Island beach, Georgia. — Southeastern Geol., **27**: 155-163.

FREY, R. W. & PINET, P. R. (1978): Calcium-carbonate content of surficial sands seaward of Altamaha and Doboy Sounds, Georgia. — J. Sed. Petrol., **48**: 1249-1256.

FÜRSICH, F. T. & HEINBERG, C. (1983): Sedimentology, biostratinomy, and palaeoecology of an Upper Jurassic offshore sand bar complex. — Bull. Geol. Soc. Denmark, **32**: 67-95.

HENDERSON, S. W. & FREY, R. W. (1986): Taphonomic redistribution of mollusk shells in a tidal inlet channel, Sapelo Island, Georgia. — Palaios, **1**: 3-16.

HOWARD, J. D. & DÖRJES, J. (1972): Animal-sediment relationships on two beach-related tidal flats; Sapelo Island, Georgia. — J. Sed. Petrol., **42**: 608-623.

HOWARD, J. D. & FREY, R. W. (1980): Holocene depositional environments of the Georgia coast and continental shelf. — In: HOWARD, J. D. & DE PRATTER, C. B. & FREY, R. W. [Eds.]: Excursions in southeastern geology: the archaeology-geology of the Georgia coast. — Georgia Geol. Survey, Guideb., **20**: 66-134.

HOWARD, J. D. & FREY, R. W. & REINECK, H.-E. (1972): Georgia coastal region, Sapelo Island, U. S. A.: sedimentology and biology. I. Introduction. — Senckenbergiana marit., **4**: 3-14.

HOWARD, J. D. & REINECK, H.-E. (1972): Georgia coastal region, Sapelo Island, U. S. A.: sedimentology and biology. IV. Physical and biogenic sedimentary structures on the nearshore shelf. — Senckenbergiana marit., **4**: 81-123.

HUBBARD, D. K. & OERTEL, G. & NUMMEDAL, D. (1979): The role of waves and tidal currents in the development of tidal-inlet sedimentary structures and sand body geometry: examples from North Carolina, South Carolina, and Georgia. — J. Sed. Petrol., **49**: 1073-1091.

JOHNSON, R. G. (1957): Experiments on the burial of shells. — J. Geol., **65**: 527-535.

KELLING, G. & WILLIAMS, P. F. (1967): Flume studies of the reorientation of pebbles and shells. — J. Geol., **75**: 243-267.

KIDWELL, S. M. & JABLONSKI, D. (1983): Taphonomic feedback, ecological consequences of shell accumulation. — In: TEVESZ, M. J. S. & MCCALL, P. L. [Eds.]: Biotic Interactions in Recent and Fossil Benthic Communities: 195-248; New York (Plenum).

KORNICKER, L. S. & ARMSTRONG, N. (1959): Mobility of partially submersed shells. — Publ. Inst. Mar. Sci., **6**: 171-185.

KORNICKER, L. S. & WISE, C. D. & WISE, J. M. (1963): Factors affecting the distribution of opposing mollusk valves. — J. Sed. Petrol., **33**: 703-712.

KURODA, R. & MARLAND, F. C. (1973): Physical and Chemical Properties of the Coastal Waters of Georgia, 62 pp. + Append. — Univ. Georgia Mar. Inst. and Georgia Inst. Technol., Environ. Res. Center.

LAWRENCE, D. R. (1968): Taphonomy and information losses in fossil communities. — Bull. Geol. Soc. Amer., **79**: 1315-1330.

— — — (1979): Valve sorting in *Dinocardium* at North Inlet, South Carolina. — Geol. Notes (South Carolina State Development Board), **23**: 50-59.

LEBER, K. M. (1982): Bivalves (Tellinacea: Donacidae) on a North Carolina beach: contrasting population size structures and tidal migrations. — Marine Ecol. Prog. Ser., **7**: 297-301.

LEVER, J. (1958): Quantitative beach research. I. The "left-right-phenomenon": sorting of lamellibranch valves on sandy beaches. — Basteria, **22**: 21-51.

LEVER, J. & THIJSSEN, R. (1968): Sorting phenomena during the transport of shell valves on sandy beaches studied with the use of artificial valves. — Symp. Zool. Soc. London, **22**: 259-271.

LEVER, J. & KESSLER, A. & OVERBEEKE, A. P. VAN & THIJSSEN, R. (1961): Quantitative beach research. II. The "hole-effect". — Netherlands J. Sea Res., **1**: 339-358.

MARTIN-KAYE, P. (1951): Sorting of lamellibranch valves on beaches in Trinidad, B. W. I. — Geol. Mag., **88**: 432-434.

MAYOU, T. V. & HOWARD, J. D. (1975): Estuaries of the Georgia coast, U. S. A.: sedimentology and biology. VI. Animal-sediment relationships of a salt marsh estuary — Doboy Sound. — Senckenbergiana marit., **7**: 205-236.

MENARD, H. W. & BOUCOT, A. J. (1951): Experiments on the movement of shells by water. — Amer. J. Sci., **249**: 131-151.

MEULEN, H. VAN DER (1947-48): Nieuwe Gezichtspunten. — Zeepaard, **7**: 10-12; **8**: 5-6.

MIDDLETON, G. V. (1967): The orientation of concavo-convex particles deposited from experimental turbidity currents. — J. Sed. Petrol., **37**: 229-232.

MIKKELSEN, P. S. (1981): A comparison of two Florida populations of the Coquina Clam, *Donax variabilis* SAY, 1822 (Bivalvia: Donacidae). I. Intertidal density, distribution and migration. — Veliger, **23**: 230-239.

— — — (1985): A comparison of two Florida populations of the Coquina Clam, *Donax variabilis* SAY, 1822 (Bivalvia: Donacidae). II. Growth rates. — Veliger, **27**: 308-311.

MILLER, W., III & KOOSER, S. (1982): The distribution of *Donax variabilis* (Bivalvia) at Ship Island, Mississippi: some paleomalacological aspects. — Nautilus, **96** (3): 113-114.

NAGLE, J. S. (1964): Differential sorting of shells in the swash zone. — Biol. Bull., **127**: 353.

NIEDORODA, A. W., & SWIFT, D. J. P. & HOPKINS, T. S. (1985): The shoreface. — In: DAVIS, R. A., Jr. [Ed.]: Coastal Sedimentary Environments: 533-624; New York (Springer-Verlag).

OERTEL, G. F. (1972): Sediment transport of estuary entrance shoals and the formation of swash platforms. — J. Sed. Petrol., **42**: 858-863.

— — — (1973a): A sedimentary framework of the substrates adjacent to Georgia tidal inlets. — In: FREY, R. W. [Ed.]: The Neogene of the Georgia coast. — Georgia Geol. Soc., Guideb., **8**: 59-66.

— — — (1973b): Examination of textures and structures of mud in layered sediments at the entrance of a Georgia tidal inlet. — J. Sed. Petrol., **43**: 33-41.

— — — (1973c): Patterns of sediment transport at nearshore zones influenced by wave and tidal currents: a study utilizing fluorescent tracers. — Southeastern Geol., **15**: 77-92.

— — — (1974): Residual currents and sediment exchange between estuary margins and the inner shelf, southeast coast of the United States. — In: International symposium on interrelationships of estuarine and continental shelf sedimentation, Bordeaux, France, 1973. — Mém. Inst. Géol. Bassin d'Aquitaine, **7**: 135-143.

— — — (1985): The barrier island system. — Mar. Geol., **63**: 1-18.

OERTEL, G. F. & HOWARD, J. D. (1972): Water circulation and sedimentation at estuary entrances on the Georgia coast. — In: SWIFT, D. J. P. & DUANE, D. B. & PILKEY, O. H. [Eds.]: Shelf Sediment Transport: Process and Pattern: 411-427; Stroudsburg, Penn. (Dowden, Hutchinson & Ross).

RICHTER, R. (1922): Flachseebeobachtungen zur Paläontologie und Geologie. III-IV. — Senckenbergiana, **4**: 103-142.

— — — (1924): Flachseebeobachtungen zur Paläontologie und Geologie. VII-XI. — Senckenbergiana, **6**: 119-165.

ROSS, D. A. (1982): Introduction to Oceanography (3rd. ed.): 544 pp.; Englewood Cliffs, N. J. (Prentice-Hall).

SEILACHER, A. (1973): Biostratinomy: the sedimentology of biologically standardized particles. — In: GINSBURG, R. N. [Ed.]: Evolving Concepts in Sedimentology: 159-177; Baltimore, Md. (The Johns Hopkins Univ. Press).

SALAZAR-JIMÉNEZ, A. & FREY, R. W. & HOWARD, J. D. (1982): Concavity orientations of bivalve shells in estuarine and nearshore shelf sediments, Georgia. — J. Sed. Petrol., **52**: 565-586.

TRUSHEIM, F. (1931): Versuche über Transport und Ablagerung von Mollusken. — In: LÜDERS, K. & TRUSHEIM, F.: Beiträge zur Ablagerung mariner Mollusken in der Flachsee. II. — Senckenbergiana, **13**: 124-139.

WOBBER, F. J. (1967): The orientation of *Donax* on an Atlantic coast beach. — J. Sed. Petrol., **37**: 1233-1235.