

## Chapter 4

# Taphonomy and Time-Averaging of Marine Shelly Faunas

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## 1. Introduction

Shelly macroinvertebrate fossils are common, locally dominant components of sedimentary rocks and their differential preservation concerns many aspects of paleontological and geological analysis. Evaluation of post-mortem effects is essential, for example, to determine the fidelity of the fossil record as an archive of biological information, whether that information is used for paleoecological, evolutionary, or biostratigraphical purposes. In addition, the post-mortem modification of shelly fossils can provide valuable insights into paleohydraulic and diagenetic conditions, including short-term cycles of deposition, erosion, and omission on the seafloor.

The abundance and composition of shelly remains are governed by the complex interaction of many factors. These can be reduced in their simplest form to (a) the source and rate of shell supply, i.e., the raw material, (b) the inherent and highly specific susceptibility of those shells to post-mortem destruction or modification, (c) the taphonomic conditions that shells are exposed to in their environment of accumulation, and (d) the time scale of accumulation (Fig. 1). The longer the period of accumulation, the more likely that the taxonomic and age-class composition of the shell assemblage will be modified by differential preservation, that shells from successive generations will be mixed (time-averaged), and that the source, rate of supply, and local environment of accumulation will change. Some of these processes will tend to inflate the diversity of the death assemblage relative to community composition at a single moment in time (for example, time-averaging), whereas others will tend to diminish diversity and variation among assemblages (for example, the removal of fragile and mineralogically unstable forms). This "taphonomic equation" (Fig. 1) also presents many opportunities for feedback among factors, most notably because of the potential of accumulating shells to influence pore-water chemistry, seafloor mass properties, and benthic colonization.

In this review we attempt to assess environmental and temporal patterns in post-mortem modification, emphasizing actualistic evidence. These data are unavoidably biased in several ways: (a) toward mollusks, which dominate many modern shelly faunas; (b) toward physical processes of shell modification, owing to their experimental tractability relative to biological processes; and (c) toward the most accessible shallow-water environments. Conclusions on patterns and especially rates of shell accumulation thus should be extrapolated to other groups and settings with caution. Such extrapolations become increasingly problematic as one moves from Cenozoic to Mesozoic and Paleozoic biotas, owing to sweeping evolutionary change among hard-part producers and destroyers. Nevertheless, Recent systems, because they are amenable to controlled experimentation, can provide a valuable baseline for determining principles and the kinds of pathways that can underlie taphonomic patterns.

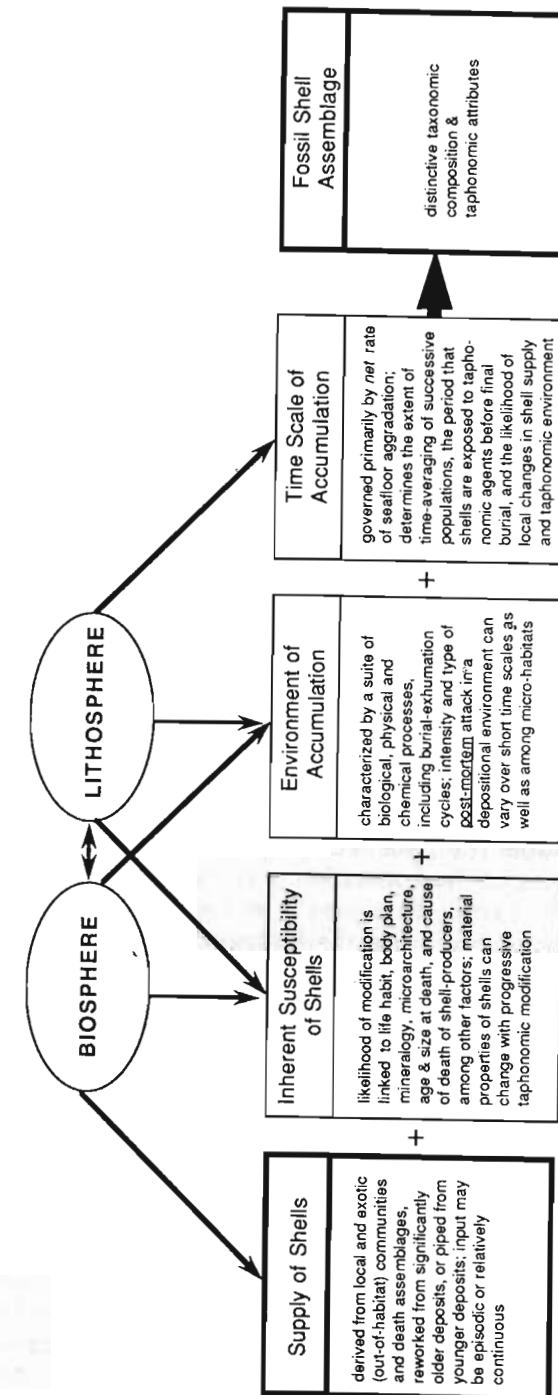


FIGURE 1. Major factors affecting the formation of shell assemblages.

### 1.1. Terminology

Post-mortem modification is a virtually unavoidable fact of fossilization: few faunas enter the record without some alteration, however minor, even those in spectacular *Lagerstätten* (Whittington and Conway Morris, 1985). Consequently, rather than reject imperfect records, paleontologists need reliable means to discriminate among degrees of bias and thus identify taphonomically comparable assemblages. Recognition of such "isotaphonomic" assemblages (*sensu* Behrensmeyer, 1988) would facilitate paleobiological interpretation by holding at least some biasing factors constant.

This is the rationale behind most classification schemes for fossil assemblages, whether they recognize (a) descriptive categories based on shell diagenesis (Koch and Sohl, 1983) and biostratigraphic features (Johnson, 1960; Brandt, 1989) or (b) inferential categories based on likely source of shells, scale of time-averaging, or complexity of post-mortem history (Table I).

Ever since Walther's (1893–1894) pioneering work on macroinvertebrate biofacies, many terms have been introduced, and variously redefined, to categorize live and dead shelly faunas (Table I). To avoid confusion, we will use the term *community* only to denote recurrent groups of living organisms, Recent or ancient. *Assemblage* will only be used for accumulations of nonliving material, that is, death assemblages. Assemblages can be of any age (e.g., modern, subfossil, or fossil) and can be composed of any mixture of transported and local shells; the unmodified term is also noncommittal with respect to ecological interactions among the former organisms. For assemblages thought to reflect ecological relationships among the preservable (i.e., shelled) portion of former communities, we prefer the paleoecological term *association* [*sensu* Fürsich (1977); following Kauffman and Scott (1976)]. This term is less ambiguous than "life assemblage," and presumes less about the biological significance of cooccurrences than terms such as "paleocommunity" and "fossil biocoenosis" (Table I).

## 2. Spatial and Temporal Variation in Recent Benthic Communities

Among many definitions of communities, that of Mills (1969) is most relevant for practical treatment of benthic faunas: "a community is a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment and separable by ecological survey from other groups." The distribution of such communities commonly can be related to areas of differing substratum (Jones, 1950; Hartnoll, 1983) or to environmental gradients in salinity (Cadée, 1968), temperature,

light, physical disturbance (Hiscock, 1983; Probert, 1984), and subaerial exposure (Price *et al.*, 1980).

Communities are recognized by visual or statistical grouping of samples on the basis of similarity in taxonomic composition and/or relative abundance of species. Unfortunately, no standard quantitative approach has yet been adopted by marine biologists and actuopaleontologists [see Gauch (1982) for review], even though multivariate methods are used to deal with the large data sets obtained from multiple sampling. These often contain tens to hundreds of taxon occurrences among tens to hundreds of sample sites.

Notwithstanding these technical problems, two models of benthic community structure have arisen, largely by analogy with terrestrial plant communities [Gray (1981) and Erwin (1983), based on Whittaker (1975)]. One model is that species abundance peaks more or less coincide across a region (Fig. 2A). In benthic systems, such a view derives from large-scale (1–10 km) studies based on widely spaced samples; community boundaries and habitat boundaries appear to be closely linked [e.g., early studies of the open shelf (Petersen, 1914; Jones, 1950)]. The alternative model is that species distributions vary independently and peak in abundance at different sites across a region (Fig. 2B). This view reflects finer-scale (10–100 m), transect-style studies [e.g., benthic zonations documented for sandy and rocky intertidal environments (Mills, 1969; Hughes and Thomas, 1971)]. This latter view has gained considerable acceptance with regard to both littoral and sublittoral settings with steeper environmental gradients (Stephenson *et al.*, 1971; Gray, 1981; Erwin, 1983).

Both models may be valid for a single environment, depending upon the scale of observation. For example: given a broad shelf with one region of rippled clean sand adjacent to another with shell gravel, it is likely (e.g., J. B. Wilson, 1986) that the two substrates would have faunas that could be distinguished by a grab or box-core kilometer-scale survey. Following Mills (1969), these would be regarded as separate communities and the distribution pattern of faunal abundances would resemble model 1 (Fig. 2A). However, if a more detailed (10-m) scale SCUBA transect survey were conducted across the boundary of these two substrata, then we would expect patterns to resemble model 2 (Fig. 2B).

The explanations offered for these patterns are diverse: some may reflect biotic interactions among species (competition, coadaptation) and others may reflect shared environmental tolerances, whereas many probably reflect a combination of causes. For example, based on a series of detailed studies (Allen, 1899; Vevers, 1952; Brun, 1969; Warner, 1971; Hiscock and Mitchell, 1980), it appears that of the 22 species in the *Ophiothrix fragilis* community of offshore British waters, five species benefit by feeding on *O. fragilis*, while the others are probably present because "environmental conditions are suitable or because another food supply is present" (Hiscock and Mitchell, 1980).

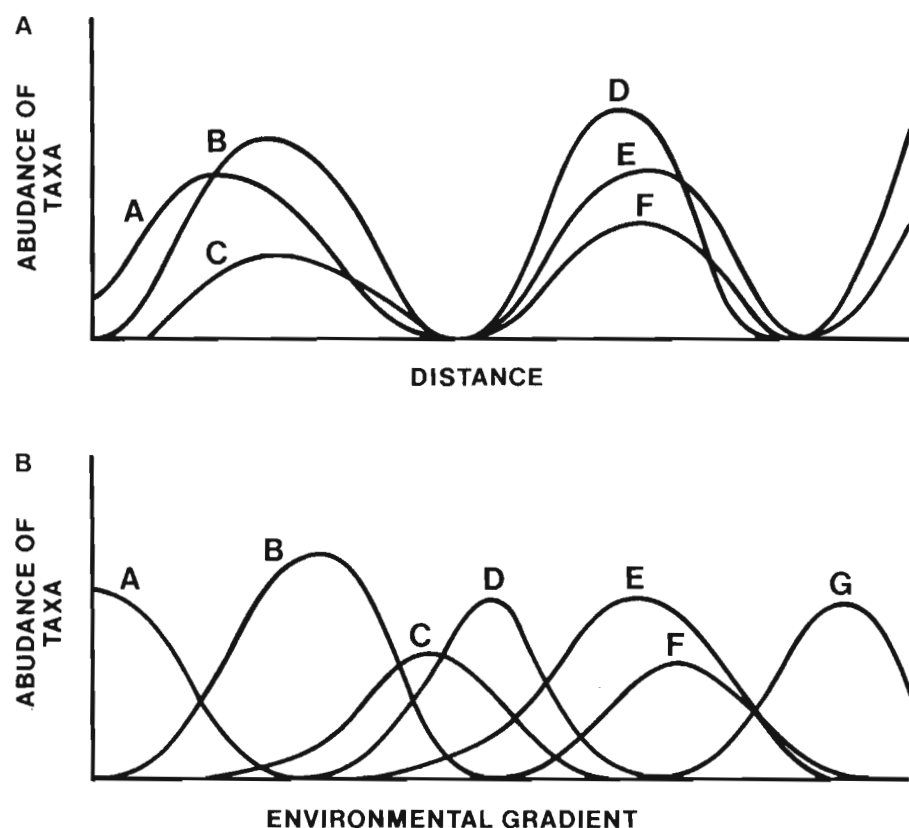


FIGURE 2. Different views of community structure: (A) Faunal abundances of different taxa occur in distinct groups A, B, C and D, E, F, possibly coinciding with environmental boundaries, (B) unrelated abundances of organisms A–G peaking separately along an environmental gradient. [After Gray (1981).]

Abundance patterns commonly are based on faunal surveys over short time scales and thus provide little insight into the temporal changes now known to characterize the structure of shelf benthic communities (Gray, 1981; Probert, 1984). Repeated sampling of shelf areas off the Northumberland coast of Britain by Buchanan *et al.* (1978), for example, indicates important seasonal and annual variation in biomass (Fig. 3A) and species abundance (Fig. 3B) attributable to larval settlement, winter mortality, and year-to-year differences in minimum winter water temperatures.

The few long-term surveys that have been carried out indicate that community structure and composition fluctuate considerably and on different time scales, and can be related to both biological disturbance (Paine, 1966) and natural cycles in the physical environment (Boesch *et al.*, 1976; Probert, 1984) (see Section 5.2.2). The data base for benthic faunas of the western English Channel, accrued over almost 100 years of sampling (Fig. 4)

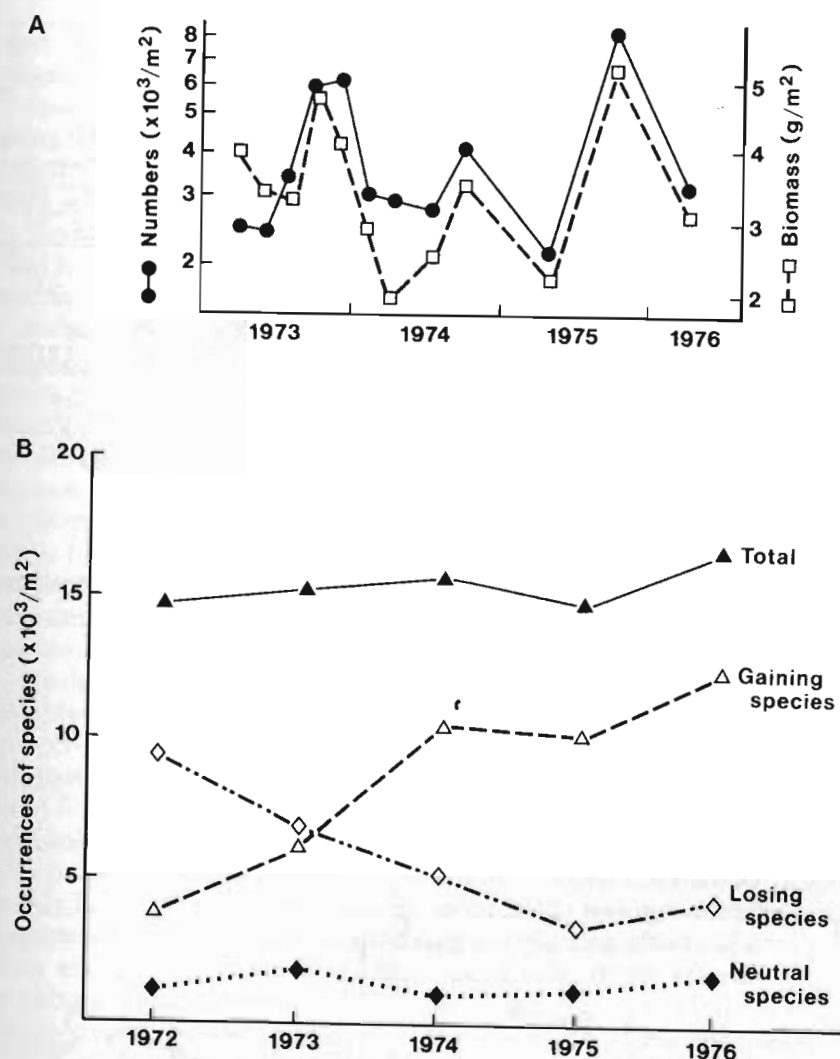
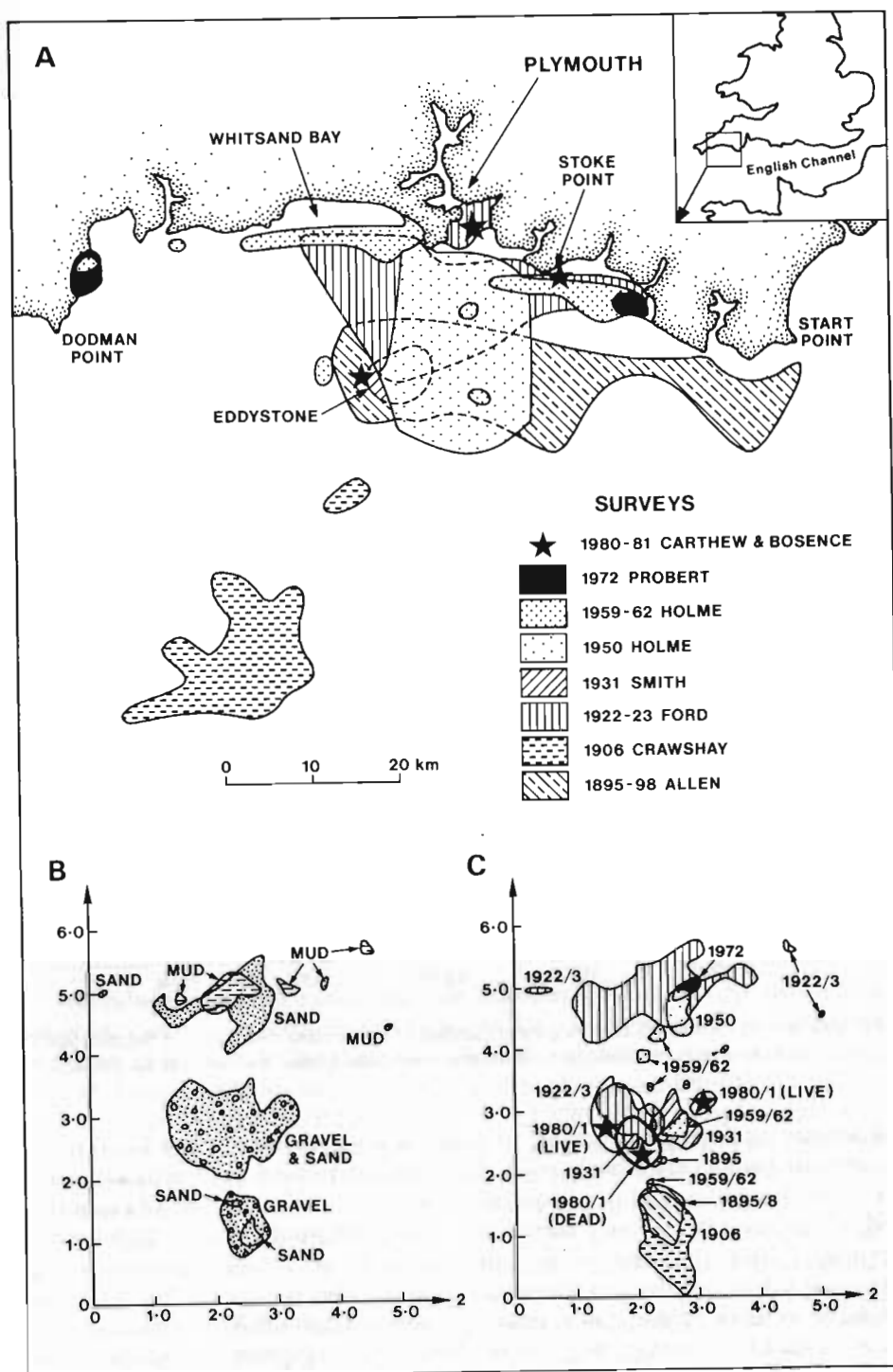


FIGURE 3. Plot of biologically long-term changes in (A) species numbers and biomass and (B) species abundances in benthos off Northumberland coast. [After Buchanan *et al.* (1978).]

(Carthew and Bosence, 1986), provides a good case in point for physical controls. Faunas are closely related to shell gravel and mud substrates (Fig. 4B) and have changed in composition over time scales of tens of years (Fig. 4C). The late 19th century faunas are clearly different from the 20th century faunas [although some of this may arise from differences in sampling techniques (Carthew and Bosence, 1986)]. The faunas of the 1920s are similar to those of the 1980s, which in turn are quite different from those of the 1930s to 1960s (Fig. 4C). These biologically long-term fluctuations (i.e., exceeding the lifespan of the organisms studied) in the composition of shell





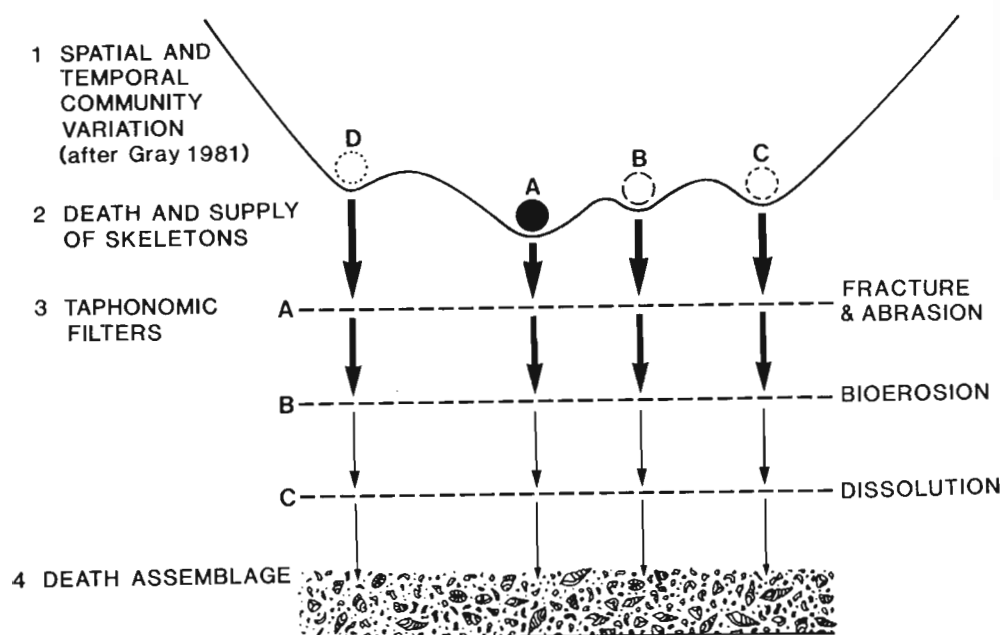
gravel communities are also reflected in the plankton communities of the western Channel (Southward, 1962, 1980). Both correlate with long-term changes in water temperature. Long-term changes in benthic faunas following the severe winter storms of 1962-1963 in the Dutch Wadden Sea and shallow German Bight, North Sea, are discussed in Beukema and Cadée (1986) and Ziegelmeier (1963, 1964), respectively.

Gray's (1981) model of temporal and spatial fluctuations is particularly useful for framing a paleoecological concept of benthic communities. This is based on Hutchinson's (1978) niche theory that organisms normally inhabit an optimal niche within a larger habitat, which may also be colonized following environmental perturbations. Gray (1981; after Holling, 1973) depicts the stable, core state of a community as a ball within a "basin of attraction" (Fig. 5) whose form is determined by disturbance and other controlling factors. Disturbance can bring about a shift in dominance and/or structure of the community to a new successional state (B in Fig. 5); the community may either revert to state A after the disturbance is removed, or change further to another state (C or D in Fig. 5) [see Johnson (1972) for a similar view]. Because these changes can be unrelated and unpredictable, community structure cannot be understood from any single survey or area; repeated sampling is required to understand the fauna at any site.

Geologically, this means that shells can be contributed to the death assemblage from any one of a community's successive states (Fig. 5). Given that soft-bottom seafloors aggrade, on average, at rates measured in only centimeters per  $10^3$  years (Schindel, 1980; Sadler, 1981), and that shells can persist for decades or centuries (see Section 5 on time-averaging), different community states should rarely be recorded as discrete assemblages in shelf environments. The details of succession and temporal coexistence of species are only likely to be preserved where aggradation was episodically rapid in decimeter-thick increments, minimizing the blurring effects of later bioturbation and physical reworking. More positively, death assemblages from soft-bottom environments can provide good pictures of the long-term average composition of communities (Peterson, 1977), comparable perhaps to those produced by summing repeated benthic surveys (Fig. 4C).

Broadly speaking, patterns of community structure on hard substrata and reefs are similar to those on soft substrata, but some of the controls on

**FIGURE 4.** Evidence for decade-scale changes in shelf benthos. (A) Locations and dates of surveys of benthic communities in waters off Plymouth, England. Where surveys overlap, the more recent survey overlies the older. (B) Plot of first and second axes of Detrended Correspondence Analysis of live benthic faunas from surveys in (A). Samples have been contoured by substrate type and this illustrates the close correspondence between samples with a similar fauna inhabiting similar substrates. (C) Plot as for (B), but samples contoured by date of survey. For the shell gravel stations in the center of the plot, note the shifts in community composition through time and the averaging of these shifts by the dead shelly fauna encircled by heavy line. Surveys are displayed by date of sampling. Publication dates are: Allen, 1899; Crawshaw, 1912; Ford, 1923; Smith, 1932; Holme, 1953, 1961, 1966; Probert, 1973; Carthew and Bosence, 1986. [After Carthew and Bosence (1986).]



**FIGURE 5.** Every benthic community has a variety of locally stable states, represented by the spheres on Gray's (1981) conceptual landscape, that differ in species abundances. Perturbations cause shifts in community composition among states A–D, each of which supplies skeletons that are subjected to a series of taphonomic filters before entering the death assemblage. Therefore the composition of the death assemblage at any given locality will depend not only upon taphonomic filters, but also upon local perturbation history and community response.

species distribution have been demonstrated more successfully. Particularly well documented has been the importance of physical disturbance (Paine and Levin, 1981; Graus *et al.*, 1984; Reichelt *et al.*, 1985), grazing pressure (Steneck, 1983; Steneck and Paine, 1986; Done, 1985), and spatial competition (Jackson, 1979; Branch, 1984). Because of rapid rates of reef growth under optimal conditions, short-term biological and physical processes have some potential for preservation in ancient reefs (Jackson, 1983), notwithstanding physical and bioerosion of the reef framework (Schroeder and Zankl, 1974; Scoffin and Garrett, 1974; Bosence, 1985). Ancient patterns of ecological succession (e.g., Rowland and Gangloff, 1988; Copper, 1988) can in some instances be compared directly with experimental evidence from field surveys and settling plates in Recent environments. For example, in the Pleistocene of Kenya, Crame (1980) found that early stages of coral reef growth showed "facilitation" succession (Connell and Slatyer, 1977) whereby early colonizers "prepare the ground" for later reef builders. Subsequent reef framework successions were less orderly, so that Crame was only able to recognize early and late colonizers following disturbance within the reef, perhaps conforming to Connell and Slatyer's (1977) "inhibition model" succession [see Kidwell and Jablonski (1983) for other examples ranging through the Phanerozoic]. On a smaller scale, Bosence (1984) was

able to show recurring overgrowth sequences of coralline algal and foraminiferal crusts in thin sections of preserved reef frameworks from patch reefs in St. Croix, Lesser Antilles. There the succession was the same as had been recorded by previous settlement plate experiments (Adey and Vassar, 1975). Disturbance created fresh substrates, which were first colonized by rapidly dispersing, fast-growing thin corallines, which were later overgrown by the more massive framework-forming coralline algae.

In cryptic hard-bottom environments, the main late-stage colonizers are often poorly mineralized and therefore would be underrepresented in fossil sequences (Rasmussen and Brett, 1985). However, in many instances interspecies spatial competition has been documented both on shells and on mobile pebble substrata (Liddell and Brett, 1982; Choi and Ginsburg, 1983; Taylor, 1984; M. A. Wilson, 1985, 1987). The high fidelity of preservation of these encrusting skeletal communities indicates the potential for studying the evolution of ecological dynamics in similar environments through time in a way that is probably impossible for soft-bottom environments.

### 3. Post-Mortem Modification of Community Structure

Benthic communities are typically composed of taxa having a variety of skeletal types and thus different preservation potentials. Macroinvertebrate groups range from those with (a) well-mineralized (= biomineralized) endo- or exoskeletons composed predominantly of calcite, aragonite, or apatite, to (b) lightly or locally mineralized proteinaceous and chitinous skeletons, (c) spiculate tissues, (d) minor mineralized hard parts, particularly feeding structures, and (e) entirely soft-tissued, hydrostatic "skeletons."

Under normal conditions of shelf sedimentation (i.e., relatively slow net aggradation of the seafloor, well-aerated overlying waters) and early diagenesis, biomineralized tissue is expected to be preserved, spiculate tissue to be dispersed, and soft tissues to decay leaving no trace (White, 1879). The first question in considering the quality of the fossil record thus must address the proportion of well-mineralized (= shelly) taxa in the benthic community: what is the maximum amount of information that a shelly assemblage can preserve from the original, total community (Section 3.1)? A second set of questions targets only the shelly portion of benthic communities: how accurately does the shelly death assemblage preserve the composition and structure of the shelled portion of the community (Section 3.2)?

#### 3.1. Proportion of Shelled Organisms in Benthic Communities

The higher the proportion of preservable taxa and individuals, the greater the likely fidelity of the death assemblage to the live community

(e.g., Lasker, 1976). Proportions of well-mineralized taxa, however, vary widely from 0 to 70% or more (e.g., Lawrence, 1968; Schopf, 1978; McCall and Tevesz, 1983) so that live : dead discrepancies in diversity can range over nearly two orders of magnitude. Based on a literature review of soft-bottom benthic faunas, Staff *et al.* (1985) found no correlation between proportion of shelly taxa and water depth or sediment grain size (Fig. 6). Even communities that contain a large number of shelly species are commonly dominated numerically by soft-bodied taxa, thus yielding poor agreement between numerical dominance-based diversity measures for the total community at a given moment and its shelly death assemblage (Peterson, 1975; Stanton, 1976; McCall and Tevesz, 1983).

Even though most individuals are not preserved, the same death assemblage can show high fidelity to the original live community if dominance is measured by biomass and if comparisons are made to a long-term picture of the benthos rather than to a single census. Because of their typically larger body sizes and temporally stable populations, shelly taxa may dominate benthic faunas in biomass even when they do not dominate in numerical abundance at any one time (Fig. 6) (Cummins *et al.*, 1986a; Staff and Powell, 1988). In Texas lagoons, Staff *et al.* (1985) found that both rank order and trophic structure of the original community could be recovered using this approach. In fact, Powell *et al.* (1989) argued that even numerical abundance data "indicate real variation in species' [ecological] success" when the compositions of both live and dead are examined over time scales exceeding a few years.

Equally reassuring is the observation that the high rates of shell dissolution documented in Texas lagoons [e.g., 50% of all new shells lost within 307 days (Powell *et al.*, 1984; Cummins *et al.*, 1986a)] are concentrated among juveniles and poorly calcified opportunists smaller than 3mm. The ecologically most persistent, and thus, it could be argued, the most characteristic species of the benthic community had immeasurably long half-lives in the same sediments, and thus dominate death assemblages much as they dominate any long-term portrait of the combined soft-bodied and shelly source community. Paleontologists therefore should not despair [contra M. V. H. Wilson (1988) and others] of the small numbers of shelly taxa or individuals normally censused in modern marine habitats: data indicate that high loss rates are focused on the ecologically most transient parts of communities, i.e., short-lived small or opportunistic forms, so that the temporally persistent core of the community is captured by the shelly death assemblage.

There have been few comparable studies in reef or hardground environments, but Brett (1988) found that shelled taxa usually represent less than 40% of species richness and only 15% of the area originally covered by encrusters. These figures are largely taken from cryptic biotas (e.g., Kobluk, 1988; Rasmussen and Brett, 1985; Kobluk and van Soest, 1989). By contrast, Jamaican reef surfaces yield an average of 70% mineralized taxa in shallow water (60 m); deeper waters yield progressively lower proportions, decreasing to 1.8% shelled taxa at 120 m depth (Liddell and Ohlhorst, 1988).

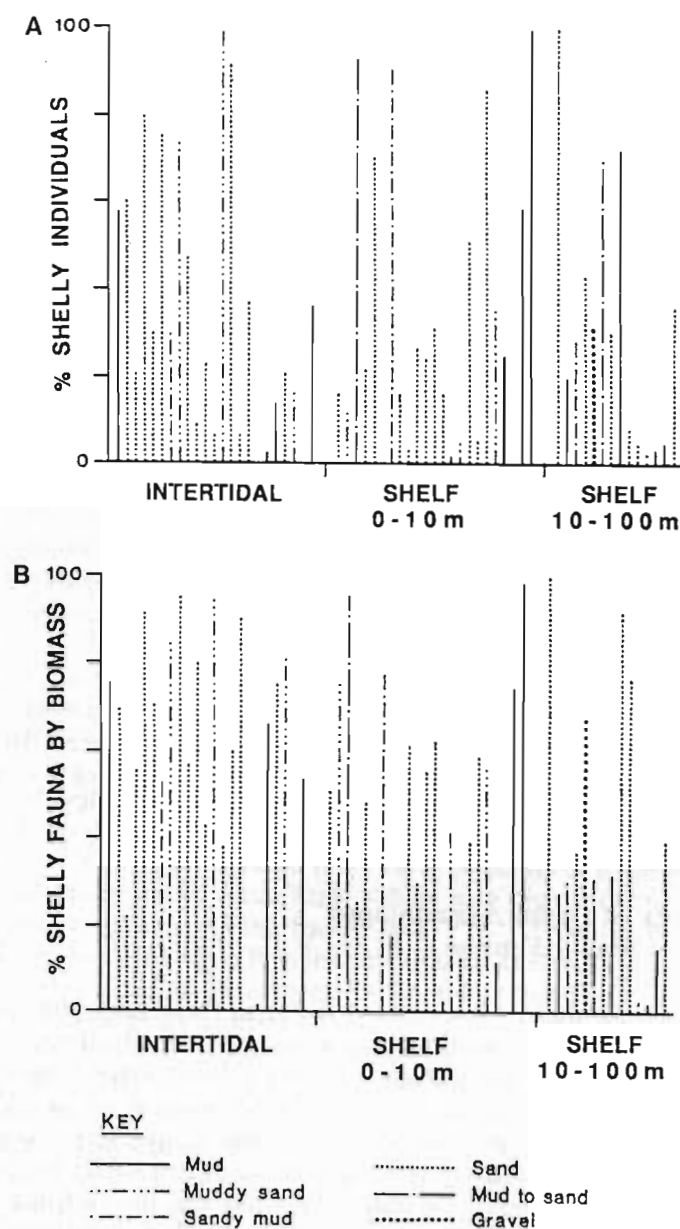


FIGURE 6. Bar charts illustrating percentages of shelly organisms in benthic communities from predominantly midlatitude soft substrata. (A) Percent of total individuals. (B) Percent of total biomass. Based on data compiled by Staff *et al.* (1985, Table 3).

Shallow-reef biotas thus have higher potential fidelities than deeper biotas. It remains to be tested how often this potential is actually achieved in death assemblages, given high water energies and intense bioerosion of live and dead skeletal material in shallow, photic waters.



### 3.1.1. Implications for Trophic Analysis

Although the temporally persistent core of the community can be captured by the shelly death assemblage, certain trophic groups and life habits will inevitably be underrepresented and thus it is unlikely that trophic structure can be satisfactorily resolved. Predators in modern shell gravel communities, for example, are mainly soft-bodied or lightly mineralized polychaetes, arthropods, echinoderms, skates, and rays (Bosence, 1979); birds are important but largely unrepresented factors in some intertidal communities (Cadée, 1989). The wide range in the proportion of low-preservation taxa even within single habitats or communities (see Section 3.1) undermines any possibility of a simple correction factor for fossil assemblages, even if benthic structures have been constant through the Phanerozoic. Reconstructing the trophic structure of the total community is further complicated by the diversity of food sources exploited by many benthic invertebrates (Cadée, 1984b).

Most trophic analyses since the late 1960s and early 1970s have not claimed to characterize the structure of the total original community (R. W. Scott, 1978; Fürsich, 1984; Fürsich and Flessa, 1987). Reconstructed trophic nuclei are used instead to describe only the shelly portion of ancient communities, and find primary application in biofacies mapping. Although in some settings such groupings may result as much from taphonomic processes as from living communities [e.g., loss of some and exotic input of others (Stanton and Dodd, 1976; Bosence, 1979)], most actualistic studies have found good agreement in the spatial distribution of live and dead shelly taxa at the biofacies scale (Section 3.2.1; Tables II–V).

### 3.2. Fidelity of Death Assemblages to Live Shelly Faunas

Even among shelly taxa, species differ in their susceptibility to post-mortem destruction (see Section 4 for processes and selectivity). Compared to the potential death assemblage, observed death assemblages can have lower species richness owing to preferential removal of small or fragile forms by predators and post-mortem processes. Conversely, they can have higher species richness than any single census of live shelly fauna owing to time-averaging of successive community states and the addition of allochthonous shells. In similar ways, size-frequency distributions of death assemblages may be more or less skewed than the raw input.

Many workers have found broad agreement between the most common occurrences in live and dead shelly faunas in a variety of environments (Johnson, 1965; Cadée, 1968; Warme, 1969; Warme *et al.*, 1976; Peterson, 1976; Bosence, 1976b; Ekdale, 1977; Carthew and Bosence, 1986). Shelly death assemblages often map communities and habitat types better than any single census of the living shelled community, suggesting both little

out-of-habitat transport of shells and little change or lateral displacement of communities during the period of shell accumulation (Column 3 in Tables II–V).

Comparisons among studies are difficult, however, because workers measure fidelity in different ways and with varying degrees of quantification. Consequently, these data are reanalyzed here using a series of standardized metrics (Tables II–V).

### 3.2.1. Fidelity with Respect to Species Richness and Taxonomic Composition

In order to assess species richness and taxonomic composition, three kinds of information are necessary: number of species found live only ( $N_L$ ), number of species found dead only ( $N_D$ ), and number of species found both live and dead ( $N_S$ ). Unfortunately, these requirements exclude several studies, most notably Johnson's (1965) seminal study of Tomales Bay, California, and Parker's (1960) data set for the Gulf of Mexico. Sixteen other studies do meet the requirements, including five from intertidal settings (Table II), five from subtidal coastal complexes (Table III), and six from open-shelf and deep-sea environments (Table IV). (Table V summarizes the data.)

Death assemblages tend to have fairly high fidelities when the question is, "what percentage of shelly species found live are also found dead at the same site?" [i.e.,  $(N_S \times 100)/(N_L + N_S)$ ; Table V]. In general, most or all well-mineralized taxa contribute to the local death assemblage: mean fidelities are 83–95% if data are summed for study areas, and are 75–98% if the focus is on individual habitats (e.g., sand channels or grass beds within an intertidal study area). Such high values also characterize Pleistocene assemblages: Valentine (1989) found that 77% of living bivalves and gastropods in the Californian Province are known as Pleistocene fossils, and that the missing species are all rare today and/or minute, fragile, or from lesser known deep-shelf habitats.

The same data sets yield lower values when the question is, "what percentage of species found dead are also found live?" [i.e.,  $(N_S \times 100)/(N_D + N_S)$ ; Table V]: 33–54% for entire study areas and 42–57% for individual facies, but the range is great (4–100%). The low fidelities are probably in part a consequence of the way living communities were (under)sampled: most studies relied upon a single census or single year of sampling. A hypothesis of sampling bias is supported by the observation that single study areas subjected to longer sampling programs showed improved agreement between live and dead with progressive sampling of live fauna. Peterson (1976) demonstrated this effect by pooling successive live samples from a 3-year study: the similarity between live and dead taxa increased from approximately 20% to 75% as live taxon records accrued over successive surveys in two warm, temperate lagoons. Knight (1988) found this same relationship over a 17-year study period in open-shelf habitats by

TABLE II. Fidelity of Recent Molluscan Death Assemblages in Intertidal Environments: Presence-Absence Data

Data set	What % live species are found dead within the STUDY AREA?	What % live species are found dead within the same FACIES?	Do dead shells cluster like live taxa?	What % dead species are found alive within the STUDY AREA?	What % dead species are found alive within the same FACIES?	What % dead individuals are from species found alive in the same FACIES?	One sampling of 11 sites, mesh unknown
West Coast North America, salt marshes and tidal creeks, 30°-47°N (MacDonald, 1969, 1976)	93% (avg.) (28/30 spp.)	Data not available	Yes	45% (28/62 spp.)	Data not available	Very high; quantitative data not available	
Yellow Sea, Korea, mud and sand flats, 37°N (Frey <i>et al.</i> , 1988, Appendixes 1 and 2)	100% (13/13 spp.)	100% mid flat (8/8 spp.) 100% outer flat (11/11 spp.)	No data	46% (13/28 spp.)	44% mid flat (8/18 spp.) 48% outer flat (11/23 spp.)	82% mid flat 79% outer flat	Mesh unknown; 2 samples each of 16 stations along single transect, one season
Seto Sea, Japan, mud, sand, and gravel flats and shoreline, 34°N (Tanabe <i>et al.</i> , 1986, and unpublished data)	45% (13/22 spp.)	62% sandy mud flat (10/16 spp.) 90% sand and gravel flat (9/10 spp.)	Yes for deep-burrowing spp.; no for shallow-burrowing spp.	100% (15/15 spp.)	100% sandy mud flat 75% sand and gravel flat	100% sandy mud flat 99% sand and gravel flat	5-mm mesh, 13 transects each dredged once
Mugu Lagoon, California, tidal flat and subtidal channel complex, 34°N (Warne, 1971; and unpublished data)	97% (38/39 spp.)	95% lower intertidal (22/23 spp.) 97% seagrass beds (31/32 spp.) 89% sand channels (16/18 spp.)	Yes	51% (38/75 spp.)	38% lower intertidal (25/58 spp.) 48% seagrass beds (31/64 spp.) 44% sand channels (16/36 spp.)	86% lower intertidal 94% seagrass beds 91% sand channels	3-mm mesh, replicate samples over one season; 55 samples
Cholla Bay, Gulf of California, sand and mud flats, 31°N (Fürsich and Flessa, 1987; and unpublished data)	80% (32/40 dominant spp.); total live spp. = 62	Data not available	Yes, in general	27% (32/119 dominant spp.); total dead spp. = 212	Data not available	Data not available	3-mm mesh, 77 samples from 4 transects, collected over 5 months
Mean	83%	90%	Yes	54%	57%	90%	

\*Based on Table I and Map 2 of Warne (1971).

TABLE III. Fidelity of Recent Molluscan Death Assemblages in Coastal Subtidal Environments: Presence-Absence Data

Data set	What % live species are found dead within the STUDY AREA?	What % live species are found dead within the same FACIES?	Do dead shells cluster like live taxa?	What % dead species are found alive in the STUDY AREA?	What % dead species are found alive within the same FACIES?	What % dead individuals are from species found alive in the same FACIES?	Sampling procedure for live fauna
Ria de Arosa, Spain, sand and clay estuary with rocky shore, and open ocean zone at mouth of estuary, 42° N(Cadée, 1968, and unpublished data)	100% (172 spp.) <sup>a</sup>	100% inner bay (10/10 spp.) 100% mid bay (20/20 spp.) 100% outer bay (17/17 spp.) 100% bay margin (24/24 spp.) 100% oceanic zone (23/23 spp.) <sup>b</sup>	Yes, except for oceanic zone	58% (172/296 spp.) <sup>a,c</sup>	53% inner bay (10/19 spp.) 100% middle bay (20/20 spp.) 71% outer bay (17/24 spp.) 89% bay margin (24/27 spp.) 88% oceanic zone (23/26 spp.) <sup>b,d</sup>	100% inner bay 100% mid bay 97% outer bay 94% bay margin >80% oceanic zone <sup>b</sup>	2-mm mesh; live collected over 3 years; 300 stations
Sapelo Island, Georgia, tidal sound and shelf, 31°N (Henderson and Frey, 1986, Appendix I)	100% (7/7 spp.)	100% sound (4/4 spp.) 100% channel (3/3 spp.) 100% shelf (4/4 spp.)	Yes?	10% (7/70 spp.)	9% sound (4/43 spp.) 4% channel (3/75 spp.) 24% shelf (4/17 spp.)	95% sound 94% channel 97% shelf	1.5-mm mesh, single samples at 8 stations in one season
Texas, Copano Bay, sandy mud, variable salinity, 26°N (Staff et al., 1985, 1986)	≥ 82% based on data for one facies only	82% (14/17 spp.) <sup>e</sup>	Not tested	≥ 23% based on data for one facies only	23% (20/88 spp.)	77% <sup>f</sup>	0.5-mm mesh, 2 samples every 6 weeks over 2 years
Texas, Laguna Madre, sand, variable salinity, 26°N (Staff et al., 1985, 1986)	≥ 97% based on data for one facies only	97% (28/29 spp.) <sup>f</sup>	Not tested	≥ 48% based on data for one facies only	48% (31/65 spp.)	99% <sup>g</sup>	0.5-mm mesh, 2 samples every 6 weeks over 2 years
Yucatan, carbonate lagoon, strait and shelf, 21°N (Warne et al., 1976; Ekdale, 1972, 1977)	97% (76/78 spp.)	95% backreef (40/42 spp.) 100% mangrove lagoon (54/54 spp.) 100% strait (29/29 spp.) 93% open sea (14/15 spp.)	Yes	26% (76/288 spp.)	19% backreef (40/213 spp.) 31% lagoon (54/173 spp.) 18% strait (29/158 spp.) 15% open sea (14/94 spp.)	78% backreef 91% lagoon 92% strait 54% open sea	3.1-mm mesh; 50 stations sampled once
Mean	95%	98%	yes?	33%	42%	89%	

<sup>a</sup>Based on Cadée (1968, Appendix).<sup>b</sup>Based on G. C. Cadée, unpublished data, for numerical dominants only.<sup>c</sup>84% (58/69 spp.) if based on unpublished data (G. C. Cadée) for numerical dominants only.<sup>d</sup>Average 45% dead spp. if based on entire fauna in Cadée (1968, Appendix).<sup>e</sup>Based on Staff et al. (1985, Table 1).<sup>f</sup>Based on Staff et al. (1985, Table 2).

TABLE IV. Fidelity of Recent Molluscan Death Assemblages in Open-Marine Environments: Presence-Absence Data

Data set	What % live species are found dead within the STUDY AREA?	What % live species are found dead within the same FACIES?	Do dead shells cluster like live taxa?	What % dead species are found alive in the STUDY AREA?	What % dead species are found alive within the same FACIES?	What % dead individuals are from species found alive in the same FACIES?	Sampling procedure for live fauna
North Sea, sand and muds at 20-50 m depth, 54°N (Cadée, 1984, and unpublished data)	97% (32/33 spp.)	95% mud, (20/21 spp.) 93% sand (13/14 spp.)	Yes, in general	51%(32/63 spp.)	84% mud, (21/25 spp.) 76% sand (13/17 spp.)	88% mud 93% sand	1-mm mesh, single samples of 21 stations, 4 sets of 10 samples over 8 months for 3 stations
Mannin Bay, Ireland, subtidal with rocky shore, 53°N (Bosence, 1976a, 1979)	92% (46/50 spp.)	86% algal bank (19/22 spp.) 92% clean algal gravel (33/36 spp.) 83% muddy algal gravel (30/36 spp.) 88% fine sand (23/26 spp.) 100% mud (7/7 spp.)	Yes	55% (46/83 spp.)	45% algal bank (19/42 spp.) 48% clean algal gravel (33/68 sp.) 60% muddy algal gravel (30/50 spp.) 36% fine sand (23/64 spp.) 22% mud (7/31 spp.)	94% algal bank 79% clean algal gravel 97% muddy algal gravel 66% fine sand 90% mud	2-mm mesh, 77 samples taken over 1 season
English Channel, open shelf, 50°N (Carthew and Bosence, 1986; and unpublished data)	≥ 92% based on data for one facies only	92% subtidal shell gravel 22/24 spp.)	Yes	≥ 23% based on data for one facies only	23% subtidal shell gravel (22/96 spp.)	66%	2-mm mesh, 4 quarterly replicates over one year; 11 sample sites
English Channel, subtidal bay, 50°N (Knight, 1988)	97% (40/41 spp.) during 1985/86	43% clean sand 60% muddy sand 69% silt 67% gravel <sup>a</sup>	Yes, but subcommunities overlap	37% if one uses live data from 1985/86 only 47% if one sums data from 1971 and 1985/86 54% if one sums data from 1968, 1971, and 1985/86	27% clean sand 27% muddy sand 44% silt 31% gravel <sup>a</sup>	6% clean sand 27% muddy sand 66% silt 67% gravel <sup>a</sup>	2-mm mesh, one sampling over 2 years (1985/86), one sampling of live in 1971, one sampling of live in 1968; all of same areas or stations; 103 total samples
Strait of Canso, Nova Scotia, 45°N (Wagner, 1975)	54% (47/87 spp.)	62% strait (35/56 spp.) 69% inner bay (25/36 spp.) 30% open bay (3/10 spp.)	No data	64% (47/73 spp.)	56% strait (35/62 spp.) 78% inner bay (25/32 spp.) 30% open bay (3/10 spp.)	No data	190 grab samples and ~50 shallow cores, one season
Gulf of California and Pacific intertidal to abyss, 21-31°N (Parker, 1963, Table I)	70% (281/403 spp.)	Data not available	Data not available	38% (281/736 spp.)	Data not available	Data not available	1-mm mesh, single samples of 270 stations over 3 years
Mean	84%	75%	yes	45%	46%	70%	

<sup>a</sup>Based on data for 12 dominant spp. in 1985/86 only.

TABLE V. Summary of Results from Tables II-IV

Setting	What % live species are found within the STUDY AREA?		Do dead shells cluster like live taxa?	What % live species are found dead within the same FACIES?		What % dead species are found alive within the STUDY AREA?		What % dead species are found alive within the same FACIES?		What % dead individuals are from species found alive in the same FACIES?	
	Mean	Range		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Intertidal	83%	45-100%		90%	62-100%		54%	27-100%	57%	38-100%	90%
Coastal	95%	82-100%	Yes	98%	82-100%	Yes	33%	10-58%	42%	4-100%	89%
subtidal											
Open marine	84%	54-97%	Yes	75%	30-100%	Yes	45%	38-64%	46%	22-84%	70%
Grand means		87%	Yes		88%	Yes		44%	48%		83%

relocating sites sampled by previous workers (Table IV). Within a single sampling program (1985/86), 37% of the dead species were found alive; this figure increased to 47% when live taxa from 1971 and 1985/86 were pooled, and increased to 54% when live taxa sampled in 1968, 1971, and 1985/86 were pooled.

This direct relationship between measured fidelity and study duration suggests that many species found "dead only" are not exotic or out-of-habitat, but simply have not yet been sampled live because of patchy or impersistent populations. Johnson (1965) and others have used the term "exotic" to designate taxa found dead only, but this term should be restricted to demonstrable instances of out-of-habitat transport. Taxa found only in death assemblages are best referred to by a more neutral term such as "dead only" (Warne, 1969), because many are simply remnants of older or very patchy indigenous populations.

Cadée (1984a, and personal communication, March 1990), for example, suggested that 26 of 32 dead-only species in molluscan assemblages of the North Sea were indigenous. The remaining 6 species not sampled live were reworked from Pleistocene intertidal deposits present 50 cm below the seafloor. Such leakage from stratigraphically older deposits is one source of discrepancy between live and dead faunas (S. W. Henderson and Frey, 1986). Another influence on fidelity is environmental change during the period of shell accumulation. Where the sedimentary environment is known to have changed during the study period, such as in Knight's (1988) study of the effects of inert clay-waste pollution in a shallow marine embayment of the English Channel (Table VI), the death assemblage differs significantly from the live community and represents an average of the older and newer communities occupying the site. It is thus essential for paleontologists to use all lines of evidence (e.g., sedimentary matrix, discontinuity surfaces, stratigraphic context, quality of shell preservation, etc.) to determine the likelihood of environmental change before death assemblages are interpreted paleobiologically (see Section 5.2.3).

Although some variation in taphonomic fidelity must reflect differences in communities, environments, and histories of shell accumulation, the positive relationship between fidelity and live-study duration described above is interesting on several accounts.

(a) It pinpoints an operational bias in data collection: because most death assemblages are time-averaged, a single live census provides an inadequate basis for comparison. Estimates of death assemblage fidelity thus should be considered to be *minimum* estimates until long-term replicate surveys of living fauna yield few new species.

(b) The between-locality variation in Tables II-IV (e.g., Mugu Lagoon versus Strait of Canso) may depend more upon how extensively live faunas were sampled than upon real differences in the fidelity of the death assemblages.

(c) Most importantly from a paleontological perspective, it provides



direct evidence for scales of time-averaging. The time period over which samples must be pooled in order for the composition of the living community to converge with the death assemblage indicates the minimum period of time-averaging recorded by modern death assemblages. For the open shelf, living benthos must be sampled over many decades before live and dead species richnesses show good agreement (Carthew and Bosence, 1986), but evidently only a few years will suffice for lagoons (Peterson, 1976). Systematic studies to determine characteristic periods of time-averaging for Recent benthic habitats could be extremely useful for extrapolation to the fossil record because these periods are not always inherently biogenic, but a consequence of the physical environment acting on both benthic ecology and taphonomy (see Section 5). Toward these ends, it is imperative (a) that samples and records from previous faunal surveys continue to be archived, and (b) that planned and current surveys of live and dead faunas accurately locate sample sites and ensure that samples are curated for future restudy.

Finally, yet another set of fidelity estimates results if the question is, "what percentage of dead individuals are from species found alive?" [i.e., (dead individuals of  $N_S \times 100$ )/(dead individuals of  $N_D + N_S$ )]. Variation in this measure of fidelity is large (6–100%), but the overall average is high (70–90%; Table V), meaning that species sampled live tend to dominate the local death assemblage. This is true even for habitats with large numbers of "dead-only" taxa. For example, only 22–60% of species found dead were sampled live in subhabitats of Mannin Bay, but these accounted for the majority of individuals in death assemblages [range 66–97%, average 85% (Bosence, 1979)] (Table IV). In other words, species not sampled live, either because they have patchy and ephemeral populations or because they are truly exotic, tend to be represented by few dead individuals.

Although assemblages can be composed exclusively of exotic species (e.g., storm-washovers and turbidites dominated by bulk flow; see Section 4.2.3 and Table IX), a low number of dead individuals prove to be exotic in level-bottom settings. For example, S. W. Henderson and Frey (1986, Appendix 1) found no exotic taxa in shallow-shelf assemblages and only 9% exotic species (accounting for 10% of dead individuals) in ebb-dominated tidal sound assemblages. On intertidal flats, Frey *et al.* (1988) found 8–25% exotic species in inner flat assemblages (accounting for 5–8% of all dead individuals), 38–50% exotic species in middle flat assemblages (only 6% of dead individuals), and 17–67% exotic species in outer flat assemblages (only 1–5% of dead individuals). Exotic individuals cannot always be reliably identified based on shell damage—rafted shells may arrive in pristine condition—but transport does tend to select shells of small-bodied, free-living epifauna and very shallow burrowing infauna (see Section 4.2.3).

The rather high fidelity of death assemblages to source live communities is encouraging for paleoecological interpretation. It also might be used to advantage in environmental impact studies (e.g., Samtleben, 1981).

### 3.2.2. Fidelity with Respect to Species Dominance

All factors being equal, the most abundant members of a living community are the ones most likely to enter the fossil record, and the most abundant fossils are the ones most likely to be sampled by paleontologists. However, taphonomic processes can alter this simple relationship by preferentially removing certain species and size classes (see Section 4). As with species richness data, comparisons among previous studies on the fidelity of relative abundances are difficult in the absence of standardized metrics, and are limited by the scarcity of appropriate data sets.

Table VI analyzes fidelity with respect to the six most abundant taxa in Recent molluscan death assemblages. This number was chosen as a basis for comparison because (a) it permitted comparison of a larger number of published data sets, and (b) in each data set the most abundant (= top) six taxa are generally confined to the peak of the skewed species-abundance distribution typical of benthic communities. For example, the top 6 living mollusk species in Copano Bay, Texas, comprise 94% of all live mollusk individuals (17 species total), and the top 6 species in nearby Laguna Madre comprise 70% of all live mollusk individuals [29 species total; data from Staff *et al.* (1985)].

For each data set, fidelity was calculated several ways: (a) the number of top six taxa in the death assemblage that are also among the six most abundant taxa in the live community; (b) the percentage of dead individuals that come from the top six taxa in the live community; (c) the number of top six taxa that occur in the same rank order in both death assemblage and live community; and (d) the percentage of dead individuals that come from taxa ranked identically both dead and live.

Results are as follows (Table VI):

(a) One-sixth to five-sixths (grand mean = one-half) of the top taxa in the death assemblage were top taxa in the source live community.

(b) The most common live taxa generally account for slightly more than half of all individuals in the death assemblage (grand mean 57%, but range of 20–99%).

(c) Very few (zero to half) of the top dead taxa occur in the same order or ranked abundance as they do in the live community.

(d) These taxa account for about one-third of all individuals in the death assemblage (grand mean 29%, but range 0–99%).

Given that most live data sets are based on only one sampling of local communities (Table VI), all of these measures of fidelity are probably minimum estimates; presumably, fidelity values would increase with study duration, much as they do for species richness (see Section 3.2.1). The low estimates nonetheless cast doubt upon biofacies discrimination based on the rank order of the numerically most abundant species. Differences in the composition of the top taxa may be biologically meaningful, but differences in the precise ordering of those top taxa are more likely to be taphonomic in origin than biologically determined.

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TABLE VI. Fidelity of Recent Molluscan Death Assemblages: Relative and Rank Abundances of the Six Most Common Species in Death Assemblages<sup>a</sup>

Location and sampling		No. of samples	Facies or community	How many of the 6 most abundant spp. in the death assemblage also rank as 6 most abundant in the source community?	What % of dead individuals come from the 6 most abundant taxa in the source community?	How many of the 6 most abundant spp. in the death assemblage occur in the same rank order as they do in the source community?	What % of dead individuals come from taxa that are ranked identically both live and dead?
Intertidal							
Yellow Sea, Korea, tidal flat (37°N) (Frey <i>et al.</i> , 1988); one sampling, unknown mesh	Muddy sand	6		5/6	81%	2/6	28%
	Sandy outer flat	10		3/6	74%	2/6	65%
Mugu Lagoon; California (34°N) (Warne <i>et al.</i> , 1976); two duplicate samples 2 years apart, 2.3-mm mesh	Eelgrass bed	8		3/6	54%	1/6	27%
	Sand channel	4		3/6	74%	3/6	74%
	Tidal creek	4		3/6	41%	1/6	8%
Seto Sea, Japan (34°N) (Tanabe <i>et al.</i> , 1986, and unpublished data); one sampling, 5-mm mesh	Sandy mud flat			6/6	99%	1/6	4%
	Sand and gravel flat			5/6	98%	NA	NA
Coastal Subtidal							
Ria de Arosa, Spain (42°N) (Cadée, 1968, and unpublished data) one sampling, 2-mm mesh	Inner bay	47		4/6	63%	0	0
	Middle bay	29		4/6	47%	2/6	24%
	Outer bay	55		4/6	49%	0	0
	Bay margin	132		1/6	10%	1/6	10%
	Oceanic zone	26		2/6	17%	0	0

Texas lagoons (26°N) (Staff <i>et al.</i> , 1986); sampling every 6 weeks over 2 years, 0.5-mm mesh	Laguna Madre sand (biomass)	14	2/6 (4/6)	36% (97%)	0 (3/6)	0 (97%)
	Copano Bay mud (biomass)	14	2/6 (4/6)	43% (98%)	0 (3/6)	0 (98%)
Yucatan coast, Mexico (21°N) (Ekdale, 1972); one sampling, 3.1-mm mesh	Backreef	21	3/6	20%	1/6	11%
	Mangrove lagoon	15	4/6	33%	3/6	24%
	High-energy strait	12	5/6	79%	2/6	70%
<b>Open Shelf</b>						
North Sea (54°N) (unpublished raw data for Cadée, 1984a); one sampling of live and dead at 21 stations, 4 quarterly samplings of 3 stations, 1-mm mesh	Muddy stations: Single-sampled Quarterly-sampled	14	4/6	40%	1/6	8%
	Sandy stations: Single-sampled Quarterly-sampled	7	2/6	52%	0	0
		8	3/6	85%	0	0
Mannin Bay, Ireland (53°N) (Bosence, 1976a,b); one sampling of live and dead faunas, 2-mm mesh	Algal bank	17	3/6	95%	1/6	78%
	Muddy algal gravel	17	2/6	91%	1/6	85%
	Clean algal gravel	21	3/6	66%	0	0
	Fine sand	11	3/6	59%	2/6	57%
	Mud	4	3/6	91%	3/6	91%
English Channel, embayment (50°N) (Knight, 1988); one sampling of live and dead faunas over 2 years, 2-mm mesh	Clean sand <sup>b</sup>	(3)	(0)	(0)	(0)	(0)
	Muddy sand <sup>b</sup>	(8)	(1/6)	(23%)	(0)	(0)
	<i>A. filiformis</i> mud	16	4/6	36%	1/6	8%
	<i>T. communis</i> mud	9	3/6	55%	3/6	55%
	Gravel (4-mm mesh)	4	3/6	78%	2/6	68%
English Channel, open shelf (50°N) (Carthew and Bosence, 1986; and unpublished data) quarterly sampling for 1 year, 2-mm mesh	Bay	15	2/6	75%	1/6	72%
	Inshore open shelf	12	3/6	40%	2/6	29%
	Offshore open shelf	13	2/6	23%	0	0
Grand means			3/6	57%	1/6	29%
Range			1/6–5/6	20–99%	0–3/6	0–91%

<sup>a</sup>Values in parentheses are based on biomass or were from communities known to have changed and, hence, were not used in calculating grand means.

<sup>b</sup>Substrate type or community known to have changed during 15 years prior to sampling (Knight, 1988; Knight and Bosence, 1988).

In a unique attempt to assess the effects of ranking species according to biomass rather than number of individuals, Staff *et al.* (1985) found that live and dead assemblages in opportunist- and juvenile-dominated Texas lagoons show greater agreement when measured in terms of biomass (parenthetical values in Table VI). Two-thirds of the top dead taxa were top taxa in the live community (up from one-third; accounted for 97–98% of dead biomass), and half of the top dead taxa occurred in the same rank order as when live (up from zero; accounted for 97–98% of biomass).

### 3.2.3. Fidelity with Respect to Age- and Size-Frequency Distributions

The extensive literature on size-frequency and survivorship analysis has been ably reviewed by Dodd and Stanton (1981). Early work in the 1950s and 1960s emphasized size-frequency data as a means of discriminating between (a) *in situ* census assemblages, thought to be characterized by polymodal or juvenile-dominated curves, and (b) allochthonous and otherwise taphonomically sorted assemblages, thought to be characterized by normal, leptokurtic curves. Work in the 1970s shifted to using size-frequency distributions as evidence for mortality patterns among different organisms (K. R. Walker and Parker, 1976; Alexander, 1977; Hutchinson, 1978) and for the same organism in different habitats (Surlyk, 1972; Richards and Bambach, 1975; Dzik, 1979).

Actualistic work in the 1980s has provided new insights into taphonomic influences on dead shells and has been largely pessimistic concerning the paleoecological value of size-frequency data. Census assemblages (*sensu* Hallam, 1972) of articulated individuals generally permit a direct reading of shelly population structure [i.e., the age-frequency distribution of living individuals (Levinton and Bambach, 1970; Tanabe and Arimura, 1987); but see Kranz (1974a) for preferential escape of juveniles], but all other assemblages are cumulative in origin, and reflect background as well as catastrophic mortalities. At best, these assemblages provide records of local mortality (i.e., age- or size-dependent survivorship) from which population structure can be back-calculated [see Dodd and Stanton (1981) for procedures].

Unfortunately for the paleoecologist, any number of different size distributions can result from a single pattern of mortality owing to taphonomic processes; moreover, any given size distribution can have several possible explanations. For example, bimodal intertidal populations can yield (a) juvenile-dominated allochthonous assemblages by current transport, (b) adult-dominated allochthonous assemblages by hermit crab and bird transport, and (c) platykurtic residual assemblages of disarticulated shells (Fig. 7).

It appears that even with little collection bias and regardless of taxonomic group and setting, juveniles are generally underrepresented in the fossil record (Olson, 1957; Kurtén, 1954; Cadée, 1982; Yochelson and Lindemann, 1986). High taphonomic loss rates for small specimens and

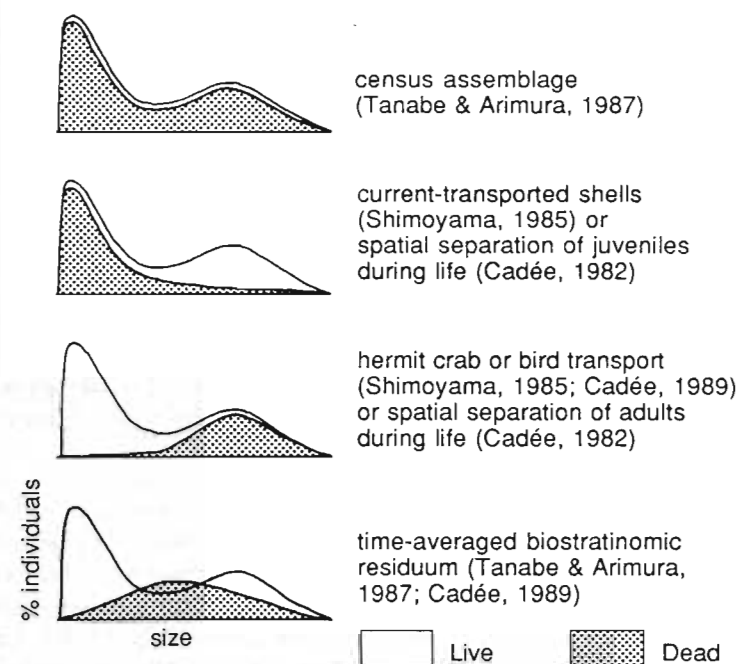


FIGURE 7. Common qualitative changes in the shape of molluscan size-frequency distributions in intertidal settings, from live (white) to dead (stippled), and documented causes.

juveniles in particular are strongly indicated by some actualistic studies (Powell *et al.*, 1982; Babcock, 1985; Cummins *et al.*, 1986a). Adults of small-bodied species are comparatively common in Recent and fossil death assemblages. The preferential loss of juveniles is possibly related not so much to size and surface area effects as it is to ontogenetic differences in degree and style of mineralization (e.g., high intraskeletal porosity and organic content associated with rapid juvenile growth).

In some circumstances, classes of small organisms may experience preferential preservation. Bosence (1979) and Arua (1982), for example, observed that small subtidal bivalves were less subject to borers and encrusters than were large specimens. Pip (1988) documented a similar bias against comparatively fragile large-shelled gastropods in freshwater sediments. Any species not showing an allometric increase in thickness relative to shell length might be expected to yield juvenile-dominated death assemblages owing to preferential loss of large specimens. Highly skewed frequency distributions for individual species can also reflect ecological phenomena such as spatial separation of juveniles and adults related to larval settlement (Cadée, 1982), unusually high (or low) juvenile mortality (Levinton, 1970), stunting of growth (Price, 1982), and dwarfing or paedomorphosis [reviewed by Mancini (1978)]. Multispecies assemblages domi-

nated by small individuals generally reflect (a) hydraulic sorting and abrasive reduction, as, for example, assemblages found in beach and washover deposits, or (b) extreme diagenetic filtering by solution or mineralization, as, for example, the phosphatic steinkern-rich "pebble necrocenoses" that characterize many Paleozoic formation boundaries in the U. S. Midcontinent (Tasch, 1955a; B. Witzke, personal communication).

Cadée (1989) suggested that in intertidal settings, size-selective predation, fragmentation, and transport are probably the rule (see also Shimoyama, 1985; Tanabe and Arimura, 1987), so that size-frequency distributions probably give little information on original population dynamics. These and other workers (Noble and Logan, 1981; Cummins *et al.*, 1986b; Westrop, 1986) have argued that size-frequency data are in general probably most revealing of post-mortem processes, except for data derived from census assemblages of articulated specimens.

Although the details of population structure are unlikely to survive taphonomic processes, data from subtidal lagoons (Cummins *et al.*, 1986b) suggest that in some instances time-averaged death assemblages provide a fairly good *qualitative* picture of molluscan mortality patterns. For example, in 10 out of 13 cases, juvenile-dominated death assemblages are associated with juvenile-dominated mortality, bimodal assemblages with bimodal mortality, and adult-dominated assemblages with adult-dominated mortality (Fig. 8). However, modes are commonly displaced by one or more size classes.

Quantitative tests of these same data yield mixed results. Based on use of the Kolmogorov-Smirnov test, a test more directly applicable to differences in the shapes of frequency distributions than the chi-square test used by Cummins *et al.* (1986b; Sokal and Rohlf, 1981), 5 of the 13 cases show no significant difference between expected and observed size distributions ( $p < 0.05$ ) (Fig. 8). Because Cummins *et al.* (1986b) note that their estimates of juvenile mortality are probably in error by 70–95%, a second Kolmogorov-Smirnov test was run excluding the 1.0-mm size class; 6 of the 13 cases showed no significant difference (Fig. 8). In summary, approximately half of the species showed no significant difference between dead size-distributions and calculated mortalities, and virtually all show good qualitative agreement.

Cummins *et al.* (1986b) stated that their data suggested a strong preservational bias acting against juveniles. However, by their own calculations, only 4 of the 11 cases in which they tracked an "input pulse" showed any significant difference between "pre- and post-taphonomic loss" (their Table 1). Juveniles also appear to be overrepresented in death assemblages relative to mortality in 8 of their 13 graphs reprinted in our Fig. 8, but this may be a consequence of underestimated mortality, as discussed above.

The good qualitative agreement, along with quantitative agreement in half of the size-frequency distributions presented by Cummins *et al.* (1986b), suggest that such data may yet be of value to paleobiologists,

although care must be taken in obtaining and interpreting these data [see, for example, the exchange between Cadée (1988) and W. Miller and DuBar (1988a,b)]. The mixed results in Texas lagoons suggest that the general conclusion that size-frequency distributions are determined primarily by taphonomy may someday prove to be overly pessimistic, even though the intertidal record does indeed appear to be strongly biased (but see Hartshorne *et al.*, 1987). Further study is warranted to determine whether time-averaged assemblages of certain taxa, life habits, or depositional environments might still yield consistently useful size-frequency data.

#### 4. Biostratinomy: Processes and Agents of Differential Shell Preservation

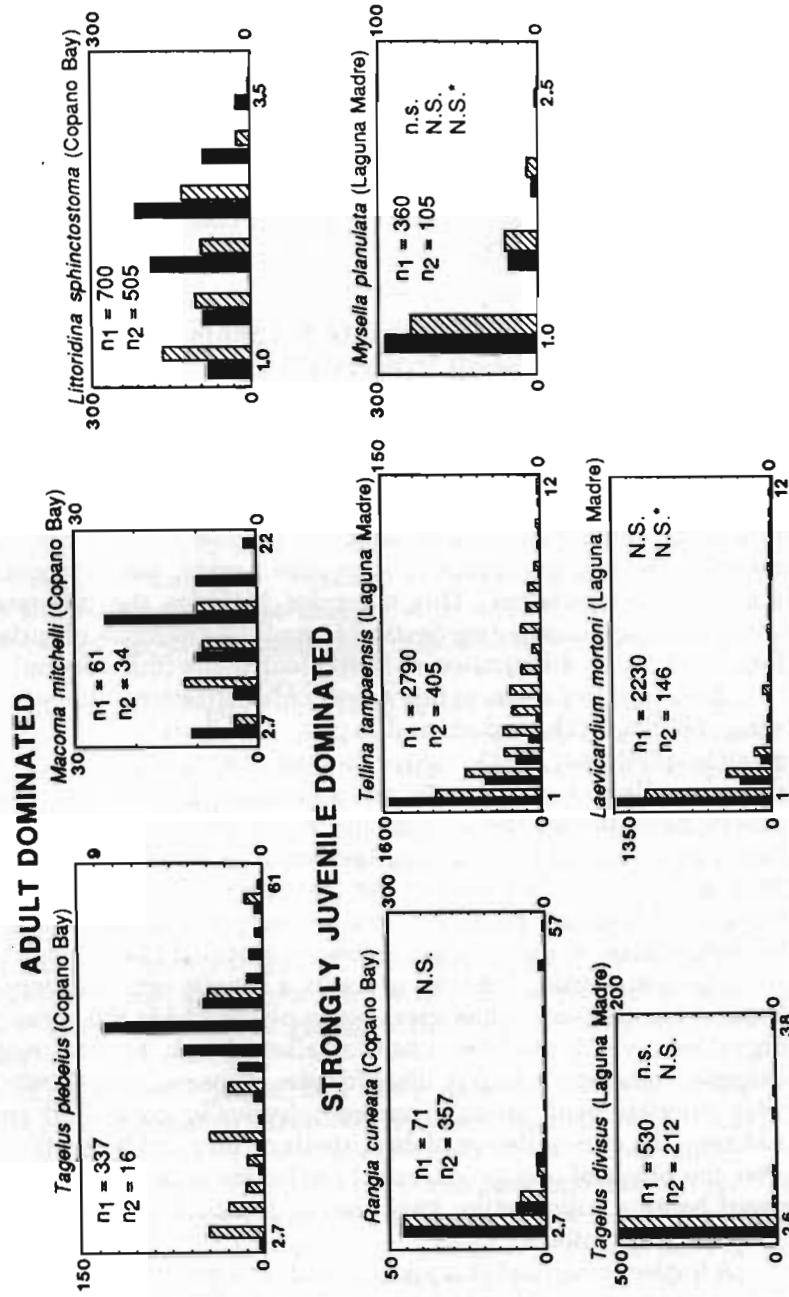
Death assemblages generally do not enter the permanent record without modification on the seafloor or within surficial sediment. Throughout this period, which can include repeated cycles of burial and exhumation, individual shells and the assemblage as a whole may acquire a taphonomic overprint related to various post-mortem agents, environments, and time scales of accumulation. This overprint includes the differential loss of species and age classes (see Section 3), and the alteration of surface features, form, and facies distribution of individual shells (this section).

Biostratinomy refers to this aspect of fossilization—literally, the embedding of biological hard parts and in particular their behavior as sedimentary particles (Seilacher, 1973, 1982a) [Weigelt (1927) originally coined the term more broadly to include death and soft-tissue decay]. Most biostratinomic studies have stressed the physical, primarily hydraulic, processes that act on carcasses and hard parts during the burial interval [see recent reviews by Brett and Baird (1986), Speyer and Brett (1988), Goldring (1990)]. Because these conditions are relatively easy to manipulate experimentally, bioclast behaviors have in some instances been quantified (see below).

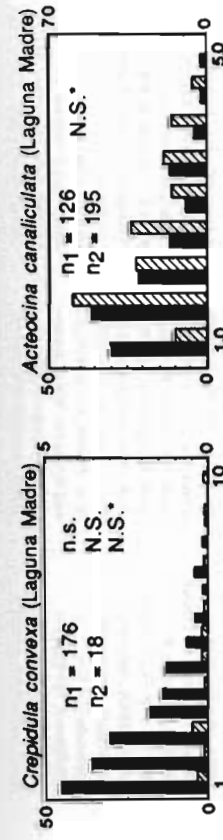
The post-mortem behavior of shells is usually not this simple, however, because biostratinomic histories commonly unfold in the presence of living organisms, which can bore, gnaw, swallow, break, encrust, reorient, bury, exhume, transport, trample, disarticulate, disperse, concentrate, and otherwise interfere with straightforward, physically controlled processes. In addition, the accumulation of dead shells on and just below the seafloor can alter the physical and geochemical environment and can influence subsequent benthic colonization [taphonomic feedback (Kidwell and Jablonski, 1983; Kidwell, 1991)].

A further analytical complication is that a given preservational state can reflect any number of life and post-mortem processes (Table VII), so that few unequivocal interpretations can be drawn in isolation. For example, high disarticulation might reflect high water energy, active scavenging, or general bioturbation of decayed carcasses. Future work should thus target

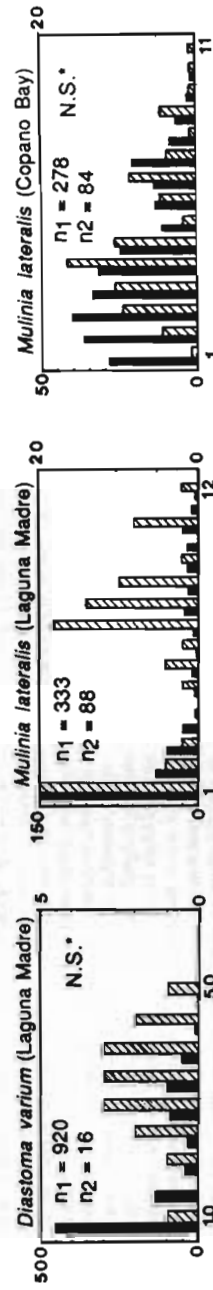




### Moderately Juvenile Dominated



### BIMODAL



**FIGURE 8.** Comparison of size-frequency distributions for shells supplied by mortality (histograms with diagonal lines) and shells observed in the locally accumulating death assemblage (black histograms) for 13 molluscan species in two Texas lagoons. Based on chi-square tests, which compare expected and observed values on a size-class by size-class basis, Cummins *et al.* (1986b) concluded that death assemblages provide poor records of mortality. However, the data suggest surprisingly good qualitative agreement in the shapes of the distributions, and a Kolmogorov-Smirnov test sensitive to curve shape indicates no statistical difference between expected and observed frequency distributions in about half the cases. n.s., not significant based on chi-square test of Cummins *et al.* (1986b); N.S., not significant ( $p > 0.05$ ) based on Kolmogorov-Smirnov test using all size classes; N.S.\*, not significant ( $p > 0.05$ ) based on Kolmogorov-Smirnov test excluding 1-mm size class;  $n_1$ , sample size of death assemblage;  $n_2$ , sample size of new additions (mortality during study period); ■, individuals in death assemblage (scaled on left axis); ▨, individuals/m<sup>2</sup> added by death during study period (right axis); mean size in mm (horizontal axis). [Adapted from Cummins *et al.* (1986b).]



TABLE VII. Origin of Biostratigraphic Features

	Behavior or ecology of shell producers	Behavior or ecology of other organisms	Physical, primarily hydraulic processes	Other seafloor processes	Postburial processes	Descriptive scales
Disarticulation	Autotomy among crinoids (Emson and Wilkie, 1980); molting (Speyer and Brett, 1985; Feldman and Tshudy, 1987)	Scavengers and predators (Meyer and Meyer, 1986; Lavoie, 1956); bioturbation? of buried carcasses	Transport or in situ reworking, particularly of decay-loosened skeletons (Menard and Boucot, 1951; Eager, 1978; Allison, 1986; Kidwell and Baumiller, 1990)	Collapse upon microbial decomposition of ligaments (Meyer and Meyer, 1986; A. B. Smith, 1984)	Compaction?	Meyer et al. (1989) (crinoids); Kidwell and Baumiller (1990) (echinoids)
Sorting	Single-cohort settlement (Levinson, 1970); gregarious adults (Waage, 1984; Speyer and Brett, 1985); remnants of anastrophic burial (Kranz, 1974a)	Selective destruction of invertebrate valves by predators (Carter, 1974); selection by tube-building worms (Recent <i>Diopatra</i> )	According to size, right-left differences, spines, perforation during transport (Kornicker et al., 1963; Martin-Kaye, 1951; Lever, 1958; Lever et al., 1961; J. B. Wilson, 1967; Bosence, 1976b; Martinell and dePorta, 1982; Aigner, 1985b); according to differential durability of skeletal parts to in situ reworking (Holland, 1988; Velbel and Brandt, 1989; Fürsich and Werner, 1989); settling rates from suspension (Middleton, 1967; Allen, 1984)		Preferential loss of small or aragonitic shells (Fürsich, 1982); preferential preservation of small shells by phosphatization	Kidwell and Holland (1991)
Perforation	Pre-mortem infestation by boring sponges, forams, bivalves, barnacles, etc. (Highsmith et al., 1983; Pisera, 1987; P. J. B. Scott, 1988; Smyth, 1988); complete abrasion of umbones and apices during life (Hollmann, 1968; Boyer, 1989; Schäfer, 1972)	Post-mortem infestation (C. M. Henderson and Styan, 1982; Akpan and Farrow, 1984, 1985; Nelson and Young, 1985; K. Vogel et al., 1987); hermit shell symbionts (Lambert and Boekschoten, 1986; S. E. Walker, 1988); boring and biting predators (gastropods, octopods, sharks, ichthyosaurs (Bishop, 1975; Alexander, 1986b; Mapes et al., 1989))	Mechanical "surf" breaks in bivalves, echinoids (Schäfer, 1972; Kidwell and Baumiller, 1990); interpenetration of telescoped nautilus and hyolithids (Tasch, 1955b; Yochelson and Fraser, 1973); localized abrasion (Pretje, 1929; Hollmann, 1968; Driscoll and Welltin, 1973)	Freshwater dissolution under holes in shell peristracum (Philippon and Piazzi, 1975)		Carrier et al. (1969); Bromley (1970); Ekdale (1985)

Fragmentation	Asexual reproduction of corals by "autotomy" (Karlson, 1986); weakening of mollusks and corals by borers (Bergman et al., 1982; Hutchings, 1986; P. J. B. Scott, 1988; Tunnicliffe, 1979; Turner, 1985)	Shell-crushing and ingestion by predatory crabs, fish, rays, etc. (Trewin and Welsh, 1976; Bertness and Cunningham, 1981; Bigelow and Schroeder, 1953; Alexander, 1986b; A. B. Smith, 1984; Hoskin, 1980); breakage on stones by otters, birds (Cadée, 1989; Hines and Pearse, 1982); bioturbation? by-product of bioerosion	Reworking of shells weakened by bioeroders; mechanical breaks in surf and high-energy situations (Hollmann, 1968); entrainment in coarse debris flows, crushed in interstices of boulder/gravel fields (Myers, 1981; S. M. Kidwell, unpublished observations, Recent and Pliocene)	Corrosion by fresh and cold waters before burial (Wiedemann, 1972; Alexander, 1972, 1978)	Compaction (Brenner and Einsele, 1976)	Hollmann (1968); Davies et al. (1989a); Pilkey et al. (1967)
Surface modification by abrasion, encrustation, and dissolution	Self-inflicted abrasion of umbones of acids, carditis (Hollmann, 1968; Boyer, 1989; Schäfer, 1972); normal wear of apices of limpets, other gastropods (S. M. Kidwell, unpublished observations, Recent); pitting by encrusting bryozoa, algae (Boekschoten, 1986; Cutler, 1987); reduction of ornamentation, creation of rasp marks by grazing limpets, echinoids, chitons, etc., during life of epifauna; symbiotic encrustation (Alvarez and Taylor, 1987)	Reduction in ornamentation by grazers, dulling of surface by micropitting encrusters and grazers on dead shells as on live, rounding by microboring and bacterial decomposition of stroma (Amerzone-Cominardi and Roux, 1987); drag marks on underside of hermit shells (S. E. Walker, 1988); partial to complete encrustation of dead shells by algae, bryozoans, corals, serpulids, etc. [both hermit and "rolling stone" colonies (Bishop, 1988; Ware, 1975; Balson and Taylor, 1982; Kissling, 1973; Taylor et al., 1989)]	Abrasive reduction and frosting on beaches (Cutler, 1987; Driscoll, 1967) and during lab tumbling (Chave, 1964; Driscoll and Welltin, 1973); impact craters on cobble beaches (S. M. Kidwell, unpublished observations)	Chalky textures from leaching in marsh and temperature marine sediments (Frey and Basan, 1981; Lewy, 1975; Meldahl, 1987a; Alexandersson, 1978); partial dissolution by acidic porewaters (Aller, 1982a); meteoric weathering (B. M. Walker, 1979)		Holland (1988); Pilkey et al. (1967, 1979); D. J. Davies et al. (1989a); Driscoll and Welltin (1973); Cutler (1987); criteria for pre- vs. post-mortem infestations: Baird et al. (1989); Sando (1984)
Orientation	Life orientation, escape postures, "death throes" (Stanley, 1970; Kranz, 1974a; Seilacher, 1984; Emig, 1986; Frey et al., 1987)	Modification by bioturbators, predators, scavengers (Salazar-Jimenez et al., 1982; Emery, 1968; Clifton, 1971); rearrangement by tube-builders and burrow back-fillers (Schäfer, 1972)	Modification by unidirectional or reversing currents, turbulent flow, redeposition, exhumation, detachment (of sessile benthos) (Moors, 1970; Müller, 1979; Raup, 1973; Seilacher, 1973; Brett and Baird, 1986; Wulff, 1990)	Orientation determined by morphology of trap (fishes, cobble interstices)	Rotation during compaction	Kidwell et al. (1986)

(continued)

TABLE VII. (Continued)

	Behavior or ecology of shell producers	Behavior or ecology of other organisms	Physical, primarily hydraulic processes	Other seafloor processes	Postburial processes	Descriptive scales
Transportation	Deposition of epifauna from floating weeds (Cadée, 1968; Bosence, 1979)	By hermit crabs (S. E. Walker, 1988; Shimoyama, 1985), birds (Cadée, 1989; Lindberg and Kellogg, 1982; Brun, 1971; Trewin and Welsh, 1976), fish and mammals (Schafer, 1972) in form of feces and epifauna; rafting on seaweed (Bosence, 1979; Cadée 1968); downslope "diffusion" by bioturbators (Bein and Fütterer, 1977)	Onshore, offshore, and longshore movement in coastal and near-shore marine zones; bulk transport on slopes including reef fronts (see Table IX); "wheeling" of ammonites in turbidity currents (Seilacher, 1963)	Post-mortem drift (Saunders and Spinosa, 1979; Reymont, 1986); ice-rafting (Spaldinaes, 1978; Aiken et al., 1988)		See terms in Table I
Exhumation	Epifaunal life habit; surfacing by moribund infauna (D. Nichols, personal communication in Aslin, 1968; Rosenberg, 1977; Steimle and Sinderman, 1978)	Hermits delay burial (S. E. Walker 1988); upward advection by bioturbators (McCave, 1988); excavation of infauna by predatory birds, rays (Carter, 1968; Gregory et al., 1979)	Erosional reworking by storms, currents, channel migration (van Straaten, 1952; Aigner, 1985a); seafloor or subaerial winnowing, bedform migration; exposure on seafloor prolonged by sediment starvation or bypassing (Akpan and Farrow, 1984; J. B. Wilson, 1988; Nelson, 1988)			Patterns of burial-exhumation cycles: Kidwell and Aigner (1985); Kidwell (1989)

Burial	Infauanal life habit	Backfill by burrowing infauna (Seibold et al., 1973); downward advection by bioturbators (Cadée, 1976; Meldahl, 1987b)	Passive infilling of burrows (Aller, 1982a; Wanless et al., 1987); anastrophic burial by storm or turbidite desposition (Peterson, 1985; Aigner, 1985a; Brett and Seilacher, 1991); bedform migration, burial to base of tractive carpet (Johnson, 1957)			
Concentration	Gregarious behavior of larvae or adults, dense opportunistic settlements (biogenic event-concentrations), reef and bioherm-forming behavior (composite concentrations)	Packrat behavior by crabs, nesting birds (Cohen, 1989; Teichert and Serventy, 1947); fecal and egested masses from predators, scavengers (Trewin and Welsh, 1976); feeding pit concentration by rays, ducks (Gregory et al., 1979; G. C. Cadée, personal communication); burrow construction and backfill (Hertweck, 1972; Seibold et al., 1973); concentrations for camouflage and antidissipation (Hart & Crowe, 1977); accretionary biogenic graded bedding (Cadée, 1976, 1979; Meldahl, 1987b)	Single-event concentration by storms, turbidites, channeled flow, bedform migration; composite shelly shoals, banks, washover fans; condensed hiatal beds produced by starvation or bypassing, associated with unconformities, flooding surfaces, condensed intervals; erosional lags (see references in Kidwell, this volume, Chapter 5)	Fissure and open burrow trapping of shell in transport (Seilacher and Westphal, 1971; Wanless et al., 1987)	Sorting and concentration by earthquake liquefaction (Bradley, 1957); preferential pressure solution of micritic matrix (Kidwell et al., 1986); diagenetic "extinction" of shells in intervening strata (Fürsich, 1982)	Aigner et al. (1978); Kidwell et al. (1986); Kidwell 1982, and this volume, Chapter 5)

development of diagnostic criteria for specific taphonomic processes at the level of both individual shells and whole assemblages, and (b) ranking the relative importance of different processes in a given environment and among environments. Essential to this work will be the development of standardized scales for describing shell condition (last column, Table VII).

This review stresses the implications of biostratinomic processes for the preservation of faunas. For reviews with fuller treatment of their geological applications, see Brett and Baird (1986), Speyer and Brett (1988; and this volume, Chapter 11), Goldring (1990), and Kidwell (this volume, Chapter 5). For a fuller review of the diagenesis of shelly assemblages, see Raiswell and Canfield (this volume, Chapter 9).

#### 4.1. Basic Patterns

In general, post-mortem modification is a function of the susceptibility of shells to a particular suite of processes and the length of time that shells are exposed to attack (Fig. 1). This susceptibility is largely inherent to the organism's life position and to the shape, size, mineralogy, microarchitecture, surface roughness, organic coats, and surface area (including porosity) of its hard parts. Consequently, it varies not only among major taxonomic groups, but among species of a single group, among different elements of a single skeleton, and among individuals at different points in ontogeny. Susceptibility can also be secondarily changed by taphonomic processes before final burial (e.g., size reduction by fragmentation, removal of periostracal coverings, early syntaxial overgrowths during temporary burial) and thus, like other major factors in the taphonomic equation (Fig. 1), it is a dynamic factor.

Both laboratory and field experiments have shown that individuals and assemblages alike suffer greater modification as the period of exposure to post-mortem agents is increased (e.g., references in Table VII). However, taphonomic damage need not be a direct function of an individual shell's age since death, because its exposure to post-mortem processes may be intermittent rather than continuous. Corrosion, for example, can characterize Recent as well as relict shells in shelf death assemblages (Nelson and Hancock, 1984), and isolated old shells may be in better condition than recently-dead shells (Powell and Davies, 1989; Flessa *et al.*, 1990).

This variability owes to several phenomena. One is that taphonomic agents themselves are not always relentless: both bioerosion and pore-water chemistry, for example, can be strongly seasonal (Aller, 1982a; Hutchings, 1986; Reaves, 1986). Second, shells can gain temporary refuge by burial or encrustation, which isolate the shell from some taphonomic agents. Temporary or permanent sanctuary from one set of post-mortem agents (e.g., from physical abrasion or undersaturated seawater at the seafloor) of course may merely expose the shell to another set [e.g., acidic pore waters in the shallow subsurface (Driscoll, 1970)]. Moreover, shells can undergo

several phases of modification related to burial-exhumation cycles and other environmental changes. Modification rates therefore probably vary during the history of individual shells and cannot readily be extrapolated from short-term experimental values; short-term values provide estimates of maximum rates. Shells do not attain true sanctuary from biostratinomic processes until final burial below the reach of bioturbation and storm reworking, at which time they enter the realm of later diagenesis.

Environments differ in their rates of shell supply and favorability for preservation, but a general correlation exists between shell condition and the short-term dynamics and net rate of sediment accumulation [for reviews see Kidwell, 1985, 1986a, and this volume, Chapter 5; Brett and Baird, 1986; Brandt, 1989]. Both continuous, rapid sedimentation and episodic deposition of thick sedimentary increments can speed the transit of shells through the biostratinomically active zone; this rapid burial favors good preservation. Conversely, slow net rates of sedimentation and repeated exhumation retard final burial, and increase the average exposure time of shells to surficial and near-surface taphonomic agents. This should lead to poorer overall preservation of the fossil assemblage, but not necessarily to a deposit with low abundance of shells, since low dilution by sediment promotes shell concentration and positive taphonomic feedback. In these ways the time-averaging, quality of shell preservation, and paleoecology of fossil assemblages may be linked (Kidwell, 1986a, and this volume, Chapter 5).




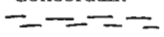

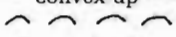

#### 4.2. Modification by Hydraulic Processes

##### 4.2.1. Reworking and Reorientation of Shells

Well-documented effects of hydraulic reworking include (a) sorting by size and shape, including right-left differences in pelecypods and brachial-pedicle differences in brachiopods (Table VII), (b) abrasive size reduction according to skeletal microarchitecture (Sorby, 1879; Force, 1969; Hoskin *et al.*, 1983; Greenstein, 1989a), and (c) reorientation into a variety of highly ordered fabrics. These fabrics include bedding-plane accumulations in which elongate elements are oriented parallel, transverse, or oblique to current, and matrix- and shell-supported fabrics in which bioclasts are concordant, oblique, or perpendicular to bedding [reviewed in Müller (1979), Kidwell *et al.* (1986), Goldring (1990)] (Table VIII).

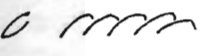


Well-ordered fabrics typically reflect steady or regularly varying flows (e.g., beach swash-backwash, tidal ebb and flood, subtidal wave oscillation), whereas poorly ordered fabrics reflect greater turbulence at the seafloor (Kellings and Williams, 1967), turbulent deposition of suspended shells (e.g., as observed in debris flows and some storm deposits and turbidites), or presumably bioturbation (Toots, 1965). Hydraulic reworking does not always result in convex-up orientations of bowl-shaped shells, and thus this is not a foolproof guide to water energy and "stratigraphic

TABLE VIII. Processes of Shell Orientation

Orientation	Hydraulic processes	Other processes
<b>PLAN VIEW</b>		
Unimodal 	Unidirectional current acting on shells (free or tethered) whose critical threshold velocities are lower than surrounding sediment; the more turbulent the flow, the greater the angular deviation (Kelling and Williams, 1967; Erickson, 1971; Brenner, 1976; Futterer, 1978a,b)	Rheotaxic life position (Frey <i>et al.</i> , 1987)
Bimodal 	As for unimodal patterns except reversing currents (wave oscillation, tidal ebb and flood); shell long axes aligned perpendicular to oscillatory current directions (Nagle, 1967; Kelling and Moshiriff, 1977)	Free-rolling <i>Oliva</i> when alive; rheotaxic life position in oscillating currents (Frey <i>et al.</i> , 1987)
No strong trend 	Flow velocities below or near critical threshold levels for shell movement (Bayer, 1978), OR sediment moves at lower velocity than shells, leading to shell burial without azimuthal reorientation (Futterer, 1978b), OR very turbulent flow conditions, OR interference among shells or between shells and other particles (Brenchley and Newall, 1970; Futterer, 1978b)	Life position (Allmon, 1988)
<b>CROSS-SECTIONAL VIEW</b>		
Concordant 	Redeposition of platey fragments and shells out of suspension, OR rotation during compaction, OR complete exhumation of vertically embedded infauna by gentle winnowing (Emig, 1986)	Life position (Stanley, 1970)
Concordant and convex-down 	Redeposition out of suspension, associated with turbidity and turbulent storm currents (Middleton, 1967; Futterer, 1978c; Allen, 1984), OR redeposition on leesides of migrating bedforms (Clifton and Boggs, 1970), OR overturning of hemispheric corals, etc. (Abbott, 1974), OR burial at sub-threshold velocities (Richter, 1942; Johnson, 1957; Futterer, 1978c)	Life position of concavoconvex brachiopods; bioturbation on seafloor (Emery, 1968; Clifton, 1971) and within sediments (Salazar-Jimenex <i>et al.</i> , 1982)
Concordant and convex-up 	Reorientation by currents on high-friction seafloor (Richter, 1942; Johnson, 1957; Futterer, 1978a)	Life position (Abbott, 1974)
Perpendicular 	Oscillatory wave and current action on abundant shells, interference effects for edgewise stacking (Grinnell, 1974; Sanderson and Donovan, 1974; Seilacher & Meischner, 1965), OR vertical embedding of nekton (Raup, 1973; Reyment, 1980)	Life position of solitary or clustered individuals (Papp, 1944; Frey <i>et al.</i> , 1987)

(continued)

TABLE VIII. (Continued)

Orientation	Hydraulic processes	Other processes
Oblique (30–60°) 	Interference effect of unidirectional or tidal current resulting in imbricate or shingled stack, with shells dipping up-current (Greensmith and Tucker, 1969; Futterer, 1978b; Seilacher, 1982b)	Life position (Alexander, 1986a)
Stacked 	Both convex-up and convex-down stacks are associated with storm-reworked concentrations; probably a result of interference among shells during transport (Kidwell <i>et al.</i> , 1986; Kidwell and Holland, 1989)	Life position of mutually attaching epifauna (e.g., anomiid bivalves)
No strong trend 	Turbulent stirring of seafloor (Greensmith and Tucker, 1969), OR rapid deposition out of high-density turbulent flows such as debris flows (Middleton, 1967), OR burial by sediment scour at subcritical velocities (Futterer, 1978b)	Life position (Allmon, 1988), OR bioturbation presumably (Elias <i>et al.</i> , 1987), OR biogenic graded bedding (van Straaten, 1956)

way-up." Moreover, organisms may be efficient rearrangers of shells on the seafloor and within the sediment (Tables VII and VIII), yielding both ordered and disordered fabrics. Biological influences thus must be ruled out before shell orientations are interpreted hydraulically. The association of well-ordered shells with physical sedimentary structures, textures, and/or hydraulically equivalent sediment often provides the best evidence in such situations.

Because hydraulic reorientation requires that shells be mobilized, the selective reorientation, flipping, and size sorting of shells in assemblages should permit paleocurrent velocities to be bracketed (Alexander, 1986a). For paleocurrent *direction* indicators to be reliable, the seafloor must be sufficiently firm for shells to move freely—that is, the threshold velocity for surrounding sediment must be higher than that for the shells—and so the most dependable measurements come from bedding plane surfaces where sediment dewatering has increased the internal "bed friction" of the sand or mud (Futterer, 1978c; Allen, 1984) and where there are few obstacles (e.g., other shells, low-amplitude bedforms). Flume studies by Futterer (1978a,b) illustrate the often surprising equilibrium orientations assumed by bioclasts, particularly when shells are in sufficient abundance to interfere with free-rolling behavior.

When the threshold velocity of surrounding sediment is lower than for shells, shells sink or rotate into the substratum by settling into scours formed around them. Appropriately oriented shells become traps for sediment in motion, further reducing the likelihood of shell transport and hastening shell burial to a lag position at the base of migrating bedforms (Johnson, 1957; Clifton and Boggs, 1970; Futterer, 1978a,b). Shells can thus be

hydraulically buried and concentrated without necessarily acquiring a "hydraulically stable" orientation [and see R. L. Watson (1971) for subaerial formation of shell lags]. Presumably, most shells on seafloors above fairweather wavebase are subject to such rapid burial [e.g., burial of 85% of dead shells within 21 days observed by Conover (1975)]. It should also be important wherever bedforms migrate more episodically in response to storms. In all cases, rates of shell burial should not be limited by the typically slow net rates of seafloor aggradation (centimeters per thousand years) that characterize level-bottom marine settings; nor should hydraulic concentration and burial of shells be limited to the rare, high-energy events capable of causing ecologically catastrophic slumps and sediment-laden plumes.

When flow exceeds shell threshold velocities, shells are set in free motion and may themselves create bedforms (see Kidwell, this volume, Chapter 5). Such hydraulic deposits include shell megaripples and trough concentrates on tide- and wave-dominated shelves (J. B. Wilson, 1986; Norris, 1986) and sheets of storm- or turbidity-emplaced shells (Meldahl, 1987a; Aigner and Reineck, 1982; Pilkey and Curran, 1986). Bioclasts will tend to be size- or shape-sorted according to their effective diameter [a function of size, aspect ratio, and density (Ruhrmann, 1971; Seibold *et al.*, 1973; Futterer, 1978c)]. When taxa differ significantly in hydraulic properties, size sorting may be misinterpreted as having an ecological rather than taphonomic origin (Westrop, 1986).

Although convex-up orientations pervade traction-dominated flow conditions (but shell orientations can be modified by organisms during slack flow; Table VIII), concave-up orientations are common in turbidites and other mass-flow deposits. Laboratory experiments (e.g., Middleton, 1967; Futterer, 1978c; Allen, 1984; Hesselbo, 1987) have shown that resuspended shells settle concave-up through both stagnant and moving water columns, and entrain suspended sediment and thus increase in effective mass during settling. Consequently, as the effective density of the fluid increases, so does the frequency of concave-up positions [23–40% in low-density flows, 50–69% in high-density flows (Middleton, 1967)], resulting in changing proportions of concave-up orientations [and of shell size (van Tassell, 1981)] within single beds. In the absence of bioturbation and tractive movement after settling, this diversity of concave-up, oblique, and vertical positions can be preserved (Jeffry and Aigner, 1982).

Because shells are often coarser than surrounding sediment, shell-rich bedforms and lags can have higher preservation potential than nonbioclastic deposits. This is a consequence of both the high threshold velocities of individual shells and the interlocking fabrics that bioclasts can assume. Such concentrations can armor sediments against subsequent erosion (Futterer, 1978a) and become basal "reference horizons" for the accumulation of complexly amalgamated coquinas (Seilacher, 1985; Kidwell and Aigner, 1985; Pickrill, 1985), thus increasing the preservation potential of shelly assemblages.

#### 4.2.2. Disarticulation and Fragmentation of Shells

These phenomena are commonly attributed to physical reworking and in particular to shell transport [e.g., the influential paper by Menard and Boucot (1951)], but until recently few systematic studies have been conducted on environmental differences and on the relative roles of physical and biological agents. In general, disarticulation should decrease with decreasing water energy, and in fact Eager (1978), S. W. Henderson and Frey (1986), and others have reported higher incidences of articulated dead bivalves in open-shelf relative to nearshore environments. Rapid burial and low-energy anoxic conditions are most frequently invoked to explain good preservation of articulated hard parts (Seilacher *et al.*, 1985).

Controlled laboratory studies indicate that disarticulation is not a simple function of water energy or distance of transport. Instead, it is strongly influenced by the life habit [e.g., epifauna are more prone than infauna (Callender *et al.*, 1990)], amount of connective tissue (Ruhrmann, 1971), and extent of organic decay before physical reworking (Schäfer, 1972; Meyer, 1971; Allison, 1986, 1990; Kidwell and Baumiller, 1990). Anoxia is relatively ineffective in preventing decay (Plotnick, 1986; Allison, 1988; Kidwell and Baumiller, 1990), but nonetheless favors preservation of articulated specimens by reducing biogenic reworking (Plotnick, 1986) and promoting early mineralization of organic connective tissues (Allison, 1986). By contrast, low temperature is very effective in retarding decay (Kidwell and Baumiller, 1990). Well-articulated specimens thus should preferentially occur in environments characterized either by frequent catastrophic burial [obstruction (Brett and Seilacher, 1991)] or by low temperature and anoxia.

Susceptibility to disarticulation is also governed by how skeletal elements fit together. For example, owing to their interlocking stereom, many echinoids fracture across plates rather than separate along plate sutures even after decay of connective tissue (A. B. Smith, 1984), and the hinges of many brachiopods must break before the valves can separate (Sheehan, 1978; Alexander, 1990). Pelecypods also vary in their tendency to disarticulate owing to phylogenetic differences in ligament size and type. If kept moist, the abductin-rich types of ligament apparently remain flexible almost indefinitely. For example, oysters from subtidal middens associated with the 18th century New Haven, Connecticut, town pier were still pliable when removed from the anoxic harbor mud in the 1960s (K. M. Waage, personal communication). Butterflied scallop shells dredged from shelf fisheries, and laminated silt fills in articulated infaunal bivalves [Fig. 7 in Kidwell (this volume, Chapter 5); see Holland (1988) for brachiopod examples] indicate that individuals can survive exhumation and exposure even on current-swept seafloors without disarticulation.

For fragmentation, waves and currents are most effective when they act against anvils such as hard-packed sand, gravel, or bedrock (Hollmann,



1966). These conditions yield distinctive "surf breaks" in thin convex shells (a single hole punctured in the arc of the shell or hollow test) and impact-cratered surfaces on thick-shelled specimens. Because of the cushioning effect of water, this method of mechanical fracture is more common in beach than in subtidal settings. Alternatively, shells can be pulverized among mobile gravel (Myers, 1981) or broken by water after becoming wedged in fissures. Much fragmentation may be biogenic rather than hydraulic in origin (e.g., Cadée, 1968; J. B. Wilson, 1967; Trewin and Welsh, 1976; Bosence, 1976a; Meldahl and Flessa, 1990), but data are sparse on the proportional contribution or environmental trends (see biological effects below, Section 4.3).

Small, light shells can be entrained in turbulence and literally float on the surface or above the benthic boundary layer (D. W. J. Bosence, personal observation), and thus might suffer disproportionately less damage from hydraulic processes than will larger shells. Certainly, large, thin shells (length:thickness  $\geq 10$ ) require significantly lower stresses to fracture (S. Vogel, 1988). Older shells are more sensitive to stress than are new (recently dead) shells: bivalve shells lose mechanical strength as they dry out (Currey, 1980) and even when held in seawater [up to 50% strength loss in the bivalve *Donax variabilis* within 3–4 days (M. LaBarbera, personal communication, June 1990)]. Resistance to fracture also varies with skeletal microarchitecture. Among mollusks, nacre is strongest under virtually all conditions (tension, compression, impact); prismatic structures are the most flexible and cross-lamellar the least; foliated structures are least able to withstand compression (Taylor and Layman, 1972; Currey, 1980, 1988). All of these observations suggest preservational bias as a function of size, age at death (proportion of mineral and organic phases may vary ontogenetically), phylogeny, and time between death and stress.

#### 4.2.3. Shell Transport: The Question of Spatial Fidelity

Out-of-habitat transport of shells is a major concern for paleontological interpretation. However, field and experimental studies indicate that mass (or bulk) flow is the most effective mechanism of transporting shells in large abundance or over great distances, so that allochthonous assemblages are most common in steeply sloped or episodically high-energy settings (Table IX). These deposits, such as storm- and tidal-surge washovers, turbidites, and slumps, are usually identifiable by their distinctive sedimentary structures and facies context, and the resulting predominantly allochthonous assemblages commonly occur in the form of concentrations. These may (but do not always) exhibit good size sorting of shells; shell orientations and concentrations typically are closely related to physical sedimentary structures.

In contrast, out-of-habitat transport is much less important in level-bottom sublittoral environments (Table IX). The literature suggests that: (a) most lateral movement is within-habitat [this is corroborated by the facies-

level fidelity of death assemblages seen in Tables II–IV (Zenetos, 1990)]; (b) most exotic shells are derived from immediately adjacent habitats; (c) tractive transport is highly selective, affecting noncemented epifauna, small, thin shells, and shallowest-burrowing infauna in particular (van Straaten, 1956, 1960; Cadée, 1968; Shuto, 1973; Bosence, 1979; Aigner and Reineck, 1982; S. W. Henderson and Frey, 1986; Knight, 1988; Kondo, 1989); and (d) even when exotic shells account for a large percentage of species, they often comprise a minority of individuals in the assemblages that receive them ( $\sim 10\%$ ; Tables II–IV). Data in Tables II–IV on the proportions of "dead only" taxa are maximum estimates of exotic (i.e., out-of-habitat) species: some of these "dead only" taxa are indigenous but were not sampled live because of patchy and/or episodic distributions, whereas others are mixed from local relict deposits (Sarnthein, 1971; Cadée, 1984a; S. W. Henderson and Frey, 1986).

The level-bottom settings with the largest exotic component seem to be those adjacent to habitats with abundant epifauna or epiphytic communities subject to rafting (Table IX). These exotic species will in some instances constitute distinctive trophic groups not otherwise represented in the recipient (soft-bottom) assemblage. Knowledge of the basic ecology of fossil taxa and of the regional facies context of the assemblage is thus of great help in anticipating the likely abundance and source of exotic elements.

While out-of-habitat transport is rare, it is obvious [and quantifiable (Cummins *et al.*, 1986c)] from the few shells preserved in life positions that small-scale, within-habitat movement of shells is extremely common. The critical question for paleontologists is the extent to which this small-scale movement limits the detail in which ecological variation in species abundance can be interpreted from the fossil record: how much of the original gradient in community composition (e.g., Fig. 2) is smeared by post-mortem disturbance of shells? That is, what is the precise spatial fidelity of shell material and how does this fidelity vary among environments?

As discussed in Section 3, analyses of Recent level-bottom assemblages have repeatedly demonstrated (a) the nonrandom distribution of dead shells, (b) their association with benthic communities of similar composition, and (c) the significant association of both live and dead with distinct habitats (i.e., lithofacies; Tables II–VI). The basic loyalty of death assemblages to life environments applies not only to generally low-energy, protected settings (Ekdale, 1977; Peterson, 1976; A. I. Miller, 1988) but also to many persistently high-energy settings such as macrotidal flats (Fürsich and Flessa, 1987; Meldahl and Flessa, 1990) and tide-swept shelves (Holme, 1961; J. B. Wilson, 1986; Carthew and Bosence, 1986). In fact, 75 years ago Kindle (1916) used a live:dead comparison of benthos from the macrotidal Bay of Fundy to prove that post-mortem transport does not homogenize death assemblages, and argued that fossils were reliable for paleoenvironmental interpretation even in such high-energy settings.

This correspondence indicates that net movements of shells in level-bottom settings are generally small compared with the time-averaged spatial

TABLE IX. Evidence for Out-of-Habitat Transport of Shells in Recent Marine Environments<sup>a</sup>

Setting	Direction, mechanism, and distance of shell transport	Selectivity of transport; net effect on assemblage at depositional site
Supratidal to nearshore		
Mesotidal estuarine sound, inter- and supratidal flats; Georgia (Wiedemann, 1972)	Onshore storm-surge transport and concentration of shells from intertidal flats and sound into beach ridges, cheniers, and washover fans on the supratidal marsh surface and marsh edge Offshore storm transport of rocky shore fauna onto adjacent tidal flats [distance of 3.7 km (M. K. Watson and Flessa, 1979)]	Preferential transport of oysters relative to other epifauna and infauna; resulting assemblages composed predominantly of exotic species Transport of epifauna (unspecified taxa or proportion of fauna); minor effect—resulting assemblages composed predominantly of indigenous species Resulting assemblage composed of 100% exotic shells
Macrotidal flats; northern Gulf of California (M. K. Watson and Flessa, 1979; Fürsich and Flessa, 1987)	Onshore storm and longshore fair-weather transport of shells from tidal flat, formation of high-tide beach and spit	
Macrotidal coast; northern Gulf of California (Meldahl, 1987a)	Onshore movement of shells from nearshore shelf onto open beach (2 spp.), into tidal inlet (5 spp.), and onto lower flats (3 spp.); no spp. transported as far onshore as inner flats	Of the 10 exotic species, all are small infaunal bivalves ( <i>Spisula</i> , <i>Donax</i> , <i>Angulus</i> , etc.)
Mesotidal flats; Wadden Sea, Netherlands, and Bay of Arachon, France (van Straaten, 1956)	(1) Onshore from flats to concentrations along edge of salt marsh; (2) Offshore from flats to floor of tidal channels; few km maximum transport	Data for transport of <i>Cerastodoma edule</i> only
Mesotidal flats; Wadden Sea (Kristensen, 1957)	Onshore transport of shell fragments from nearshore shelf to inner? flats	Spines and broken plates of the fragile infaunal echinoid <i>Echinocardium</i> ; exotic specimens are minor component of assemblages
Macrotidal flats, strong currents; Solway Firth, Scotland (J. B. Wilson, 1965)	(1) Offshore transport of small shells from sandflats to tidal channel; (2) onshore transport of large shells to mudflats by hermit crabs	Study limited to single species of trochid gastropod ( <i>Umbonium</i> )
Mesotidal inlet with strong currents, associated flats, and open beach; Kyushu, Japan (Shimoyama, 1985)	Onshore transport of shells from intertidal flats to adjacent supratidal areas by birds; maximum distance 8 km	No size selection in transport of <i>Mytilus</i> or <i>Cerastoderma</i> by Oystercatchers; size-selective transport and smashing of large <i>Mytilus</i> by Herring Gulls; supratidal accumulations are 100% exotic
Mesotidal flats; Wadden Sea, Netherlands (Leopold et al., 1985; Cadée, 1989)		
Supratidal; southeast Farallon Island, California (Lindberg and Kellogg, 1982)	Onshore transport of shelf species to supratidal rookeries by diving birds that prey upon molluscivorous fish	No data; supratidal accumulations are 100% exotic
Supratidal; Western Australia (Teichert and Serventy, 1947)	Onshore transport, presumably by Pacific Gulls, of shelly epifauna from exposed offshore "reefs" to rock ledges of 0–70 feet elevation	Opercula and broken shells of <i>Turbo</i> most common, plus small patellid gastropods and chitons; 100% exotic
Supratidal; Alacran Reef, Mexico (Wright and Kornicker, 1962)	Onshore transport of dead shells from beach to supratidal nesting sites by birds	Nesting material determined by availability of dead specimens (none are food items); selection against coral; assemblages are 100% exotic
Mesotidal flat; Essex coast of North Sea, England (Green-smith and Tucker, 1966, 1969)	Onshore flood-tide transport of estuarine channel species into stable banks at low-water mark, then movement onto upper flats and mobile cheniers at marsh edge; shells moved over several km	No data; bivalve <i>Cerastoderma</i> dominates (ca. 70% of individuals in subtidal banks, 50–90% in cheniers)
Mesotidal flats and adjacent shelf, to 40 m depth; Liverpool Bay, Irish Sea (Lingwood, 1976)	(1) Onshore transport from subtidal (0–40 m) to intertidal flats (46 spp.) (2) Offshore transport from intertidal (8 spp.) or from nearshore (4 spp., 0–10 m) to deeper subtidal	None apparent; exotic spp. include epifauna, interstitial forms, borers, and both shallow- and deep-burrowing infauna; exotics outnumber indigenous spp. in intertidal (46:8), but represent <10% of subtidal diversity No data
Normal salinity lagoon; Mauritania (Einsele et al., 1974)	Onshore transport of shells from lower intertidal and subtidal parts of bay and of eelgrass epibionts into strandline concentrations; all transport is within bay	(1) Epiphytic gastropods; exotic individuals = 1% of bay assemblage; (2) rocky shore epifauna, especially <i>Mytilus</i> , which alone comprises 10% of shelf death assemblage
Mesotidal estuary and open shelf, both with rocky shoreline; Ria de Arosa, Spain (Cadée, 1968)	(1) Offshore transport by weed drift from rocky margin to subtidal central bay; (2) no transport detectable within central bay; (3) offshore transport of shallow-water epifauna to open shelf	(1) small gastropods?; (2) small (<2.5 mm) bivalve <i>Corbula</i> ; (3) small shells ( <i>Gibbula</i> , <i>Hydrobia</i> , <i>Cerastoderma</i> , <i>Abra</i> )
Low-energy, microtidal shoreline and shelf; Rhone Delta, France (van Straaten, 1960)	(1) Downstream transport of land and freshwater spp. to lagoon, less commonly to beach and to nearshore; (2) transverse mixing within nearshore zone above fair-weather wave base; (3) longshore transport within the nearshore zone; several km movement; (4) no transport on Rhone shelf beyond nearshore zone; little difference between live community and death assemblage	

(continued)

TABLE IX. (Continued)

Setting	Direction, mechanism, and distance of shell transport	Selectivity of transport; net effect on assemblage at depositional site
Mesotidal beach; Georgia (Dörjes et al., 1986)	Onshore transport of some shells from nearshore shelf to beach; few if any shells in beach assemblage were derived from back-barrier environments, none originated from middle to outer shelf	No data
Mesotidal, ebb-dominated tidal inlet channel, estuary and adjacent shelf; Georgia (S. W. Henderson and Frey, 1986)	(1) Onshore transport of 4 spp. from shelf to estuarine sound via tidal inlet channel; (2) no offshore transport from sound or inlet channel to shelf; all spp. in shelf dead assemblages are from spp. reported living there, although some dead may be older relicts	(1) All transported spp. are small, thin-shelled infauna ( <i>Parvilucina</i> , <i>Pleuromeris</i> , <i>Spisula</i> , <i>Tellina</i> ); exotic shells account for 11% of spp. and 10% of individuals in sound death assemblage
Open and embayed shelf		Unspecified mollusks
Nearshore; Kattegat Channel of east Denmark, and Faeroe Island off Iceland (Johansen, 1901, cited by Cadée, 1968)	Both onshore and offshore transport within the 0-15 m depth nearshore zone; the more protected the coast, the narrower the zone of tranverse mixing	
Nearshore and offshore zone (to 15 m depth) along mesotidal, low-energy open coast; Georgia (Frey and Howard, 1986)	(1) Onshore movement of some offshore shells into nearshore area; (2) no transport offshore; offshore assemblages composed of offshore shells only	No quantitative data
Macrotidal open marine embayment, storm-influenced; Helgoland Bight, North Sea (Aigner and Reineck, 1982)	Offshore storm transport of shells from tidal flats and inlets: (a) common to shoreface sands; generally within 10 km of low-water mark (b) less common to 7-15 m transition zone between shoreface and self muds (proximal tempestites; within 15 km of low-water mark) (c) rare transport to shelf mud areas (distal tempestites)	(a) Mixed fauna of indigenous and allochthonous spp.; (b) most shells are from indigenous spp.; exotic species are thin-shelled borers ( <i>Barnea</i> , <i>Petricola</i> ) from channels and small intertidal specimens (infaunal <i>Cerastodoma</i> and epifaunal <i>Littorina</i> , <i>Mytilus</i> , <i>Hydrobia</i> ); (c) virtually all shells from indigenous spp. Transport is quantitatively "insignificant"; spp. that dominate living communities are reflected in distribution of dead
30-75 m deep tide-swept channels in 10-20 m deep open marine embayment; Kiel Bay, North Sea (Arntz et al., 1976)	Downslope movement of shells onto channel floors where concentrated	

Macrotidal open marine embayment; Mannin Bay, Ireland (Bosence, 1979)	Offshore transport by weed-drift and storm back-surge from rocky shore to sublittoral soft-sediment seafloors; 1 km maximum	Epifaunal gastropods ( <i>Patellidae</i> , <i>Littorinidae</i> , <i>Rissoidae</i> )
Current-swept pass and open shelf; Sound of Jura and edge of Irish Sea, Scotland (Brown, 1979, reported in Akpan and Farrow, 1984)	(1) Onshore transport from 8 m depth onto shore; (2) offshore transport from intertidal to 46 m depth, both by wave-induced currents	(1) "Sublittoral dead shells observed on beach"; (2) small epifaunal gastropods <i>Patella</i> and <i>Littorina</i> ; no information on relative importance of exotic spp. in death assemblages
Meso?tidal estuaries and open shelf; Firth of Clyde, Firth of Lorne, Orkney Shelf, Scotland (Akpan and Farrow, 1984)	(1) Transverse transport confined to <5 m water depth in sheltered estuary but extends down to $\geq 12$ m depth in less sheltered parts of shelf; (2) no transport on sheltered parts of shelf; (3) ambiguous evidence of transport on exposed parts of shelf exposed to high wave energy and strong tidal currents	(1) Epifaunal gastropods <i>Patella</i> and <i>Littorina</i> , fragments of bivalves; (3) large numbers of polished shells locally, but could be produced by passage of sandwaves
Backreef sand and mud embayment, Salt River Bay, Virgin Islands (A. I. Miller et al., 1990 and A. I. Miller, personal communication, 1990)	Onshore transport of dead shells from shallow sandy habitats into slightly deeper "muck pit" mud habitat during Hurricane Hugo; lateral displacement tens of meters	(1) Prestorm assemblage had 8/14 spp. exotic, = 7% of dead individuals; (2) post-storm assemblage had 21/27 spp. exotic, accounting for 20% of dead individuals, all from nearby sands
Other settings		
Fringing reef and foreereef slope to 75 m, subject to hurricanes; Discovery Bay, Jamaica (Boss and Liddell, 1987)	(1) Minimal differential transport of bioclasts across reef and backreef lagoon; transport from reef framework into adjacent sand channels; (2) limited downslope (off-reef) transport of bioclastic sand on foreereef escarpment and lower foreereef slope (>14 m depth); possibly storm-driven	(1) Good agreement in relative abundance of species found alive and in nearby sand-sized sediments; (2) assemblages contain minor quantities of shallow-water grain types
Carbonate bank and slope to 600 m; Bahamas (Hoskin et al., 1986)	Downslope transport of bank-edge fauna as bedload in chutes to 45 m, then by-pass wall for deposition on mud apron below 120 m	Mollusk grains up to 1 cm diameter are transported up to 2 km offshore
Microtidal deep marine embayment, with rocky shore, narrow shelf and deep basin to 50 m; Bay of Naples, Adriatic Sea (Holliman, 1966)	(1) Downslope transport of surf-zone shells to 50 m depth by gravity and return flow of surf; slumps transport shells offshore to basin floor; (2) no landward or long-shore transport; most shells are destroyed in surf zone	Fragments of epifauna broken in surf zone; Bursa

(continued)

TABLE IX. (Continued)

Setting	Direction, mechanism, and distance of shell transport	Selectivity of transport; net effect on assemblage at depositional site
Continental slope, to 615 m; Adriatic Sea (van Straaten, 1967)	Downslope transport by turbidity currents(?) of shallow-water benthos to 615 m, where mixed with indigenous but fragmented benthos and plankton	Exotic <i>Bitium</i> , <i>Turritella</i> , and <i>Macra</i> reworked from relict Pleistocene; mixed with diverse indigenous epifaunal assemblage (no quantitative data)
Microtidal lagoon, beach, and deep borderland basin, to 2000 m depth; San Pedro and Catalina Island area, California (A. Clark, in Natland, 1957)	(1) Onshore transport from shelf to nearshore and beach; (2) offshore, downslope transport from beach and nearshore to deeper shelf	(1) Transport limited to 3 spp. ( <i>Bursa</i> , <i>Conus</i> , and <i>Lucina</i> ), rare individuals; (2) transport limited to 6 spp. (epifauna and shallow-burrowing infauna); total tabulated molluscan fauna = 225 spp.
Submarine canyon and continental rise; Atlantic continental margin, North Carolina (Pilkey and Curran, 1986)	Downslope, offshore turbidity-current transport of relict, estuarine and shallow-marine shells from middle? or outer? shelf deposits to 500 m depth on abyssal plain; 500-km lateral transport ("Black Shell Turbidite")	Exotic specimens dominated by $\leq 1.5$ -cm <i>Mulinia</i> and <i>Nassarius</i> ; final assemblage is presumably entirely allochthonous in composition
Continental shelf, slope, and rise; northwestern Africa (Bein and Fütterer, 1977)	Downslope transport of relict shells from shelf to slope and basin by actions of benthic organisms, which resuspend and inject sediments into overlying water, redeposition deeper on slope	No data
Deep sea; western Pacific Ocean (Saunders and Spinosa, 1979)	Pelagic drift of dead <i>Nautilus</i> from Palau (Caroline Island) to northern Philippines; 1000 km transport in 138 days (contrasted with up to 150 km in 332 days when alive); beach strand deposits?	Nektonic cephalopods

\*Most hydraulic transport removes shells only to adjacent habitats and selects for small specimens and/or epifaunal species; exotic species are usually only minor components of recipient assemblages. The major exceptions are transport by mass-flow processes associated with steep gradients (long-distance transport of entire assemblages is possible) or unusual surge conditions (large quantities of shells typically moved short distances) and transport by predators (small quantities, highly localized deposits); exotic shells typically dominate these assemblages.

range of live individuals. A. I. Miller and Cummins (1989, 1990), for example, found that physically and ecologically discrete habitat patches 10 m wide (seagrass beds) and 50–60 m wide (sandy areas) were readily detected by abundance changes in death assemblages in back-reef areas of St. Croix (also see Masse *et al.*, 1989). Smaller-scale, within-habitat ecological variability was not detectable in death assemblages, but presumably had been smeared by limited transport and temporal patchiness in benthic settlement. Spatial resolution on the low-gradient macrotidal flats of Cholla Bay, Mexico (Fürsich and Flessa, 1987) is on average coarser (five assemblage types can be discriminated across a 3-km shore-to-sea transect; habitat patches range from 10 m to hundreds of meters), but local peaks in live abundance of some species are often matched by peaks of dead individuals. On the hurricane-stirred Texas continental margin, high-fidelity death assemblages distinguish three habitats [a 15-km-wide inner shelf, 100-km-wide middle shelf, and 25-km-wide outer shelf (S. E. Walker *et al.*, 1989)]. Death assemblages thus commonly show good fidelity to life habitat, and the spatial resolution of these assemblages varies from very fine in very patchy shallow-water settings (on the order of tens of meters) to much coarser on more homogeneous open shelves (tens of kilometers to 100 km).

Experiments on hydraulic transport generally corroborate inferences from live:dead studies, although complex relationships abound. For example, J. B. Wilson (1967) found that under identical conditions small shells (10–14 mm) of *Cerastoderma edule* were rapidly buried, larger specimens (14–17 mm) were transported, and the largest specimens (17–24 mm) were slowly buried. Cain (1968) suggested that crinoid ossicles undergoing aerobic decomposition have different hydraulic behaviors than those under anaerobic decomposition, owing to differences in specific gravity.

Shell transport by organisms [see review by Boucot (1981, p. 333)] and passive post-mortem drift of carcasses are less well-appreciated mechanisms but highly significant for some environments and groups (Tables VII and VIII). Although rare instances of post-mortem drift have been documented for benthic organisms (Reyment, 1986), greatest drift has been documented for cephalopods. Saunders and Spinosa (1979), for example, documented 1000 km of drift among Recent *Nautilus*, underscoring the potential of taphonomic processes to increase the biostratigraphic utility of some groups (Kennedy and Cobban, 1976). Propensity for drift among cephalopods depends upon shell form, rate of epizoan growth, and mode of death (Kennedy and Cobban, 1976, and references therein; Hewitt, 1988; Donovan, 1989).

#### 4.3. Modification by Other Organisms

Many features conventionally attributed to physical processes can be created or mimicked by biological processes (Table VII). These processes include the ecology of the shell producer, the effects of duraphagous



predation and pathological infestations by endobionts, and an array of post-mortem live:dead interactions. Many live:dead interactions reflect highly selective behavior [e.g., species- and surface-selective settlement of bryozoa on dead bivalves (Bishop, 1988, 1989; Ward and Thorpe, 1989)] and possibly obligate behavior in some cases [e.g., deep-sea limpets that graze exclusively on dead squid beaks, fish, and whale bones (Hickman, 1983; Marshall, 1987)]. Other organisms select dead substrata more opportunistically on the basis of size or shape [e.g., choice of shell domiciles by hermit crabs and octopods (McClintock, 1985; Mather, 1982; Iribarne, 1990), choice of camouflage/stilt shells by *Xenophora* spp. (Ponder, 1983)], whereas still other live:dead interactions seem to be nothing more than post-mortem bad luck. This latter category would include dead shells exhumed by bioadvection (McCave, 1988; Oliver *et al.*, 1985) or inadvertently crushed by durophagous crabs (S. E. Walker, 1988) and rays (Gregory *et al.*, 1979) (Table VII). Schäfer (1962, 1972) noted many of these factors in his North Sea studies, but few have been thoroughly examined or had their importance quantified in different environments.

Recent shelly deposits commonly show both bioerosion and biofragmentation (J. B. Wilson, 1967; Cadée, 1968; Trewin and Welsh, 1976; Bosence, 1979; P. J. Davies and Hutchings, 1983), but the importance of these processes relative to physical ones is poorly known (but see Meldahl and Flessa, 1990). Wignall and Myers (1988) make a good argument for exclusively biogenic fragmentation in Jurassic mudstones where they found a consistent correlation between fragmentation and bioturbation. Compared with organic-rich laminated shales, the organic-poor bioturbated mudstones contain higher-diversity shell layers with extensive fragmentation, suggesting that fragmentation was linked with oxygenation and thus with improved access to benthic prey by predators. Extensive fragmentation is not correlated with coarser-grained layers such as would be expected had fragmentation been hydraulic or the shells exotic.

Bioturbation is a commonly invoked agent of post-mortem modification of shelly faunas and is thought to have multiple effects, but none has been adequately tested. Bulldozing species are thought to disarticulate and rotate shells within the sediment, yielding random orientations (Toots, 1965; Brett and Baird, 1986). In our separate studies of shell gravels, however, we have encountered many shallow-water accumulations with large proportions of concave-up shells, suggesting that predators and bioturbators might preferentially create concave-up rather than random fabrics within the sediment (also see Salazar-Jimenez *et al.*, 1982). Concave-up orientations on the seafloor have been attributed to "flipping" by scavengers (Emery, 1968; Clifton, 1971; J. B. Wilson, 1986) [but see Callender *et al.* (1990), who postulate that this is an artifact of human fishing activity].

Other postulated effects of bioturbators on the preservation of shelly fauna are fragmentation (Knight, 1988), dispersion of small-scale concentrations (Kidwell, 1986a), and burial +/- concentration of shells by subsurface deposit feeders (van Straaten, 1952; Rhoads and Stanley, 1965;

Trewin and Welsh, 1976; Cadée, 1976; Meldahl, 1987b). None of these effects has been tested in aquaria or under controlled field conditions. The only rigorously tested relationship between bioturbation and shell preservation is that sediment irrigation by macrobenthos can increase dissolution rates (Aller, 1982a; Raiswell and Canfield, this volume, Chapter 9).

Predators and scavengers are responsible for an undetermined amount of shell breakage, disarticulation, and dispersion. Organisms that exhume shelled infauna expose these shells to post-mortem conditions on the seafloor that they might otherwise have avoided, and some predators are capable long-distance transporters (Tables VII and IX). Digestive acids presumably accelerate destruction, as may organic coating of egested and defecated material. Such coats may make shells more attractive to microbial communities and thus to rasping grazers [see discussion in Scoffin (1987, p. 65)]. Coralline algal coats, on the other hand, seem to significantly reduce shell damage by borers (Smyth, 1989).

Algal and other organic coatings do not necessarily seal the post-mortem fates of exposed shells. For example, Cutler (1989) found that a critical density of dead shells is required to support a community of grazers; at subcritical densities, shells escape attack and thus have significantly higher likelihood of preservation. Organic coatings might actually enhance preservation potential by sealing shell carbonate from ambient, corrosive waters (Henrich and Wefer, 1986), much as periostraca protect freshwater mollusks from dissolution before death (Philippon and Plaziat, 1975; Hunter, 1990). Many encrusting organisms may actually strengthen dead shells (Stachowitsch, 1980).

Bioeroders attack live and dead shell material alike, although some are highly selective. Endobionts (boring fungi, algae, sponges, barnacles, bivalves, echinoids, various worms, bryozoa) perforate shells, thereby reducing shell strength and increasing surface area exposed to abrasion, dissolution, and maceration [see review by Young and Nelson (1988)]; raspers alter the shell surface, exposing shell layers more susceptible to dissolution (Table VII). Encrusters and other epibionts with penetrating attachment structures [e.g., lichens, byssate bivalves, foraminifera (Boeckh, 1966; Poag, 1969)] might also hasten destruction. Measured rates of sediment production by bioeroders in carbonate habitats vary from 0.2 to 16 kg/m<sup>2</sup> per year (Scoffin, 1987), indicating the very large amounts of carbonate that can be removed by these processes [often equal to biogenic carbonate production (e.g., Bak, 1990)]. Some of these organisms produce distinctive shell damage (e.g., clionid and spionid borings, crab peel marks, whelk chips, bird attack), but not all fragments of such activity are diagnostic and many organisms generate as yet unrecognizable debris (especially predators that ingest and internally crush shells). Even distinctive fragments and perforations become nondescript with further breakage and bioerosion, until physical disintegration is so complete that the shell is unidentifiable (Adjas *et al.*, 1990).

The extent of shell damage by borers and encrusters and their frequency



within an assemblage are usually interpreted as proportional to exposure time on the seafloor (e.g., Driscoll, 1970); this is one criterion among many commonly used to infer net rates and dynamics of sediment aggradation (Kidwell and Aigner, 1985; Brett and Baird, 1986; Brandt, 1989; Kidwell, this volume, Chapter 5, Section 3.1.1). However, not all infesters leave an identifiable skeleton or trace (some encrusters leave only vague attachment scars; Cutler, 1987), and infesting groups vary in abundance along depth and salinity gradients and over ecological time (Lawrence, 1969; Budd and Perkins, 1980; Scoffin *et al.*, 1980; P. J. Davies and Hutchings, 1983; Akpan and Farrow, 1984, 1985; Hutchings, 1986; Kobluk and van Soest, 1989; Sammarco and Risk, 1990; Günther, 1990). Inferences on relative periods of exposure thus should only be made among samples from similar environments.

Taphonomic damage must be distinguished from damage incurred while the host was alive. Infested interior surfaces of shells or of any surface thought to have been covered by soft tissues during life are the most reliable evidence. Exterior surfaces of infauna as well as epifauna may be infested during life, particularly the posterior margins of shallow-burrowers (Schäfer, 1972; Hertweck, 1979; Peterson, 1983). The distribution and orientations of infesters may in some instances be used to distinguish between life and post-mortem attack (Seilacher, 1969, 1982b; Sando, 1984; Elias, 1986; Baird *et al.*, 1989).

Some further caveats may be made on the biostratigraphic influence of living organisms.

(a) Some encrusters and borers can thrive below the sediment surface, particularly within coarse rubbly deposits (Scoffin and Henry, 1984), and thus shell modification does not always cease with "burial."

(b) Many encrusters prefer cryptic areas on the undersides of shells as a means of avoiding competition with algae and rasping organisms (Bosence, 1979; Jackson, 1977; Ward and Thorpe, 1989; K. McKinney, personal communication) or avoiding sedimentation (Bishop, 1988; Cadée, 1991). Heavily encrusted surfaces thus do not provide clear-cut evidence for "way-up" (*contra* Brett and Baird, 1986); they are at least as likely to indicate "way-down."

(c) Encrusters and borers modify the hydraulic behavior of dead shells. For example, circumrotary overgrowths by bryozoans, hydroids, and corals transform plate- and stick-form fragments into spheres and add weight (Kissling, 1973; Balson and Taylor, 1982). Perforated bivalve shells have different transport characteristics than intact shells (Lever and Thijssen, 1968).

(d) Hermit crabs (a Jurassic innovation) carry dead shells, particularly from gastropods, on their backs as domiciles, thereby transporting, delaying burial, and facilitating damage and modification that create a number of distributional anomalies (Conover, 1975; Shimoyama, 1985; S. E. Walker, 1988, 1989). These shells can be identified by distinctive patterns of boring,

encrustation, and physical abrasion (S. E. Walker, 1988; Smyth, 1990) and should be evaluated separately from other parts of the death assemblage.

(e) To corroborate whole-assemblage data, individual bioclasts should be examined for multiple-phase, post-mortem histories consistent with delayed burial or repeated burial-exhumation cycles. Not all individuals will exhibit such features (Frey and Howard, 1986). In fact, the hallmark of time-averaged shell accumulations having complex histories is the admixture of shells in different states of preservation, from fresh to completely altered (Kidwell and Aigner, 1985; Kidwell, this volume, Chapter 5).

#### 4.3.1. Discrimination of Physical and Biogenic Effects

In general, shell assemblages influenced by physical processes should bear some imprint of such or have an appropriate stratigraphic context, e.g., high-energy sedimentary structures. If post-mortem processes are predominantly hydraulic, then all shells of similar or lower critical threshold velocities should be affected, whereas biological processes, if selective at all, will tend to select on other features, such as sizes and shapes most vulnerable or rewarding to infestation. With careful study, results of different processes can be distinguished. Scoffin (1987), for example, found that *in situ* mechanical breakdown of skeletons yields a broad range of grain sizes, whereas boring produces predominantly fine grains (also see Sammarco and Risk, 1990).

As exposure to post-mortem processes increases, taphonomic features tend to become less readily interpretable because of progressive destruction. In addition, shells can be recycled from one post-mortem environment to another through vertical reworking and time-averaging as well as by transport, and thus can accrue a succession of different taphonomic signatures. This is particularly true in concentrations of exotic shells, where taphonomic features may be more informative of shell source than of the final depositional process and thus should be interpreted with caution. For example, shells in the Recent Black Shell Turbidite (Prince *et al.*, 1987) show all stages of abrasion and have a range of radiocarbon ages, suggesting that fragmentation reflects not only downslope transport, but also initial accumulation as a time-averaged shallow-water assemblage [also see D. J. Davies *et al.* (1989a) for similar conclusions for shallow-water tempestites]. This is why stratigraphic workers have consistently used bedding features—physical scale, geometry, microstratigraphic complexity, overall bioclastic fabric, facies context—as the primary evidence for modes of shell concentration rather than relying solely upon features of component shells (see Kidwell, this volume, Chapter 5).

#### 4.4. Geochemical Modification

The breakdown of carbonate shells into their constituent microscopic elements (prisms, needles, fibers, flakes, and granules) can proceed both on

the seafloor and during shallow burial. Shells exposed on the seafloor are subject to the chemistry of overlying waters. Most open marine waters at shelf depths are saturated or oversaturated with respect to calcium carbonate and are slightly alkaline, so that aragonitic and calcitic bioclasts are chemically stable. Under such conditions, shell breakdown is largely by boring, although these pits can become micritized in warm oversaturated waters (Alexandersson, 1972; Gunatilaka, 1976). Chemical leaching or microbial decay of organic matrix can also be a factor, leading to chalky textures (Alexandersson, 1972; Lewy, 1981).

In undersaturated seawater (cold water, whether shallow or deep) and in acidic brackish and freshwater settings, carbonate shells can be etched and leached (Alexandersson, 1972; Pip, 1988) (Table VIII). Microscopic (and preferably SEM) inspection of shell surface features is almost always required in order to distinguish among the effects of chemical dissolution of crystallites, organic leaching, fungal or algal microboring, and physical abrasion [Cutler (1987); *contra* 12 $\times$  magnification used by D. J. Davies *et al.* (1989a); Staff and Powell (1990)]. Brett and Baird (1986) used the term corrosion (combining abrasion and corrosion) for dulled surfaces of uncertain origin.

Upon shallow burial, shells may pass through a series of pore-water zones whose chemistries are determined by the quantity of buried reactive organic matter and iron and by fluid exchange with overlying waters [reviews by Aller (1982b), Allison (1988), Raiswell and Canfield (this volume, Chapter 9)]. Near-surface pore waters are generally oxidizing and supersaturated owing to good exchange with saturated overlying water; the effects of this exchange generally overcompensate for acids produced by aerobic decomposition of organics. Carbonate shells thus should suffer little dissolution in this thin surficial zone unless overlying waters are undersaturated (D. E. Canfield, personal communication, March 1989).

In contrast, actively bioturbated sediments just below the surface (and extending some tens of centimeters to the depth of active burrowing) are characterized by undersaturated pore waters of high  $p\text{CO}_2$  and low pH which promote carbonate dissolution (Aller, 1982a). Sediments are so well irrigated with sulfate-rich overlying waters that little alkalinity can build up, notwithstanding high rates of sulfate reduction and bicarbonate ion production. The accumulation of  $\text{Ca}^{2+}$  in these pore waters (Aller, 1982a) and SEM evidence of shell pitting indicate that shell dissolution occurs within the bioturbated zone. This is recorded even in sites of net carbonate accumulation such as Florida Bay, where dissolution has been reported to remove fine particles of high-Sr aragonite (Walter and Morse, 1984; Walter and Burton, 1990). If reactive detrital iron is present (as in most siliciclastic marine sediments), diagenetic pyrite forms locally by sulfate reduction; later oxidation of these reduced pockets yields sulfuric acid, which further lowers pore-water pH to levels inimical to carbonate preservation (Aller, 1982a). Where bioturbation is intense, at least seasonally, even sediment molds of dissolved shells have low likelihood of preservation.

Below the zone of sediment irrigation, anaerobic decomposition can lead to high bicarbonate levels (high alkalinity) in both carbonate and siliciclastic sediments (Raiswell and Canfield, this volume, Chapter 9). This creates supersaturated conditions that favor carbonate shell preservation. Presumably, shells must be moved quickly into this zone if they are to become part of the fossilized shelly fauna (Aller, 1982a; D. J. Davies *et al.*, 1989b). This may be accomplished by the piping of shells down open burrows (Aller, 1982a; Seibold *et al.*, 1973; Wanless *et al.*, 1987), downward advection by surface and subsurface deposit feeders (Cadée, 1976), scouring to the base of migrating bedforms (Johnson, 1957; Clifton and Boggs, 1970), and catastrophic burial by storms, slumps, and turbidites (Aigner, 1985a).

Sedimentary environments that favor carbonate shell preservation are thus those with little reactive organic matter and iron, e.g., carbonate grainstones, where any local undersaturation can be quickly buffered by dissolution of carbonate mud or can be corrected by flushing with overlying saturated seawater. Similarly, local clusters of shells in otherwise disadvantageous sediments might create their own favorable pore-water microenvironment by partial dissolution and bicarbonate buffering. There thus is potential for a positive diagenetic feedback between shell abundance and shell preservation potential [see discussion in Kidwell (1986a, 1989, and this volume, Chapter 5). Sediments with bioturbated zones that are thin, heterogeneous (i.e., characterized by discrete burrows rather than by thorough admixing), or highly seasonal in development should also favor carbonate shell preservation by providing various time and space windows for shells to escape undersaturated pore-water conditions (Kidwell, 1989).

Alternatively, shells can persist in the face of antagonistic geochemical conditions if their reactivities are modified soon after death. Although the mineralogies of shells are generally well known (Milliman, 1974; Scoffin, 1987; Lowenstam and Weiner, 1989; Saelen, 1989), the kinetics of shell dissolution is less well understood, inasmuch as species are not always lost in the order or at the rates predicted by their chemical activities (Berner and Morse, 1974; Walter and Morse, 1984, 1985; Walter, 1985; Morse, 1986). Peterson (1976), for example, estimated the differential preservability of shelly benthos from Mugu Lagoon (California) by tracking weight loss of individual shells over 7.5 months (shells  $\geq 2$  cm) (C. H. Peterson, personal communication, June 1990). After 50-cm-deep burial in either sand or muddy sand, high-Mg calcite echinoids and some aragonitic gastropods had suffered 10–20% weight loss, but most aragonitic species lost only 0–4%, and the only low-Mg calcite scallop lost 0.14%. Linear extrapolation suggests that the post-mortem longevities of the different taxa ranged from 4 to 894 years.

High surface area and disseminated organic material tend to speed shell destruction, and may even reverse the susceptibilities of aragonitic and calcitic bioclasts (Flessa and Brown, 1983; Walter and Morse, 1984, 1985; Ameziane-Cominardi and Roux, 1987; Schott *et al.*, 1989). High organic content, for example, appears to be an important factor in the rapid

post-mortem destruction of calcitic brachiopods relative to many aragonitic bivalves (Collins, 1985; Gaspard, 1989; Curry *et al.*, 1989; Emig, 1990; Kidwell, 1990). On the other hand, organic coatings on shells (Henrich and Wefer, 1986; Morse, 1986), adsorption of less soluble ions [surface "poisoning" by Zn, Mg,  $\text{PO}_4$ , and others (Bernier and Morse, 1974; Walter and Hanor, 1979; Morse, 1986)], periostracal coverings (Phillippon and Plaziat, 1975; Hunter, 1990), and conchiolin layers within shells (Lewy and Samtleben, 1979) can significantly impede dissolution. Rapid conversion of high-Mg calcite to low-Mg calcite quickly stabilizes the tests of some echinoderms and bryozoans (Nelson, 1978), but not all [e.g., rapid destruction of ophiuroids (Jensen and Thomsen, 1987)].

The importance of kinetics in determining shell loss rates is underscored by the abundance of shells that accumulate in sites where water chemistry should not permit shell preservation. Deep-sea oozes, for example, can accumulate on seafloors overlain by undersaturated water despite metastable mineralogies (Morse, 1986). Kinetics is also implicated in the persistence of shell carbonate on and shallowly buried within modern shelf sediments at low, middle, and high latitudes (Nelson, 1988), even where total carbonate production rates are low.

Work in Long Island Sound (New York) on carbonate productivity and carbonate dissolution illustrates this apparent paradox of preservation in estuarine siliciclastic muds. Macrobenthic carbonate production has a mean of  $67 \text{ g CaCO}_3/\text{m}^2$  per year [ranging from 6 to  $180 \text{ g}/\text{m}^2$  per year (Sanders, 1956)], similar to rates established from other temperate level-bottom environments (Bosence, 1980). In the same area, carbonate dissolution rates of  $10\text{--}70 \text{ g CaCO}_3/\text{m}^2$  per year (Aller, 1982a) have been measured from pore waters, depending on season and bioturbation intensity. Similar budgets have been documented for Californian and Texan lagoons (Peterson, 1976; Cummins *et al.*, 1986a).

Based on measured oxygen demands in muds, D. J. Davies *et al.* (1989b) calculated that the potential for dissolution is much more extreme on continental shelves—ranging from 400 to  $>2000 \text{ g CaCO}_3/\text{m}^2$  per year and usually  $>1000 \text{ g}/\text{m}^2$  per year in surficial, bioturbated sediments. Because these values exceed average rates of carbonate production ( $300\text{--}500 \text{ g}/\text{m}^2$  per year), they predicted that shells should only be preserved if they are quickly buried to a depth below the bioturbated zone. Although logical, and certainly one viable scenario for shell preservation often invoked in the paleontological literature, this conclusion is belied by the presence of abundant old shells in surficial sediments across many clastic-starved shelves (Nelson, 1988; Kidwell, this volume, Chapter 5) (see data in Section 5.1) and even in the bioturbated, organic- and clastic-rich Texas shelf (S. E. Walker *et al.*, 1989). In addition, field studies demonstrate that much of early diagenetic dissolution is probably focused on fine particulate carbonate (e.g., Walter and Morse, 1985), leaving shells of several millimeters or larger intact. It is thus clear that, notwithstanding high rates of carbonate dissolution measured for single seasons or burrow systems, and the high

rates that can be calculated if these short-term rates are multiplied out to their annual values (e.g., D. J. Davies *et al.*, 1989b), individual shells face a temporally and spatially heterogeneous diagenetic environment and can survive by many pathways other than immediate deep burial. These pathways include very early post-mortem modification of shell structure and composition that alter the kinetics of dissolution.

Loss rates definitely are high for many juvenile mollusks: notwithstanding high juvenile mortality following large larval settlements, juveniles are rare in most Recent and fossil death assemblages (Section 3.2.3). Shell loss is thus not a simple matter of shell size or surface area, but also of microarchitecture, including organic content. Based on a capture/recapture method (Powell *et al.*, 1982), Cummins *et al.* (1986a, Table III) estimated that small ( $0.8\text{--}3.12 \text{ mm}$ ) aragonitic mollusks have post-mortem "half-lives" of less than 40–307 days in two Texas lagoons (half-life = length of time for half the members of a larval cohort to disappear from the death assemblage). It should be noted, however, that variance is very high: three out of the four taxa that occur in both lagoons (*Acteocina*, *Caecum*, *Laevicardium*) showed high loss in one but no loss (i.e., immeasurably long half-lives) in the other lagoon, even after 20 months of study. Four other numerically dominant taxa in the Texas death assemblages also showed no loss (all size classes of *Anomalocardia*, *Chione*, and *Brachiodontes*; *Tagelus plebius*  $>16 \text{ mm}$ ). Because the shortest half-lives and highest loss rates are documented for the most juvenile and presumably most susceptible members of the shelly fauna, these values should not be taken as typical of all aragonitic taxa and all size classes (*contra* M. V. H. Wilson, 1988, and Brett and Baird, 1986).

## 5. Estimating Relative and Absolute Scales of Time-Averaging

Most benthic fossil assemblages are time-averaged accumulations dominated by indigenous material: instantaneous census assemblages are rare, as are assemblages composed entirely of exotic shells. One of the major challenges in taphonomic analysis, then, is to recognize and quantify degrees of time-averaging in fossil assemblages [and see Fürsich and Aberhan (1990); which appeared as this volume went into production].

Time-averaging was defined by K. R. Walker and Bambach (1971) for "fossil assemblages . . . that accumulate from the [local] live community during the time required to deposit the containing sediment." They argued that because sediment accumulation rates are slow relative to organism life spans, such assemblages do not reflect community structure at any instant, but instead are composites spanning decades, and that short-term fluctuations in populations are canceled out by the predominance of ecologically persistent, long-term trends. This concept quickly gained wide acceptance



and, corroborated by actualistic studies (Peterson, 1977; Staff *et al.*, 1986; Staff and Powell, 1988), has become a cornerstone of paleoecological analysis.

### 5.1. Controlling Factors

Given sufficiently durable shells, the fundamental control on scales of time-averaging should be the rate of sediment accumulation, which determines the approximate stratigraphic separation of successive faunas. Because deposition is generally episodic on short time scales (e.g., Barrell, 1917; Sadler, 1981), the time span encompassed by a given deposit and its fossil assemblage cannot simply be back-calculated from longer-term sediment accumulation rates (*sensu* Schindel, 1980, 1982). Moreover, shells of several ages may be incorporated even into rapidly deposited beds [e.g., reworking of new and old shells into a single storm-bed (Kidwell, this volume, Chapter 5)], and presumably may be added later by bioadvection and other stratigraphic leakage [e.g., stratigraphic disordering *sensu* Flessa *et al.* (1989; Cutler and Flessa, 1990)]. Thus, to reconstruct the likely scale of time-averaging for a specific assemblage, the short-term dynamics of sediment accumulation must be evaluated along with shell sources and histories. This requires a variety of biostratigraphic, paleoecological, sedimentological, and stratigraphic lines of evidence (e.g., Goldring, 1964; Einsele and Seilacher, 1982; Behrensmeyer, 1982; Kidwell, 1982, 1986a, this volume, Chapter 5; Kidwell and Aigner, 1985; Brett and Baird, 1986; Parsons *et al.*, 1988).

The mixed ages of shells found in surficial sediments of Recent environments indicate that many shells can endure periods of time-averaging of up to tens of thousands of years. For example, mid-shelf shell gravels from around the British Isles yield radiocarbon dates of up to ~10,000 years BP (J. B. Wilson, 1982; Sturrock, 1982), and shell gravels from the clastic-starved outer shelf of the southeastern United States yield dates as old as 10,000–15,000 years BP (Milliman *et al.*, 1972). Shells sampled from surficial carbonate-rich sediments in warm temperate and subtropical settings yield radiocarbon dates of 0–3100 years BP in south Florida, 1425–1600 years BP in the Bahamas, and 1000–4805 years BP in coastal Baja California (Taft and Harbaugh, 1964). Sealevel flooding curves for areas where Holocene sediments are still being reworked, such as Florida Bay (Bosence, 1989a,b), also indicate time-averaging over a period of 3000–4000 years, as do direct dates on beach accumulations of shells (Gould and McFarlan, 1959; Albertzart and Wilkinson, 1989; Powell and Davies, 1989) and intertidal biogenic graded beds (Meldahl, 1987b; Flessa *et al.*, 1990). In deep-sea cores, Broecker *et al.* (1988) found that even among assemblages of coexisting planktonic foraminifera, radiocarbon ages differ by 60–3100 years within sampling horizons. Assemblages composed of shells of mixed ages, formed under conditions of slow net aggradation, commonly record more than one community (owing to environmental change during the period of accumulation) and several different states of degradation [see

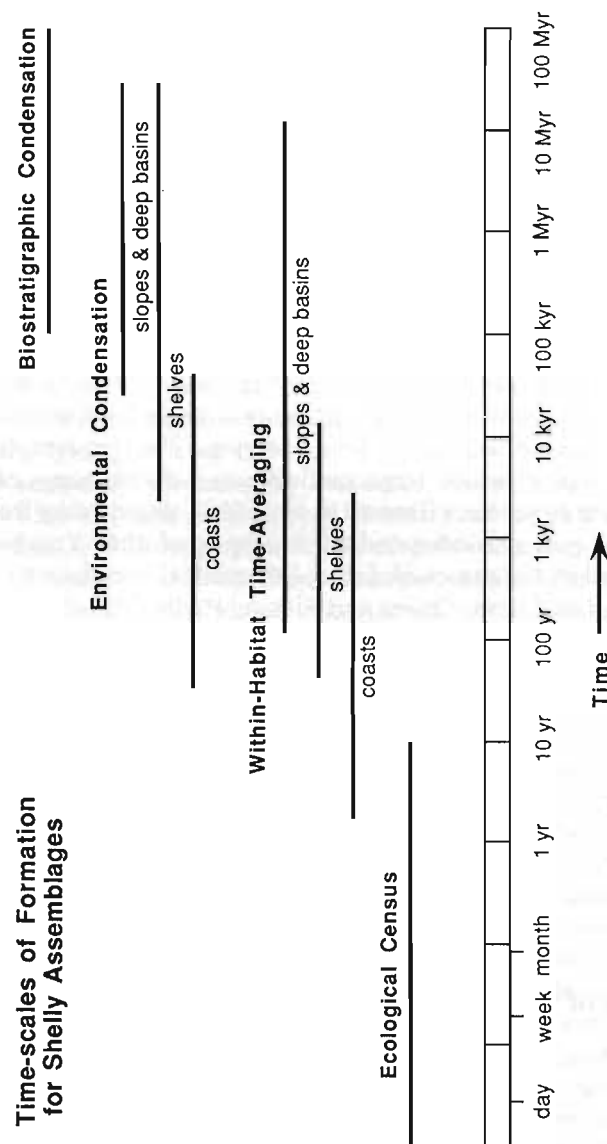
Kidwell and Aigner (1985) for fossil examples; Kidwell (this volume, Chapter 5)].

Many authors have postulated that time-averaging is also governed by the depth of sediment (and presumably faunal) reworking by bioturbators [for recent examples, see Schiffelbein (1985), Backman (1986), Meldahl (1987b)]. This model, although often invoked, has yet to be tested for macroinvertebrates; some recent analyses suggest that bioturbation can yield a far more complex record. Kershaw *et al.* (1988), for example, found that only fine carbonate particles are vertically mixed by bioturbators in areas of slow clastic sedimentation (0.02–0.3 cm/year) within the Irish Sea. Notwithstanding a deep-burrowing shrimp (*Callianassa subterranea*) which moves sediment to the surface from depths  $\geq 140$  cm and an echiuran worm (*Maxmuelleria lankesteri*) which moves surface sediment to depth, large *Turritella communis* shells increased in age down-core from 270 to 4250 years BP. In contrast, radiocarbon ages of bulk carbonate (particles  $< 1$  mm) were roughly constant at 10,000–15,000 years BP throughout each 0.6- to 2.7-m-long core. These results suggest that the large *Turritella communis* retained their stratigraphic positions, whereas fine-grained sediment and shell fragments were homogenized by advection. The preservation of a relative age stratigraphy among large molluscs in ~70-cm cores of bioturbated sediment from Texas bays [Powell *et al.* (1989), dated using free amino acids] provides a second, independent example of this “no-homogenization” model within the errors of dating. Numerical simulation of bioadvection by Flessa *et al.* (1989; Cutler and Flessa, 1990) yielded comparable, well-ordered synthetic stratigraphies.

Many of the consequences of time-averaging for shelly faunas have already been discussed (see Sections 2 and 3). These include heightened species richnesses in death assemblages, relative abundances that reflect long-term averages rather than successional states, and poor records of short-term ecological structure. The following discussion focuses on methods of estimating absolute scales of time-averaging and on criteria for identifying taphonomically comparable assemblages. [Contrary to Fürsich and Aberhan (1990), we have found little evidence that time-averaging lowers the species richness of death assemblages (see Tables II–IV).]

### 5.2. Magnitudes of Time-Averaging

Census assemblages and biostratigraphically condensed assemblages are end members in the spectrum of time-averaging (Fig. 9; Table I). Assemblages that accumulate over intermediate time scales may form: (a) during periods in which the physical environment remained stable (*within-habitat* assemblages); such assemblages sum within-habitat perturbations in community state or physical environment; or (b) during periods of significant physical environmental change at the site of accumulation [*environmental condensation sensu* Fürsich (1975)]; these assemblages are derived from two or more successive communities and reflect taphonomic overprints of two or more environments. [Compare with Fig. 6 of Fürsich and Aberhan (1990).]



**FIGURE 9.** Estimates for relative and absolute scales of time-averaging in census, within-habitat, environmentally condensed, and biostratigraphically condensed assemblages. See text for explanation.

### 5.2.1. Census Assemblages

Sudden burial ["obruption"; for review see Brett and Seilacher (1991)] can entomb a benthic community, yielding a census assemblage that has undergone little or no time-averaging. Such assemblages provide the highest resolution records of community structure, including virtual "snapshots" of species relative abundances and size-frequency distributions. Other ecological features such as commensal relationships, substratum preferences for byssate or pediculate taxa, and individual spacing can also be preserved.

The hallmarks of such assemblages should be high proportions of articulated specimens, with many in life position, and sedimentary evidence of rapid permanent burial or asphyxiation (graded sediment caps, "smothering" black mud, early concretion formation, escape traces). Census assemblages are typically associated with single beds or bedding planes and, if shells are densely packed, these concentrations are typically thin and local in distribution [pods, pavements, and thin beds; local overgrowths on hard substrata; = simple event-concentrations in Kidwell (this volume, Chapter 5)].

Catastrophic mortality and/or burial can be an important mode of assemblage formation in environments of variable oxygenation, salinity, or temperature such as lagoons, deep basins, and inland seas (Noe-Nygaard *et al.*, 1987; Oschmann, 1988). In higher-energy and persistently aerobic soft-bottom environments, recognizable census assemblages are less likely to be preserved, owing to physical reworking and bioturbation, even though mass mortality may be common.

Preservation of discrete census assemblages depends upon the immediacy, thickness, and permanence of burial sediments (Kidwell, 1990). In the presence of burrowing organisms, burial increments must be at least tens of centimeters thick to sequester the death assemblage from taphonomic modification and time-averaging (Bjerstedt and Erickson, 1989). A minimum thickness of sedimentary cover [ $\sim 30$  cm for Recent infauna (Nichols *et al.*, 1978)] is also necessary to limit the number of organisms that can escape entombing sediments, with mobile epifauna fleeing the scene and infauna burrowing up to a new equilibrium position; such behaviors have considerable potential to bias census assemblages (Kranz, 1974a,b). The lack of an entombing sedimentary increment may explain in part the failure of the extraordinary 1983–1984 mass mortality of the Caribbean urchin *Diadema antillarum* to leave a signal in the record (Greenstein, 1989b). Census assemblages are probably more common on hard substrata where encrusters and largely sessile borers and cavity dwellers can be entombed by later encrustations and organic frameworks, although cross-cutting relationships must be carefully distinguished before the true census community can be recognized (Fürsich, 1979; Jackson, 1983; Brett and Brookfield, 1984; M. A. Wilson, 1985).

Biological interpretation of census assemblages is not necessarily



straightforward: buried along with the catastrophically censused community will be the shelly remains of any earlier colonists of the site together with introduced shelly material. Moreover, few mass mortalities kill all individuals of a species or all species in a community (e.g., Rees *et al.*, 1977; Von Esternhagen and Dethlefsen, 1983; Hunte *et al.*, 1986; Mah and Stearn, 1986; Stebbins, 1987; Lessios, 1988), with local exceptions (Tsuchiya, 1983), and nonobtrusion types can be markedly diachronous or involve time lags in mortality (Knowlton *et al.*, 1981; Lessios, 1988), or even fail to leave a record (Greenstein, 1989b). Thus, strictly speaking, only some of all assemblages conventionally categorized as census types are likely to reflect complete censuses or truly zero time-averaging of shelly faunas. Absolute time resolution for census assemblages therefore ranges from zero to perhaps a few decades (Fig. 9).

### 5.2.2. Within-Habitat Time-Averaged Assemblages

Death assemblages that accumulate through sporadic, attritional mortality or that sum several census events are necessarily more complex, both biologically and taphonomically. The longer the period of accumulation, the greater the number of biological processes that can influence shell supply and preservation even within a single environment, and the greater the likelihood of both short- and long-term changes in the local physical environment, whether driven by external forces, by the community itself (sediment baffling, growth up into shallower waters), or by live/dead interactions (taphonomic feedback) (Figs. 1 and 5).

Time-averaged indigenous assemblages from a single environment, here termed within-habitat assemblages, should be good sources of paleoecological information, judging by analyses of Recent examples (e.g., most entries in Tables II–VI). Environmental conditions during the period of shell accumulation need not be static: the background or average state may be punctuated by short-term events and natural oscillations in water energy, emersion, salinity, temperature, and oxygenation, any of which might have ecological and taphonomic consequences for the time-averaged assemblage. Equally important, the substratum itself might change, owing to erosion, dewatering (firming), cementation, deposition of new sediment, or accumulation of shells; many of these processes can be biologically mediated.

Low-density fossil assemblages embedded within a larger homogeneous sedimentary body [e.g., Thorson's (1957) stereotypic *Venus* community in a bioturbated muddy sand facies] are likely to reflect within-habitat time-averaging. Other typical features include (a) diverse mixture of shells supplied by different community states (*sensu* Johnson, 1972, and Gray, 1981) (Fig. 5), (b) mixture of shells with differing degrees of physical, biological, or chemical damage, (c) association of apparently indigenous but ecologically disparate forms, such as soft-bottom and shell-gravel taxa in shell-rich intervals, owing to taphonomic feedback [Kidwell and Jablonski (1983); one pathway of faunal condensation *sensu* Fürsich (1978)], and (d)

fine-scale heterogeneity in composition owing to incomplete mixing of successive states by physical or biogenic reworking [another pathway of faunal condensation *sensu* Fürsich (1978)].

The repetitive and distinctive associations of taxa [recurrent assemblages of Johnson (1962); Valentine and Mallory (1965)] that characterize stratigraphic facies provide strong circumstantial evidence that many fossil assemblages are time-averaged over periods that encompass the entire range of within-community variability (K. R. Walker and Bambach, 1971), i.e., over at least decades to centuries on the open shelf. If fossil assemblages typically formed over shorter time scales, then the record should be far more mosaic in its composition and less likely to yield recurrent associations in a given facies type.

The fossil record of a community or habitat can be made more complex by taphonomic feedback between accumulating dead shells and living benthos (Kidwell and Jablonski, 1983; Kidwell, 1986b; K. B. Miller *et al.*, 1988). Dead shells, whether supplied by local mortality or by transport from adjacent habitats, provide substrata for attachment and might eventually transform a soft substratum into coarser, firmer seafloor. Such a change could inhibit the initial soft-bottom fauna and facilitate colonization and survival of new taxa that tolerate or prefer shell-gravel conditions (e.g., J. B. Wilson, 1988), modifying both the lithofacies and community structure. Actualistic studies suggest that changes driven by live/dead interactions require many decades to accomplish. Knight (1988; Knight and Bosence, 1988), working in a coastal shelf embayment where the timing of clastic deposition was well known, found that while shell accumulation over several decades resulted in some changes in the benthic fauna (facilitation of encrusters and borers not otherwise present in the soft-bottom habitat), longer periods would be required to generate a community-wide change in faunal composition by live/dead interactions.

Absolute scales for within-habitat time-averaging can be estimated in a number of ways from Recent faunas. One approach (Section 3.2.1) measures the number of years over which a local fauna must be sampled before its cumulative species richness approximates that of the local death assemblage. By this method, data from the English Channel suggest at least 70 years of time-averaging in shell gravel habitats (Carthew and Bosence, 1986), whereas the less diverse faunas of Californian lagoons with higher sedimentation rates require only 3 years of pooled data (Peterson, 1976).

Another approach that provides minimum estimates of time-averaging is based on the temporal scale of physical and biological variability in modern environments. For example, the natural hydrographic period for coastal environments, over which storms and other perturbations become a steady-state process, is on the order of a few decades, whereas the natural period for the depth-buffered open shelf is on the order of a century (Moore and Curray, 1964; Swift, 1970, 1976). From a sedimentological perspective, only those sampling programs that span these long cycles can reveal the true "average condition" of the coast or shelf as a depositional system, and

detect the infrequent but high-energy processes that disproportionately influence the permanent rock record. Because benthic populations commonly track physical environmental fluctuations even on seasonal scales (e.g., Nichols and Thompson, 1985), these long-term scales almost certainly influence the composition of death assemblages.

Analyses of benthic ecosystems yield virtually identical estimates for the minimum period over which a community must be studied for its entire range of states to be sampled (e.g., Livingstone, 1987). Pearson and Barnett (1987) suggested that observations along coasts of western Europe should span  $\geq 25$  years and preferably 50–70 years, and that in general the minimum length of study should equal the lifespan of the longest-lived organisms in the target community (also see Connell and Sousa, 1983). Because populations can oscillate over periods of several years or more, even benthic surveys separated by several decades cannot always differentiate between short-term “noise” and long-term unidirectional trends or stasis (Gray and Christie, 1983; Nichols and Thompson, 1985; Shillabeer and Tapp, 1990).

All of these lines of evidence estimate the *minimum* period over which communities and their within-habitat death assemblages are time-averaged: from years to decades in coastal environments and from many decades to centuries on the open shelf (Fig. 9). Maximum periods may be estimated from rates of habitat migration and change. Coastal environments can shift rapidly, in part because of their mosaic nature, so that a single habitat is unlikely to persist at a single site for time-averaging over more than a few thousand years. In contrast, open-shelf habitats are typically more extensive and more intergradational in nature, so that time scales of habitat migration will more closely approximate those of transgression and regression, yielding within-habitat scales of time-averaging up to tens of thousands of years (Fig. 9). These minimum and maximum estimates thus bracket time-averaging values derived from absolute dating of individual shells (see Section 5.1).

### 5.2.3. Environmentally Condensed Assemblages

When environmental change is rapid relative to net rates of sediment aggradation, faunas from successive habitats can accumulate *in situ* to form a single fossil assemblage. These assemblages, such as might be formed during salinity fluctuations in marine embayments (e.g., Fürsich and Kauffman, 1984) or marine transgression of a sediment-starved shelf (e.g., J. B. Wilson, 1988; Kidwell, 1989), are examples of environmental condensation as defined by Fürsich (1975; Fürsich and Kauffman, 1984, p. 505): “faunas representing different environments in time are telescoped into one stratigraphic horizon.”

Environmental condensation should be suspected for assemblages that (a) lie along facies boundaries or along discontinuity surfaces of any type, (b) occur as dense concentrations, particularly if these coquinas are microstratigraphically complex and extend laterally into adjacent facies, (c) have

shell infills that differ from the surrounding matrix, or (d) include shells showing a wide range of preservational states (Fürsich, 1978; Kidwell and Aigner, 1985). On both hard and soft substrata, these assemblages commonly show features consistent with multiple cycles of burial and exhumation, early diagenesis, and benthic recolonization including taphonomic feedback. In carbonate settings, the matrix can undergo early cementation and thus may also be subjected to dissolution, bioerosion, and encrustation (e.g., Schroeder and Zankl, 1974; Scoffin and Garrett, 1974; Palmer and Fürsich, 1974; Fürsich, 1978; Walker and Diehl, 1985).

Almost by definition, time scales of environmental condensation fall at the high end of those estimated for within-habitat time-averaging (Fig. 9). These processes operate on time scales that approach or exceed the limits of direct observation, so that Quaternary cores and surficial deposits are the chief evidence. Up to 15,000 years of *in situ* time-averaging during the Holocene transgression are recorded by mixed nearshore and shelf faunas (see Section 5.1). Similarly, thousands of years of shell accumulation with only microstratigraphic separation of successive faunas has been documented in a variety of Holocene coastal settings. Examples include the amalgamation of open marine and lagoonal assemblages off Mauritania (Einsele *et al.*, 1974), the reworking of ~9000-year-old intertidal shells into modern subtidal communities in the North Sea (Cadée, 1984a), and biogenic mixing of upper and lower intertidal shells whose ages range from 0 to ~4000 years in the Gulf of California (Meldahl, 1987b).

### 5.2.4. Biostratigraphically Condensed Assemblages

If net rates of sediment aggradation are so slow that a time-averaged assemblage includes taxa that ordinarily have mutually exclusive geological ranges (i.e., taxa from different biozones), then that assemblage is more precisely described as biostratigraphically condensed (Wendt, 1970; Jenkyns, 1971) (Fig. 9). Assemblages can also be mixed biostratigraphically in the absence of time-averaging, for example by stratigraphic leakage (exhumation, reworking) of older taxa into a young assemblage (Middlemiss, 1962; Frey *et al.*, 1975; W. Miller, 1983; Goldring, 1990; Ruffell, 1990), or by piping of young taxa into an older assemblage (Garrison *et al.*, 1987) (Table I). These phenomena, along with a number of others discussed in Sections 5.2.2 and 5.2.3, all fall under the general concept of faunal condensation *sensu* Fürsich (1978).

Given that biostratigraphically condensed deposits must encompass evolutionarily significant periods of time (perhaps 100,000 years or more), most shelf-depth and shallower examples will record environmental condensation as well (Machalski and Walaszczyk, 1987). Within-habitat biostratigraphic condensation, in contrast, is most likely to occur in deep-sea sediments, where time scales of facies change can be slow relative to evolutionary rates, although environmental condensation can occur even here (Wendt, 1970, 1988; Bernoulli and Jenkyns, 1974; Urlichs, 1975; Bergner *et al.*, 1982).

### 5.3. Identifying Taphonomically Comparable Assemblages

In his paleoecological analyses of Jurassic molluscan faunas, Fürsich (1977, 1984, 1986) focused on beds containing relatively few, dispersed shells and on monospecific shell pavements. By avoiding the most shell-rich beds, even though these are conspicuous, he restricted his paleobiological interpretations to the taphonomically most comparable census and within-habitat accumulations. This strategy could be applied effectively in many other settings.

When shell gravels are the predominant lithofacies or are the benthic habitat of interest, some degree of taphonomic comparability can be achieved by grouping them according to the inferred process and time scale of concentration (Kidwell, 1982, 1986a, this volume, Chapter 5). Shell assemblages can be time-averaged to varying degrees before final deposition, of course, and so there will not always be a precise correlation between the time scale over which the concentration formed and the age spectrum of constituent shells. For example, a Recent tempestite could incorporate shells from a single mass mortality (i.e., census assemblage), from a time-averaged indigenous assemblage, from exotic sources, from relict Pleistocene deposits, from eroded Miocene strata, or from any combination of these.

Nonetheless, simple event-concentrations formed by brief episodes of shell influx or reworking should generally be taphonomically more straightforward than shell concentrations formed by the amalgamation or stacking of many event-concentrations. Such multiple-event, composite concentrations commonly involve environmental condensation and other mixing processes, so that samples that are taphonomically comparable to those from simple event-concentrations will be difficult to extract, even by microstratigraphic dissection. The cumulative effects of taphonomic processes should tend to be most pronounced in stratigraphically condensed hiatus concentrations and in erosional lags (Kidwell, 1982, and this volume, Chapter 5).

## 6. Bathymetric Variation in the Preservation of Shelly Faunas

All factors in the basic taphonomic equation—quantity and susceptibility of shells, post-mortem environment, time scale of accumulation (Fig. 1)—are likely to vary over ecological time scales, among environments, and through the Phanerozoic. Comparative actualistic studies are rare, however, and, owing to little standardization or quantification in the description of taphonomic features, it is difficult to compare among published accounts and thus to characterize bathymetric and other gradients in much detail. Moreover, because many actualistic studies describe taphonomic end-prod-

ucts rather than processes, extrapolation to the fossil record is uncertain, particularly for Mesozoic and Paleozoic strata.

Figure 10 summarizes bathymetric trends in the taphonomy of benthic marine faunas, as developed in an aggradational facies tract. Long-term condensed accumulations are excluded (see Kidwell, this volume, Chapter 5, Fig. 16), as are anaerobic and dysaerobic environments. Environments within tidal range and within SCUBA depths are best known; reef work is only getting underway, and very little evidence is available for deeper-shelf environments.

In terms of shell condition, soft substrata of the outer shelf and presumably the slope evidently yield the best preservation: low frequency of fragmentation, virtually no abrasion or bioerosion, and deep infauna articulated though generally not in life positions (S. E. Walker *et al.*, 1989, and unpublished data). Nearshore, beach, and other shoal environments within the photic zone show the poorest preservation, whereas intertidal, sheltered coast, and middle-shelf environments are highly variable (Fig. 10).

Bathymetric trends in time-averaging can only be postulated on the basis of stratigraphic evidence and a handful of direct-dated assemblages. Within-habitat assemblages should occur in all settings, whereas censuses are likely to be preserved only in areas of rapid and/or substantial episodic deposition; these include lagoons, reefs, and the transitional zones of open shelves. Environmentally condensed assemblages should be most common in higher-energy and shallow-water environments where environments shift most rapidly. These trends broadly correspond with bathymetric patterns in shell concentration (Kidwell, this volume, Chapter 5, Fig. 15). [Compare with Fig. 6 of Fürsich and Aberhan (1990).]

Dissolution rates are poorly constrained, as indicated by the ranges in Fig. 10, with rates varying from low in sands to high in muds. Precipitation within micrite envelopes, between particles, and in intraskeletal pores is better documented. In tropical and subtropical environments, early precipitation is found in fully marine environments characterized by frequent wave pumping through pore spaces.

Despite poorly understood limitations on applicability to the pre-Cenozoic fossil record, owing to the evolution of shell-producing and shell-destroying organisms (Efremov, 1940; Behrensmeier and Kidwell, 1985; Speyer and Brett, 1988; Kidwell, 1990), actualistic studies provide valuable insights into the variety of end-products that can arise under a set of relatively well-understood and tightly constrained conditions. Some of this variation is environmentally arrayed, although the broad range of preservational quality even within single environments underscores just how difficult it will be to characterize taphofacies uniquely. This does not mean that taphofacies analysis (e.g., Speyer and Brett, 1986, 1988; Norris, 1986; Kidwell *et al.*, 1986; D. J. Davies *et al.*, 1989a; Staff and Powell, 1990) is premature, but its state of development resembles that of conventional facies analysis in the early 1960s. It is also more difficult, simply because patterns and effects can be generated by more than one agent, shells can



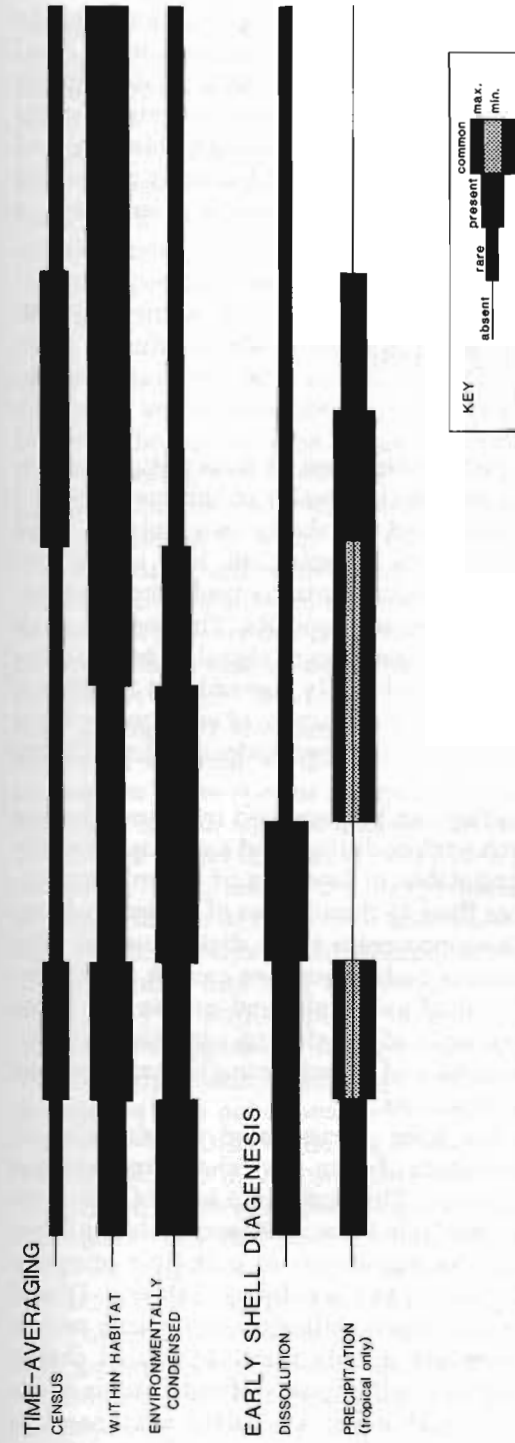
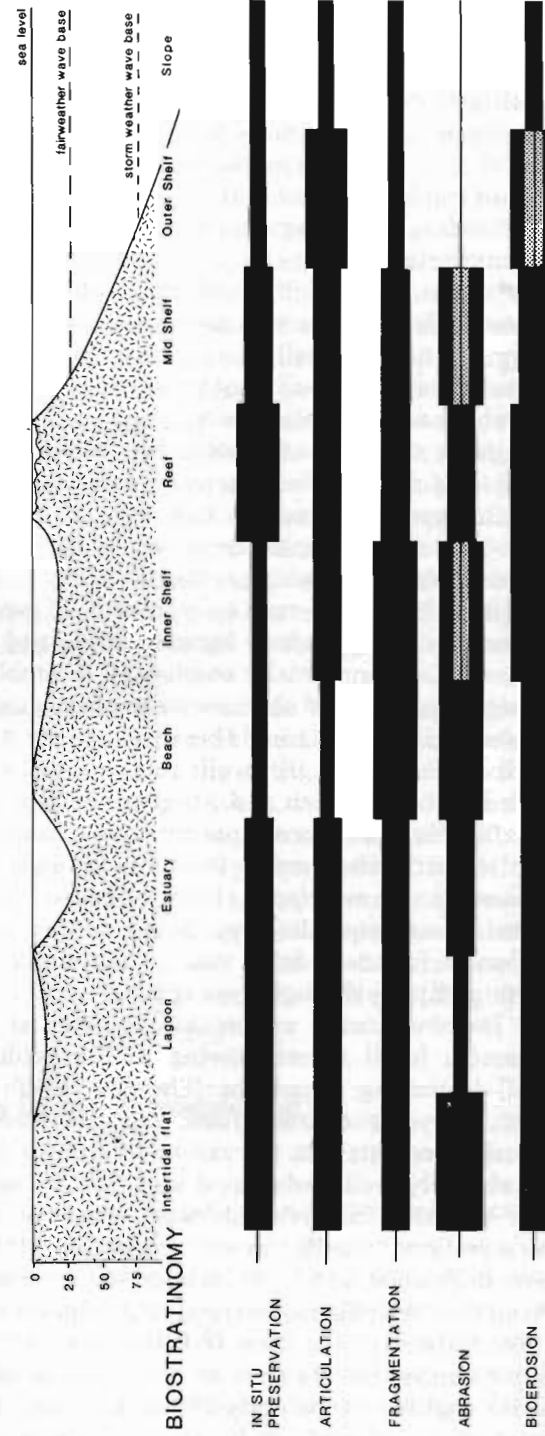


FIGURE 10. Bathymetric trends in taphonomy and time-averaging of predominantly molluscan assemblages.

experience more than one cycle of modification, and generations can be time-averaged to many different degrees. These complications make it all the more important to establish objective, preferably quantitative descriptors of post-mortem alteration (see references in Table VII), and to design studies that directly link taphonomic patterns and effects to processes. Meldahl and Flessa (1990), for example, focused on the taphonomic behavior of a single bivalve species into order to rank the relative importance of diverse factors among intertidal to shallow subtidal environments.

## 7. Interpretation of the Fossil Record: Conclusions and Strategy

1. After decades of stressing post-mortem loss of information, taphonomic studies provide ample evidence for the wealth of sedimentological and paleoecological information preserved in shelly assemblages. One major challenge for taphonomy in the 1990s is geological: how to improve the reliability and sophistication of taphonomic criteria bearing on depositional and diagenetic histories of sedimentary deposits. The second challenge is biological and lies in quantifying the ratio of signal to noise in the paleontological record: what is the fidelity of shelly assemblages to original biological patterns, how does fidelity vary as a function of environment and scale of time-averaging, and how are these values best estimated for different assemblages?

2. Many kinds of shell modification can be generated by more than one agent (Table VII). For example, much surface dulling and shell loss casually referred to as "dissolution" is attributable to leaching of organic matrix, microboring, and bioabrasion rather than to dissolution of mineral phases alone; SEM examination allows these processes to be distinguished. The origin of many shell fragments remains ambiguous: we cannot yet distinguish the effects of different mechanical and biological processes. These complications underscore the importance of developing objective, quantitative descriptors of taphonomic features and of improving the criteria used to recognize the effects of separate processes.

3. Although shell transport has been documented in virtually all environments, its effect on the composition of open-shelf shelly assemblages appears to be minor at the scale of facies. This justifies a host of paleontological applications, from biofacies analysis to evolutionary paleoecology. Except for settings characterized by steep gradients or bulk-flow phenomena, death assemblages show strong loyalty to life habitats (Tables II–IV and VIII). Out-of-habitat transport in level-bottom settings usually only moves shells into adjacent habitats and involves mainly small, epifaunal shells; these exotic shells generally constitute a small minority of individuals in the recipient assemblage. Shell movement within habitats, on the other hand, is pervasive, as evidenced by the scarcity of fossils preserved in life positions.

These processes (small-scale transport, disruption by bioturbators) smear ecological patterns, so that within-habitat details of community structure usually must be derived from exceptional, instantaneously buried communities.

4. The temporal resolution of shelly assemblages varies immensely, from high-resolution census assemblages to low-resolution biostratigraphically condensed accumulations. Intermediate scales of time-averaging characterize most of the fossil record. These assemblages can form either (a) during a period of environmental stability (within-habitat time-averaging), or (b) during a period of environmental change (environmental condensation). Absolute scales of time-averaging can be bracketed on the basis of rates of environmental and community change in Recent settings, and these estimates are corroborated by direct-dated shells in Recent death assemblages. The sparse data suggest some systematic variation in scales of time-averaging among environments (Figs. 9 and 10).

5. Actualistic investigations indicate that the compositions of death assemblages are in many respects faithful reflections of long-term community structure, further justifying certain kinds of paleobiological interpretation. Based on studies of level-bottom soft-substrata conducted over the last 25 years, it appears that (a) virtually all live shelly taxa leave some record in the local death assemblage, whether examined at the facies or larger scale, (b) species found "dead only" are usually low-abundance taxa, indicating that ecologically transient and exotic species will only dominate assemblages in unusual situations, even though they may constitute a large proportion of the species richness of an assemblage, and (c) only half of the top (most abundant) dead taxa are top taxa in the living community (Tables II–VI). The longer the period over which live data are pooled, the higher the measured fidelities of the death assemblages, underscoring the time-averaged nature of most shell accumulations in surficial marine sediments and the importance of long-term baselines of live data for comparison. Consequently, much of the variance and many of the low resemblance values may be attributable to inappropriate comparisons of time-averaged death assemblages with living communities sampled for only 1 or 2 years. Surprisingly, fidelity with respect to species presence/absence and relative abundance does not appear to vary strongly across environmental gradients (Tables II–VI). Discriminating biofacies and interpreting community structure on the basis of the rank abundance of the most common species (rather than of the entire assemblage) cannot be justified actualistically (Table VI). The fidelity of size-frequency data in time-averaged assemblages is highly variable; further work might yet demonstrate such data to be biologically meaningful, at least in some environments.

The results of actualistic studies are fundamentally encouraging for both geologists and paleontologists. Taphonomic criteria for paleoenvironmental interpretation show great promise, although still in an early stage of development. Moreover, when viewed at the appropriate scale, the record clearly yields more biological signal than noise, and this can be scaled



quantitatively for Recent environments. The greatest difficulty in extrapolating these results to the older fossil record, whether for geological or paleontological application, will be biological factors—namely, evolutionary changes in the behavior and environmental deployment of organisms as producers, utilizers, and destroyers of dead hard parts. A strategy informed rather than ruled by actualism will thus be the most fruitful.

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## References

- Abbott, B. M., 1974, Flume studies on the stability of model corals as an aid to quantitative paleoecology, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **15**:1-27.
- Adey, W. H., and Vassar, J. M., 1975, Colonization, succession and growth rates of tropical coralline algae (Rhodophyta, Cryptonemiales), *Phycologia* **14**:55-69.
- Adjas, A., Masse, J.-P., and Montaggioni, L. F., 1990, Fine-grained carbonates in nearly closed reef environments: Mataiva and Takapoto atolls, central Pacific Ocean, *Sediment. Geol.* **67**:115-132.
- Aigner, T., 1985a, *Storm Depositional Systems: Dynamic Stratigraphy in Modern and Ancient Shallow-Marine Sequences*, Springer-Verlag, Berlin.
- Aigner, T., 1985b, Biofabrics as dynamic indicators in nummulite accumulations, *J. Sediment. Petrol.* **55**:131-134.
- Aigner, T., and Reineck, H.-E., 1982, Proximity trends in modern storm sands from the Helgoland Bight (North Sea) and their implications for basin analysis, *Senckenb. Marit.* **14**:183-213.
- Aigner, T., Hagdorn, H., and Mundlos, R., 1978, Biohermal, biostromal and storm-generated coquinas in the Upper Muschelkalk, *Neues Jahrb. Geol. Paläontol. Abh.* **157**:42-52.
- Aitken, A. E., Risk, M. J., and Howard, J. D., 1988, Animal-sediment relationships on a subarctic intertidal flat, Pangnirtung Fjord, Baffin Island, Canada, *J. Sediment. Petrol.* **58**:969-978.
- Akpan, E. B., and Farrow, G. E., 1984, Shell-boring algae on the Scottish continental shelf: Identification, distribution, bathymetric zonation, *Trans. R. Soc. Ed. Earth Sci.* **75**:1-12.
- Akpan, E. B., and Farrow, G. E., 1985, Shell bioerosion in high-latitude low-energy environments: Firths of Clyde and Lorne, Scotland, *Mar. Geol.* **67**:139-150.
- Albertzart, L. S., and Wilkinson, B. H., 1989, Genesis of Holocene shell assemblages along barrier backbeaches of the central Texas coast, *Geol. Soc. Am. Abstr. Progr.* **21A**:A290-A291.
- Alexander, R. R., 1977, Growth morphology, and ecology of Paleozoic and Mesozoic opportunistic species of brachiopods from Idaho-Utah, *J. Paleontol.* **51**:1133-1149.
- Alexander, R. R., 1986a, Life orientation and post-mortem reorientation of Chesterian brachiopod shells by paleocurrents, *Palaios* **1**:303-311.
- Alexander, R. R., 1986b, Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods, *J. Paleontol.* **60**:273-285.
- Alexander, R. R., 1990, Disarticulated shells of Late Ordovician brachiopods: Inferences on strength of hinge and valve architecture, *J. Paleontol.* **64**:524-532.
- Alexandersson, T., 1972, Micritization of carbonate particles: Processes of precipitation and dissolution in modern shallow-marine sediments, *Bull. Geol. Inst. Univ. Uppsala N. S.* **3**(7):201-236.
- Alexandersson, T., 1978, Destructive diagenesis of carbonate sediments in the eastern Skagerrak, North Sea, *Geology* **6**:324-327.
- Allen, E. J., 1899, On the fauna and bottom deposits near the thirty fathom line from the Eddystone grounds to Start Point, *J. Mar. Biol. Assoc. U. K.* **5**:365-541.
- Allen, J. R. L., 1984, Experiments on the settling, overturning and entrainment of bivalve shells and related models, *Sedimentology* **31**:227-250.
- Aller, R. C., 1982a, Carbonate dissolution in nearshore terrigenous muds: The role of physical and biological reworking, *J. Geol.* **90**:79-95.
- Aller, R. C., 1982b, The effects of macrobenthos on chemical properties of marine sediment and overlying water, in: *Animal-Sediment Relations* (P. L. McCall and M. J. S. Tevesz, eds.), Plenum Press, New York, pp. 53-102.
- Allison, P. A., 1986, Soft-bodied animals in the fossil record: The role of decay in fragmentation during transport, *Geology* **14**:979-981.
- Allison, P. A., 1988, The role of anoxia in decay and mineralization of proteinaceous microfossils, *Paleobiology* **14**:139-154.
- Allison, P. A., 1990, Variation in rates of decay and disarticulation of Echinodermata: Implications for the application of actualistic data, *Palaios* **5**:432-440.
- Allmon, W. D., 1988, Ecology of Recent turritellid gastropods (Prosobranchia, Turritellidae): Current knowledge and paleontological implications, *Palaios* **3**:259-284.
- Alvarez, F., and Taylor, P. D., 1987, Epizoan ecology and interactions in the Devonian of Spain, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **61**:17-31.
- Ameziane-Cominardi, N., and Roux, M., 1987, Biocorrosion et micritisation des ossicules d'Echinodermes en milieu bathyal au large de la Nouvelle-Calédonie, *C. R. Acad. Sci. Paris Sér. II* **305**:701-705.
- Arntz, W. E., Brunswig, P., and Sannthern, M., 1976, Zonierung um Mollusken und Schill im Rinnensystem der Kieler Bucht (Westliche Ostsee), *Senckenb. Marit.* **8**:189-269.
- Arua, I., 1982, Borings and shell damage in Eocene Gastropoda: Southeastern Nigeria, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **38**:269-282.
- Aslin, C. J., 1968, Echinoid preservation in the Upper Estuarine Limestone of Blisworth, Northamptonshire, *Geol. Mag.* **105**:506-518.
- Babcock, R. C., 1985, Growth and mortality in juvenile corals (*Goniastrea*, *Platygyra* and *Acropora*): The first year, in: *Proceedings 5th International Coral Reef Congress, Tahiti*, Volume 4, pp. 355-360.
- Backman, J., 1986, Accumulation patterns of Tertiary calcareous nannofossils around extinctions, *Geol. Rundsch.* **75**:185-196.
- Baird, G. C., Brett, C. E., and Frey, R. C., 1989, "Hitchhiking" epizoans on orthoconic cephalopods: Preliminary renewal of the evidence and its implications, *Senckenb. Lethaea* **69**:439-465.
- Bak, R. P. M., 1990, Patterns of echinoid bioerosion in two Pacific coral reef lagoons, *Mar. Ecol. Progr. Ser.* **66**:267-272.
- Balson, P. S., and Taylor, P. D., 1982, Palaeobiology and systematics of large cyclostome bryozoans from the Pliocene Coralline Crag of Suffolk, *Palaeontology* **25**:529-554.
- Barrell, J., 1917, Rhythms and the measurement of geologic time, *Geol. Soc. Am. Bull.* **28**:745-904.
- Bayer, U., 1978, Multimodale Häufigkeitsverteilung bei der Analyse von Strömungseinregelungen, *Neues Jahrb. Geol. Paläontol. Monatsh.* **1978**:747-748.
- Behrensmeier, A. K., 1982, Time resolution in fluvial vertebrate assemblages, *Paleobiology* **8**:211-227.
- Behrensmeier, A. K., 1988, The Pull of the Recent analogue, *Palaios* **3**:373.
- Behrensmeier, A. K., and Kidwell, S. M., 1985, Taphonomy's contributions to paleobiology, *Paleobiology* **11**:105-119.
- Bein, A., and Fütterer, D., 1977, Texture and composition of continental shelf to rise sediments off the northwestern coast of Africa: An indication for downslope transportation, *Meteor. Forschungsergeb. Reihe C* **27**:46-74.

- Bergman, K. M., Elner, R. W., and Risk, M. J., 1982, The influence of *Polydora websteri* borings on the strength of the shell of the sea scallop, *Placopecten magellanicus*, *Can. J. Zool.* **60**:2551-2556.
- Bergner, H. D., Gebhard, G., and Wiedmann, J., 1982, Kondensationerscheinungen in der marokkanischen und alpinen Mittelkreide (Apt, Alb), *Neues Jahrb. Geol. Paläontol. Abh.* **165**:102-124.
- Berner, R. A., and Morse, J. A., 1974, Dissolution kinetics of calcium carbonate in sea water IV. Theory of calcite dissolution, *Am. J. Sci.* **274**:108-134.
- Bernoulli, D., and Jenkyns, H. C., 1974, Alpine, Mediterranean, and central Atlantic Mesozoic facies in relation to the early evolution of the Tethys, *Soc. Econ. Paleontol. Mineral. Spec. Publ.* **19**:129-160.
- Bertness, M. D., and Cunningham, C., 1981, Crab shell-crushing predation and gastropod architectural defense, *J. Exp. Mar. Biol. Ecol.* **50**:213-230.
- Beukema, J. J., and Cadée, G. H., 1986, Zoobenthos responses to eutrophication of the Dutch Wadden Sea, *Ophelia* **26**:55-64.
- Bigelow, H. B., and Schroeder, W. C., 1953, Sawfishes, guitarfishes, skates, rays, and chimaeroids, *Mem. Sears Found. Mar. Res.* **2**:1-514.
- Bishop, G. A., 1975, Traces of predation, in: *The Study of Trace Fossils* (R. W. Frey, ed.), Springer-Verlag, New York, pp. 261-281.
- Bishop, J. D. D., 1988, Disarticulated bivalve shells as substrates for encrustation by the Bryozoan *Cribrilina puncturata* in the Plio-Pleistocene Red Crag of Eastern England, *Palaeontology* **31**:237-253.
- Bishop, J. D. D., 1989, Colony form and the exploitation of spatial refuges by encrusting bryozoa, *Biol. Rev.* **64**:197-218.
- Bjerstedt, T. W., and Erickson, J. M., 1989, Trace fossils and bioturbation in peritidal facies of the Potsdam-Theresa Formations (Cambrian-Ordovician), Northwest Adirondacks, *Palaios* **4**:203-224.
- Boeschoten, G. J., 1966, Shell borings of sessile epibiontic organisms as paleoecological guides (with examples from the Dutch coast), *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **3**:333-379.
- Boesch, D. F., Wass, M. L., and Virnstein, R. W., 1976, The dynamics of estuarine benthic communities, in: *Estuarine Processes* (M. Wiley, ed.), Academic Press, New York, Volume 1, pp. 177-196.
- Bosence, D. W. J., 1976a, Ecological and sedimentological studies on some carbonate sediment producing organisms, Co. Galway, Ireland, Ph.D. thesis, University of Reading, Reading, United Kingdom.
- Bosence, D. W. J., 1976b, Ecological studies on two unattached coralline algae from Western Ireland, *Palaeontology* **19**:365-395.
- Bosence, D. W. J., 1979, Live and dead faunas from coralline algal gravels, Co. Galway, Eire, *Palaeontology* **22**:449-478.
- Bosence, D. W. J., 1980, Sedimentary facies, production rates and facies models for Recent coralline algal gravels, Co. Galway, Ireland, *Geol. J.* **15**:91-111.
- Bosence, D. W. J., 1984, Construction and preservation of two Recent algal reefs, St. Croix, Caribbean, *Palaeontology* **27**:549-574.
- Bosence, D. W. J., 1985, Preservation of coralline algal reef frameworks, in: *Proceedings 5th International Coral Reef Congress, Tahiti*, Volume 6, pp. 623-628.
- Bosence, D. W. J., 1989a, Surface sublittoral sediments of Florida Bay, *Bull. Mar. Sci.* **44**:434-453.
- Bosence, D. W. J., 1989b, Carbonate budgets for carbonate mounds, Florida, U.S.A., in: *Proceedings 6th International Coral Reef Symposium, Townsville*.
- Boss, S. K., and Liddell, W. D., 1987, Patterns of sediment composition of Jamaican fringing reef facies, *Sedimentology* **34**:77-87.
- Boucot, A. J., 1953, Life and death assemblages among fossils, *Am. J. Sci.* **251**:25-40.
- Boucot, A. J., 1981, *Principles of Benthic Marine Paleocology*, Academic Press, New York.
- Boyer, P. S., 1969, Pelecypod beak wear: An indicator of postmortem transport, *Texas J. Sci.* **20**:385-388.

- Bradley, W. H., 1957, Physical and ecologic features of the Sagadahoc Bay tidal flat, Georgetown, Maine, *Geol. Soc. Am. Mem.* **67**(2):641-682.
- Branch, G. M., 1984, Competition between marine organisms: Ecological and evolutionary implications, *Oceanogr. Mar. Biol. Annu. Rev.* **22**:429-593.
- Brandt, D. S., 1989, Taphonomic grades as a classification for fossiliferous assemblages and implications for paleoecology, *Palaios* **4**:303-309.
- Brandt Velbel, D., 1984, On defining limits to paleoecological interpretation in the fossil record, *Géobios Mém. Spéc.* **8**:415-418.
- Brenchley, P. J., and Newall, G., 1970, Flume experiments on the orientation and transport of models and shell valves, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **7**:185-220.
- Brenner, K., 1976, Ammoniten-Gehäuse als Anzeiger von Palaeo-strömungen, *Neues Jahrb. Geol. Paläontol. Abh.* **151**:101-118.
- Brenner, K., and Einsele, G., 1976, Schalenbruch im Experiment, *Zentralbl. Geol. Paläontol. II* **1976**:349-354.
- Brett, C. E., 1988, Palaeoecology and evolution of marine hard substrate communities: An overview, *Palaios* **3**:374-378.
- Brett, C. E., and Baird, G. C., 1986, Comparative taphonomy: A key to paleoenvironmental interpretation based on fossil preservation, *Palaios* **1**:207-227.
- Brett, C. E., and Brookfield, M. E., 1984, Morphology, faunas and genesis of Ordovician hardgrounds from southern Ontario, Canada, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **46**:233-290.
- Brett, C. E., and Seilacher, A., 1991, Obrution deposits: A taphonomic consequence of event sedimentation, in: *Cycles and Events in Stratigraphy* (G. Einsele, W. Ricken, and A. Seilacher, eds.), Springer-Verlag, Berlin, in press.
- Broecker, W. S., Andree, M., Bonani, G., Wolfli, W., Klas, M., Mix, A., and Oeschger, H., 1988, Comparison between radiocarbon ages obtained on coexisting planktonic foraminifera, *Paleoceanography* **3**:647-657.
- Bromley, R. G., 1970, Borings as trace fossils and *Entobia cretacea* Portlock, as an example, in: *Trace Fossils: Geological Journal Special Issue 3* (T. P. Crimes and J. C. Harper, eds.), Liverpool, pp. 49-90.
- Brouwer, A., 1959, *General Palaeontology*, University of Chicago Press, Chicago.
- Brown, B. J., 1979, Shell transport and community composition in modern shelf seas, Ph. D. thesis, Glasgow University, Glasgow.
- Brun, E., 1969, Aggregation of *Ophiotrix fragilis* (Abildgaard) (Echinodermata: Ophiuroidea), *Nytt Mag. Zool.* **17**:153-160.
- Brun, E., 1971, Predation of *Chlamys islandica* (O. F. Müller) by eiders (*Somateria* spp.), *Astarte* **4**:23-29.
- Buchanan, J. B., Shearer, M., and Kingston, P. R., 1978, Sources of variability in the benthic macrofauna off the south Northumberland coast, 1971-6, *J. Mar. Biol. Assoc. U. K.* **58**:191-210.
- Budd, D. A., and Perkins, R. D., 1980, Bathymetric zonation and paleoecological significance of microborings in Puerto Rican shelf and slope sediments, *J. Sediment. Petrol.* **50**:881-903.
- Cadée, G. C., 1968, Molluscan biocoenoses and thanatocoenoses in the Ria de Arosa, Galicia, Spain, *Rijksmus. Nat. Hist. Leiden Zool. Verhandl.* **95**:1-121.
- Cadée, G. C., 1976, Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea, *Neth. J. Sea Res.* **10**:440-460.
- Cadée, G. C., 1979, Sediment reworking by the polychaete *Heteromastus filiformis* on a tidal flat in the Dutch Wadden Sea, *Neth. J. Sea Res.* **13**:441-456.
- Cadée, G. C., 1982, Low juvenile mortality in fossil brachiopods, some comments, *Interne Verslagen Ned. Inst. Onderzoek Zee, Texel* **3**:1-29.
- Cadée, G. C., 1984a, Macrobenthos and macrobenthic remains on the Oyster Ground, North Sea, *Neth. J. Sea Res.* **18**:160-178.
- Cadée, G. C., 1984b, 'Opportunistic feeding', a serious pitfall in trophic structure analysis of (paleo)-faunas, *Lethaia* **17**:289-292.
- Cadée, G. C., 1988, The use of size frequency distribution in paleoecology, *Lethaia* **21**:289-290.

- Cadée, G. C., 1989, Size-selective transport of shells by birds and its palaeoecological implications, *Palaeontology* **32**:429-437.
- Cadée, G. C., 1991, Carapaces of the shore crab *Carcinus maenas* as a habitat for encrusting organisms, in: *8th International Bryozoological Association Conference*, Paris, in press.
- Cain, J. D. B., 1968, Aspects of the depositional environment and paleoecology of crinoidal limestones, *Scot. J. Geol.* **4**:191-208.
- Callender, W. R., Staff, G. M., Powell, E., and MacDonald, I. R., 1990, Gulf of Mexico hydrocarbon seep communities V. Biofacies and shell orientation of autochthonous shell beds below storm wave base, *Palaos* **5**:2-14.
- Carriker, M. R., Smith, E. H., and Wilce, R. T. (eds.), 1969, Penetration of calcium carbonate substrates by lower plants and invertebrates, *Am. Zool.* **9**(3):629-1020.
- Carter, R. M., 1968, On the biology and paleontology of some predators of bivalve molluscs, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **4**:29-65.
- Carter, R. W. G., 1974, Feeding sea birds as a factor in lamellibranch valve sorting patterns, *J. Sediment. Petrol.* **44**:689-692.
- Carthew, R., and Bosence, D. W. J., 1986, Community preservation in Recent shell-gravels, English Channel, *Palaeontology* **29**:243-268.
- Chave, K. E., 1964, Skeletal durability and preservation, in: *Approaches to Paleoecology* (J. Imbrie and N. D. Newell, eds.), Wiley, New York, pp. 377-387.
- Choi, D. R., and Ginsburg, R. N., 1983, Distribution of coelobites (cavity dwellers) in coral rubble across the Florida reef tract, *Coral Reefs* **2**:165-172.
- Clifton, H. E., 1971, Orientation of empty pelecypod shells and shell fragments in quiet waters, *J. Sediment. Petrol.* **41**:671-682.
- Clifton, H. E., and Boggs, S., Jr., 1970, Concave-up pelecypod (*Psephidea*) shells in shallow marine sand, Elk River Beds, southwestern Oregon, *J. Sediment. Petrol.* **40**:888-897.
- Cohen, A. S., 1989, The taphonomy of gastropod shell accumulations in large lakes: An example from Lake Tanganyika, Africa, *Paleobiology* **15**:26-45.
- Collins, M. J., 1985, Post mortality strength loss in shells of the Recent articulate brachiopod *Terebratulina retusa* (L.) from the west coast of Scotland, in: *Les Brachiopodes fossiles et actuels* (P. R. Racheboeuf and C. C. Emig, eds.), *Biostratigr. Paléozoïque* **4**:209-218.
- Connell, J. H., and Slatyer, R. O., 1977, Mechanisms of succession in natural communities and their roles in community stability and organization, *Am. Nat.* **111**:1119-1144.
- Connell, J. H., and Sousa, W. P., 1983, On the evidence needed to judge ecological stability or persistence, *Am. Nat.* **121**:789-824.
- Conover, M. R., 1975, Prevention of shell burial as a benefit hermit crabs provide their symbionts (Decapoda, Paguridea), *Crustaceana* **29**:311-313.
- Copper, P., 1988, Ecological succession in Phanerozoic reef ecosystems: Is it real?, *Palaos* **3**:136-152.
- Craig, G. Y., 1953, Discussion: Fossil communities and assemblages, *Am. J. Sci.* **251**:547-548.
- Craig, G. Y., and Hallam, A., 1963, Size frequency and growth ring analysis of *Mytilus edulis* and *Cardium edule* and their palaeoecological significance, *Palaeontology* **6**:731-750.
- Crame, J. A., 1980, Succession and diversity in the Pleistocene coral reefs of the Kenya coast, *Palaeontology* **23**:1-37.
- Crawshaw, L. R., 1912, On the fauna of the western outer area of the English Channel, *J. Mar. Biol. Assoc. U. K.* **9**:292-393.
- Cummins, H., Powell, E. N., Stanton, R. J., and Staff, G., 1986a, The rate of taphonomic loss in modern benthic habitats: How much of the potentially preservable community is preserved?, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **52**:291-320.
- Cummins, H., Powell, E. N., Stanton, R. J., and Staff, G., 1986b, The size frequency distribution in palaeoecology: Effects of taphonomic processes during formation of molluscan death assemblages in Texas bays, *Palaeontology* **29**:495-518.
- Cummins, H., Powell, E. N., Newton, H. J., Stanton, R. J., Jr., and Staff, G., 1986c, Assessing transportation by the covariance of species with comments on contagious and random distributions, *Lethaia* **19**:1-22.
- Currey, J. D., 1980, Mechanical properties of the mollusc shell, *Symp. Soc. Exp. Biol.* **34**:75-97.

- Currey, J. D., 1988, Shell form and strength, in: *The Mollusca* **11** (E. R. Trueman and M. R. Clarke, eds.), Academic Press, San Diego, pp. 183-210.
- Curry, G. B., Ansell, A. D., James, M., and Peck, L., 1989, Physiological constraints on living and fossil brachiopods, *Trans. R. Soc. Ed. Earth Sci.* **80**:255-262.
- Cutler, A. H., 1987, Surface textures of shells as taphonomic indicators, *Paleontol. Soc. Spec. Publ.* **2**:164-176.
- Cutler, A. H., 1989, Shells survive—Loss, persistence and accumulation of hardparts in shallow marine sediments, *Geol. Soc. Am. Abstr. Progr.* **21**:A71.
- Cutler, A. H., and Flessa, K. W., 1990, Fossils out of sequence: Computer simulations and strategies for dealing with stratigraphic disorder, *Palaos* **5**:227-235.
- Davies, D. J., Powell, E. N., and Stanton, R. J., Jr., 1989a, Taphonomic signature as a function of environmental process: Shells and shell beds in a hurricane-influenced inlet on the Texas coast, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **72**:317-356.
- Davies, D. J., Powell, E. N., and Stanton, R. J., Jr., 1989b, Relative rates of shell dissolution and net sediment accumulation—A commentary: Can shell beds form by the gradual accumulation of biogenic debris on the sea floor?, *Lethaia* **22**:207-212.
- Davies, P. J., and Hutchings, P. A., 1983, Initial colonization, erosion and accretion on coral substrate. Experimental results, Lizard Island, Great Barrier Reef, *Coral Reefs* **2**:27-35.
- Dodd, J. R., and Stanton, R. J., Jr., 1981, *Paleoecology, Concepts and Applications*, Wiley, New York.
- Done, T. J., 1985, Effects of two *Acanthaster* outbreaks on coral community structure. The meaning of devastation, in: *Proceedings 5th International Coral Reef Congress Tahiti*, Volume 5, pp. 315-320.
- Donovan, S. K., 1989, Taphonomic significance of the encrustation of the dead shell of Recent *Spirula spirula* (Linné) (Cephalopoda: Coleoidea) by *Lepas anatifera* Linné (Cirripedia: Thoracia), *J. Paleontol.* **63**:698-702.
- Dörjes, J., Frey, R. W., and Howard, J. D., 1986, Origins of, and mechanisms for, mollusk shell accumulations on Georgia beaches, *Senckenb. Marit.* **18**:1-43.
- Driscoll, E. G., 1967, Experimental field study of shell abrasion, *J. Sediment. Petrol.* **37**:1117-1123.
- Driscoll, E. G., 1970, Selective bivalve shell destruction in marine environments, a field study, *J. Sediment. Petrol.* **40**:898-905.
- Driscoll, E. G., and Weltin, T. P., 1973, Sedimentary parameters as factors in abrasive shell reduction, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **13**:275-288.
- Dzik, J., 1979, Some terebratulid populations from the Lower Kimmeridgian of Poland and their relations to the biotic environment, *Acta Paleontol. Polon.* **24**:473-492.
- Eagar, R. M. C., 1978, Shape and function of the shell: A comparison of some living and fossil bivalve molluscs, *Biol. Rev.* **53**:169-210.
- Efremov, J. A., 1940, Taphonomy: New branch of paleontology, *Pan Am. Geol.* **74**:81-93.
- Einsele, G., and Seilacher, A. (eds.), 1982, *Cyclic and Event Stratification*, Springer-Verlag, Berlin.
- Einsele, G., Herm, D., and Schwartz, H. U., 1974, Holocene eustatic(?) sea level fluctuation at the coast of Mauritania, *Meteor. Forschungsergeb. Reihe C* **18**:43-62.
- Ekdale, A. A., 1972, Ecology and paleoecology of marine invertebrate communities in calcareous substrates, northeast Quintana Roo, Mexico, Ph. D. thesis, Rice University, Houston, Texas.
- Ekdale, A. A., 1977, Quantitative paleoecological aspects of modern marine mollusk distribution, northeast Yucatan coast, Mexico, *Am. Assoc. Petroleum Geol. Stud. Geol.* **4**:195-207.
- Ekdale, A. A., 1985, Paleoecology of the marine endobenthos, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **50**:63-81.
- Elias, R. J., 1986, Symbiotic relationships between worms and solitary rugose corals in the Late Ordovician, *Paleobiology* **12**:32-45.
- Elias, R. J., McAuley, R. J., and Mattison, B. W., 1987, Directional orientations of solitary rugose corals, *Can. J. Earth Sci.* **24**:806-812.
- Emery, K. O., 1968, Positions of empty pelecypod valves on the continental shelf, *J. Sediment. Petrol.* **38**:1264-1269.



- Emig, C. C., 1986, Conditions de fossilisation de genre *Lingula* (Brachiopoda) et implications paléocéologiques, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **53**:245-253.
- Emig, C. C., 1990, Examples of post-mortality alteration in Recent brachiopod shells and (paleo)ecological consequences, *Mar. Biol.* **104**:233-238.
- Emson, R. H., and Wilkie, I. C., 1980, Fission and autotomy in echinoderms, *Oceanogr. Mar. Biol. Annu. Rev.* **18**:155-250.
- Erickson, J. M., 1971, Wind-oriented gastropod shells as indicators of paleowind direction, *J. Sediment. Petrol.* **41**:589-593.
- Erwin, D. G., 1983, The community concept, in: *Sublittoral Ecology, The Ecology of the Shallow Sublittoral Benthos* (R. Earll and D. G. Erwin, eds.), Clarendon Press, Oxford, pp. 144-164.
- Fagerstrom, J. A., 1964, Fossil communities in paleoecology: Their recognition and significance, *Geol. Soc. Am. Bull.* **75**:1197-1216.
- Feldmann, R. M., and Tshudy, D., 1987, Ultrastructure in cuticle from *Hoploparia stokesi* (Decapoda: Nephropidae) from the Lopez de Bertodano Fornatira (Late Cretaceous-Paleocene) of Seymour Island, Antarctica, *J. Paleontol.* **61**:1194-1203.
- Flessa, K. W., and Brown, T. J., 1983, Selective solution of macro-invertebrate calcareous hard parts, *Lethaia* **16**:193-205.
- Flessa, K. W., Cutler, A. H., Meldahl, K. H., and Fürsich, F. T., 1989, Taphonomic processes and stratigraphic disorder, in: *Abstracts, 28th International Geological Congress, Volume I*, Washington, D.C., pp. 493-494.
- Flessa, K. W., Meldahl, K. H., and Cutler, A. H., 1990, Quantitative estimates of stratigraphic disorder and time-averaging in a shallow marine habitat, *Geol. Soc. Am. Abstr. Progr.* **22**:A83.
- Force, L. M., 1969, Calcium carbonate size distribution on the West Florida shelf and experimental studies on the microarchitectural control of skeletal breakdown, *J. Sediment. Petrol.* **39**:902-934.
- Ford, E., 1923, Animal communities of the level sea bottom in the waters adjacent to Plymouth, *J. Mar. Biol. Assoc. U. K.* **13**:164-224.
- Frey, R. W., and Basan, P. B., 1981, Taphonomy of relict Holocene salt marsh deposits, Cabretta Island, Georgia, *Senckenb. Marit.* **13**:111-155.
- Frey, R. W., and Howard, J. D., 1986, Taphonomic characteristics of offshore mollusk shells, Sapelo Island, Georgia, *Tulane Stud. Geol. Paleontol.* **19**:51-61.
- Frey, R. W., Voorhies, M. R., and Howard, J. D., 1975, Estuaries of the Georgia coast, U.S.A.: Sedimentology and biology. VII. Fossil and recent skeletal remains in Georgia estuaries, *Senckenb. Marit.* **7**:257-295.
- Frey, R. W., Basan, P. B., and Smith, J. M., 1987, Rheotaxis and distribution of oysters and mussels, Georgia tidal creeks and salt marshes, U.S.A., *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **61**:1-16.
- Frey, R. W., Hong, J.-S., and Hayes, W. B., 1988, Physical and biological aspects of shell accumulation on a modern macrotidal flat, Inchon, Korea, *Neth. J. Sea Res.* **22**: 267-278.
- Fürsich, F. T., 1975, Trace fossils as environmental indicators in the Corallian of England and Normandy, *Lethaia* **8**:151-172.
- Fürsich, F. T., 1977, Corallian (Upper Jurassic) marine benthic associations from England and Normandy, *Palaeontology* **20**:337-386.
- Fürsich, F. T., 1978, The influence of faunal condensation and mixing on the preservation of fossil benthic communities, *Lethaia* **11**:243-250.
- Fürsich, F. T., 1979, Genesis, environments and ecology of Jurassic hardgrounds, *Neues Jahrb. Geol. Paläontol. Abh.* **158**:1-63.
- Fürsich, F. T., 1982, Rhythmic bedding and shell bed formation in the Upper Jurassic of east Greenland, in: *Cyclic and Event Stratification* (G. Einsele and A. Seilacher, eds.), Springer-Verlag, Berlin, pp. 208-222.
- Fürsich, F. T., 1984, Palaeoecology of boreal invertebrate faunas from the Upper Jurassic of central east Greenland, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **48**:309-364.
- Fürsich, F. T., 1986, Benthic associations and their environmental significance in the

- Lusitanian Basin (Upper Jurassic, Portugal), *Neues Jahrb. Geol. Paläontol. Abh.* **172**:271-329.
- Fürsich, F. T., 1990, Fossil concentrations and life and death assemblages, in: *Paleobiology: A Synthesis* (D. E. G. Briggs and P. R. Crowther, eds.), Blackwell Scientific Publications, Oxford, pp. 235-238.
- Fürsich, F. T., and Aberhan, M., 1990, Significance of time-averaging for palaeocommunity analysis, *Lethaia* **23**:143-152.
- 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, *Palaos* **2**:543-559.
- Fürsich, F. T., and Kauffman, E. G., 1984, Palaeoecology of marginal marine sedimentary cycles in the Albian Bear River Formation of south-western Wyoming, *Palaeontology* **27**:501-536.
- Fürsich, F. T., and Werner, W., 1989, Taxonomy and ecology of *Juranomia calcibyssata* gen. et sp. nov.—A widespread anomiid bivalve from the Upper Jurassic of Portugal, *Géobios* **22**:325-337.
- Futterer, E., 1978a, Hydrodynamic behavior of biogenic particles, *Neues Jahrb. Geol. Paläontol. Abh.* **157**:37-42.
- Futterer, E., 1978b, Studien über die Einregelung, Anlagerung und Einbettung biogener Hartteile im Strömungskanal, *Neues Jahrb. Geol. Paläontol. Abh.* **156**:87-131.
- Futterer, E., 1978c, Untersuchungen über die Sink- und Transportgeschwindigkeit biogener Hartteile, *Neues Jahrb. Geol. Paläontol. Abh.* **155**:318-359.
- Garrison, R. E., Kennedy, W. J., and Palmer, T. J., 1987, Early lithification and hardgrounds in Upper Albian and Cenomanian calcarenites, southwest England, *Cretaceous Res.* **8**:103-140.
- Gaspard, D., 1989, Quelques aspects de la biodégradation des coquilles de brachiopodes; Conséquences sur leur fossilisation, *Bull. Soc. Géol. Fr. Sér. 8*, **5**:1207-1216.
- Gauch, H. G., 1982, *Multivariate Analysis in Community Ecology*, Cambridge University Press, Cambridge.
- Goldring, R., 1964, Trace fossils and the sedimentary surface in shallow water marine environments, in: *Deltaic and Shallow Marine Deposits* (L. M. J. U. van Straaten, ed.), Elsevier, Amsterdam, pp. 136-143.
- Goldring, R., 1990, *Fossils in the Field: Information Potential and Analogues*, Longman, London.
- Gould, H. R., and McFarlan, E., Jr., 1959, Geologic history of the chenier plain, southwestern Louisiana, *Trans. Gulf Coast Assoc. Geol. Soc.* **9**:261-270.
- Graus, R. R., MacIntyre, I. G., and Herchenroder, B. E., 1984, Computer simulation of reef zonation at Discovery Bay, Jamaica: Hurricane disruption and long term physical oceanographic controls, *Coral Reefs* **3**:59-68.
- Gray, J. S., 1981, *The Ecology of Marine Sediments*, Cambridge University Press, Cambridge.
- Gray, J. S., and Christie, H., 1983, Predicting long-term changes in marine benthic communities, *Mar. Ecol. Progr. Ser.* **13**:87-94.
- Greensmith, J. T., and Tucker, E. V., 1966, Morphology and evolution of inshore shell ridges and mud-mounds on modern intertidal flats, near Bradwell, Essex, *Proc. Geol. Assoc.* **77**:329-346.
- Greensmith, J. T., and Tucker, E. V., 1969, The origin of Holocene shell deposits in the chenier plain facies of Essex (Great Britain), *Mar. Geol.* **7**:403-425.
- Greenstein, B. J., 1989a, The effect of taphonomic bias on the fossil record of echinoids, *Geol. Soc. Am. Abstr. Progr.* **21**:A70-A71.
- Greenstein, B. J., 1989b, Mass mortality of the West-Indian echinoid *Diadema antillarum* (Echinodermata: Echinoidea): A natural experiment in taphonomy, *Palaos* **4**:487-492.
- Gregory, M. R., Ballance, P. F., Gibson, G. W., and Ayling, A. M., 1979, On how some rays (Elasmobranchia) excavate feeding depressions by jetting water, *J. Sediment. Petrol.* **49**:1125-1130.
- Grinnell, R. S., Jr., 1974, Vertical orientation of shells on some Florida oyster reefs, *J. Sediment. Petrol.* **41**:116-122.

- Gunatilaka, A., 1976, Thallopiphyte boring and micritization within skeletal sands from Connemara, western Ireland, *J. Sediment. Petrol.* **46**:548-554.
- Günther, A., 1990, Distribution and bathymetric zonation of shell-boring endoliths in Recent reef and shelf environments: Cozumel, Yucatan (Mexico), *Facies* **22**:233-262.
- Hallam, A., 1972, Models involving population dynamics, in: *Models in Paleobiology* (T. J. M. Schopf, ed.), Freeman, Cooper and Co., San Francisco, pp. 62-80.
- Hart, C. E., and Crowe, J. H., 1977, The effect of attached gravel on survival of intertidal anemones, *Trans. Am. Microsc. Soc.* **96**:28-41.
- Hartnoll, R. G., 1983, Substratum, in: *Sublittoral Ecology, The Ecology of the Shallow Sublittoral Benthos* (R. Earll and D. G. Erwin, eds.), Clarendon Press, Oxford, pp. 97-124.
- Hartshorne, P. M., Gillespie, W. B., and Flessa, K. W., 1987, Population structure of live and dead gastropods from Bahia la Choya, in: *Paleoecology and Taphonomy of Recent to Pleistocene Intertidal Deposits, Gulf of California* (K. W. Flessa, ed.), *Paleontol. Soc. Spec. Publ.* **2**:139-149.
- Henderson, C. M., and Styann, W. B., 1982, Description and ecology of Recent endolithic biota from the Gulf Islands and banks in the Strait of Juan de Fuca, British Columbia, *Can. J. Earth Sci.* **19**:1382-1394.
- Henderson, S. W., and Frey, R. W., 1986, Taphonomic redistribution of mollusk shells in a tidal inlet channel, Sapelo Island, Georgia, *Palaaios* **1**:3-16.
- Henrich, R., and Wefer, G., 1986, Dissolution of biogenic carbonates: Effects of skeletal structure, *Mar. Geol.* **71**:341-362.
- Hertweck, G., 1972, Georgia coastal region, Sapelo Island, USA: Sedimentology and biology. V. Distribution and environmental significance of lebensspuren and in-situ skeletal remains, *Senckenb. Marit.* **4**:125-167.
- Hertweck, G., 1979, Aufwuchs von See-pocken auf Hartteilen anderer Tiere, Teil I, *Nat. Mus.* **109**:305-311.
- Hesselbo, S. P., 1987, The biostratigraphy of *Kikelocephalus* sclerites: Implications for the use of trilobite attitude data, *Palaaios* **2**:605-608.
- Hewitt, R. A., 1988, Nautiloid shell taphonomy: Interpretations based on water pressure, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **63**:15-25.
- Hickman, C. S., 1983, Radular patterns, systematics, diversity, and ecology of deep-sea limpets, *Veliger* **26**:73-92.
- Highsmith, R. C., Lueptow, R. L., and Schonberg, S. C., 1983, Growth and bioerosion of three massive corals on the Belize barrier reef, *Mar. Ecol. Progr. Ser.* **13**:261-271.
- Hines, A. H., and Pearse, J. S., 1982, Abalones, shells, and sea otters: Dynamics of prey populations in central California, *Ecology* **63**:1547-1560.
- Hiscock, K., 1983, Water movement, in: *Sublittoral Ecology, The Ecology of the Shallow Sublittoral Benthos* (R. Earll and D. G. Erwin, eds.), Clarendon Press, Oxford, pp. 58-96.
- Hiscock, K., and Mitchell, R., 1980, The description and classification of sublittoral epibenthic ecosystems, in: *The Shore Environment* (J. H. Price, D. E. G. Irvine, and W. F. Farnham, eds.), Academic Press, London, pp. 323-370.
- Holland, S. M., 1988, Taphonomic effects of sea-floor exposure on an Ordovician brachiopod assemblage, *Palaaios* **3**:588-597.
- Holling, C. S., 1973, Resilience and stability of ecological systems, *Annu. Rev. Ecol. Syst.* **4**:1-23.
- Hollmann, R., 1966, Tauchbeobachtungen zur Mollusken-Verbreitung und Sediment-Umlagerung im Golf von Neapel, *Neues Jahrb. Geol. Paläontol. Abh.* **125**:499-526.
- Hollmann, R., 1968, Zur morphologie rezenter mollusken-bruchschille, *Paläontol. Z.* **42**:217-235.
- Holme, N. A., 1953, The biomass of the bottom fauna in the English Channel off Plymouth, *J. Mar. Biol. Assoc. U. K.* **32**:1-49.
- Holme, N. A., 1961, The bottom fauna of the English Channel, *J. Mar. Biol. Assoc. U. K.* **41**:397-461.
- Holme, N. A., 1966, The bottom fauna of the English Channel, *J. Mar. Biol. Assoc. U. K.* **46**:401-496.

- Hoskin, C. M., 1980, Flux of barnacle plate fragments and fecal pellets measured by sediment traps, *J. Sediment. Petrol.* **50**:1213-1218.
- Hoskin, C. M., Geier, J. C., and Reed, J. K., 1983, Sediment produced from abrasion of the branching stony coral *Oculina varicosa*, *J. Sediment. Petrol.* **53**:779-786.
- Hoskin, C. M., Reed, J. K., and Mook, D. H., 1986, Production and off-bank transport of carbonate sediment, Black Rock, southwest Little Bahama Bank, *Mar. Geol.* **73**:125-144.
- Hughes, R. G., and Thomas, M. L., 1971, The classification and ordination of shallow water benthic samples from Prince Edward Island, Canada, *J. Exp. Mar. Biol. Ecol.* **7**:1-39.
- Hunte, W., Cote, I., and Tomascik, T., 1986, On the dynamics of the mass mortality of *Diadema antillarum* in Barbados, *Coral Reefs* **4**:135-139.
- Hunter, R. D., 1990, Shell dissolution rate in freshwater pulmonate snails: Influence of periostracum and water chemistry, *Nautilus* **104**:87-91.
- Hutchings, P. A., 1986, Biological destruction of coral reefs, *Coral Reefs* **4**:239-252.
- Hutchinson, G. E., 1978, *An Introduction to Population Ecology*, Yale University Press, New Haven, Connecticut.
- Iribarne, O. O., 1990, Use of shelter by the small Patagonian octopus *Octopus tehuelchus*: Availability, selection, and effects on fecundity, *Mar. Ecol. Progr. Ser.* **66**:251-258.
- Jackson, J. B. C., 1977, Habitat area, colonization, and development of epibenthic community structure, in: *Biology of Benthic Organisms* (B. F. Keegan, P. O'Ceidigh, and P. J. S. Boaden, eds.), Pergamon Press, Oxford, pp. 349-358.
- Jackson, J. B. C., 1979, Morphological strategies of sessile animals, in: *Biology and Systematics of Colonial Organisms* (G. Larwood and B. R. Rosen, eds.), Academic Press, London, pp. 499-556.
- Jackson, J. B. C., 1983, Biological determinants of present and past sessile animal distributions, in: *Biotic Interactions in Recent and Fossil Benthic Communities* (M. J. S. Tevesz and P. L. McCall, eds.), Plenum Press, New York, pp. 39-120.
- Järvinen, O., Babin, C., Bambach, R. K., Flügel, E., Fürsich, F. T., Futuyma, D. J., Niklas, K. J., Panchen, A. L., Simberloff, D., Underwood, A. J., and Weidich, K. F., 1986, The neontologico-paleontological interface of community evolution: How do the pieces in the kaleidoscopic biosphere move?, in: *Patterns and Processes in the History of Life* (D. M. Raup and D. Jablonski, eds.), Springer, Berlin, pp. 331-350.
- Jeffrey, D., and Aigner, T., 1982, Storm sedimentation in the Carboniferous limestones near Weston-Super-Mare (Dinantian, SW-England), in: *Cyclic and Event Stratification* (G. Einsele and A. Seilacher, eds.), Springer, Berlin, pp. 240-247.
- Jenkyns, H. C., 1971, The genesis of condensed sequences in the Tethyan Jurassic, *Lethaia* **4**:327-352.
- Jensen, M., and Thomsen, E., 1987, Ultrastructure, dissolution and "pyritization" of Late Quaternary and Recent echinoderms, *Bull. Geol. Soc. Den.* **36**:275-287.
- Johansen, A. C., 1901, Om aflejungene af molluskernes skaller i indooer og i havet, *Vidensk. Medd. Dansk. Naturh. Foren.* **53**:5-46.
- Johnson, R. G., 1957, Experiments on the burial of shells, *J. Geol.* **65**:527-535.
- Johnson, R. G., 1960, Models and methods for analysis of the mode of formation of fossil assemblages, *Geol. Soc. Am. Bull.* **71**:1075-1086.
- Johnson, R. G., 1962, Interspecific associations in Pennsylvanian fossil assemblages, *J. Geol.* **70**:32-55.
- Johnson, R. G., 1965, Pelecypod death assemblages in Tomales Bay, California, *J. Paleontol.* **39**:80-85.
- Johnson, R. G., 1972, Conceptual models of benthic marine communities, in: *Models in Paleobiology* (T. J. M. Schopf, ed.), Freeman, Cooper and Co., San Francisco, pp. 148-159.
- Jones, N. F., 1950, Marine bottom communities, *Biol. Rev.* **25**:283-313.
- Karlson, R., 1986, Disturbance, colonial fragmentation, and size-dependent life history variation in two coral reef cnidarians, *Mar. Ecol. Progr. Ser.* **28**:245-249.
- Kauffman, E. G., and Scott, R. W., 1976, Basic concepts of community paleoecology, in: *Structure and Classification of Paleocommunities* (R. W. Scott and R. R. West, eds.), Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 1-28.



- Kelling, G., and Moshrif, M. A., 1977, The orientation of fossil bivalves in a pene-littoral sequence (the Rhaetian of South Wales), *J. Sediment. Petrol.* **47**:1342-1346.
- Kelling, G., and Williams, P. F., 1967, Flume studies of the reorientation of pebbles and shells, *J. Geol.* **75**:243-267.
- Kennedy, W. J., and Cobban, W. A., 1976, Aspects of ammonite biology, biogeography, and biostratigraphy, *Spec. Pap. Palaeontol.* **17**:1-94.
- Kershaw, P. J., Swift, D. J., and Denoon, D. C., 1988, Evidence of recent sedimentation in the eastern Irish Sea, *Mar. Geol.* **85**:1-14.
- Kidwell, S. M., 1982, Time scales of fossil accumulation: Patterns from Miocene benthic assemblages, in: *Proceedings 3rd North American Paleontological Convention, Montreal*, Volume 1, pp. 295-300.
- Kidwell, S. M., 1985, Palaeobiological and sedimentological implications of fossil concentrations, *Nature* **318**:457-460.
- Kidwell, S. M., 1986a, Models for fossil concentrations: Paleobiologic implications, *Paleobiology* **12**:6-24.
- Kidwell, S. M., 1986b, Taphonomic feedback in Miocene assemblages: Testing the role of dead hardparts in benthic communities, *Palaios* **1**:239-255.
- Kidwell, S. M., 1989, Stratigraphic condensation of marine transgressive records: Origin of major shell deposits in the Miocene of Maryland, *J. Geol.* **97**:1-24.
- Kidwell, S. M., 1990, Phanerozoic evolution of macroinvertebrate shell accumulations: Preliminary data from the Jurassic of Great Britain, in: *Paleocommunity Temporal Dynamics* (W. M. Miller, III, ed.), *Paleontol. Soc. Spec. Publ.* **5**:309-327.
- Kidwell, S. M., 1991, Taphonomic feedback (live/dead interactions) in the genesis of bioclastic deposits: Keys to reconstructing sedimentary dynamics, in: *Cycles and Events in Stratigraphy* (G. Einsele, W. Ricken, and A. Seilacher, eds.), Springer, Berlin, pp. 268-281.
- Kidwell, S. M., and Aigner, T., 1985, Sedimentary dynamics of complex shell beds: Implications for ecological and evolutionary patterns, in: *Sedimentary and Evolutionary Cycles* (U. Bayer and A. Seilacher, eds.), Springer-Verlag, Berlin, pp. 382-395.
- Kidwell, S. M., and Baumiller, T., 1990, Experimental disintegration of regular echinoids: Roles of temperature, oxygen and decay thresholds, *Paleobiology* **16**:247-271.
- Kidwell, S. M., and Holland, S. M., 1991, Field description of coarse bioclastic fabrics, *Palaios* **6**(4):in press.
- Kidwell, S. M., and Jablonski, D., 1983, Taphonomic feedback: Ecological consequences of shell accumulation, in: *Biotic Interactions in Recent and Fossil Benthic Communities* (M. J. S. Tevesz and P. L. McCall, eds.), Plenum Press, New York, pp. 195-248.
- Kidwell, S. M., Fürsich, F. T., and Aigner, T., 1986, Conceptual framework for the analysis of fossil concentrations, *Palaios* **1**:228-238.
- Kindle, E. M., 1916, Bottom control of marine faunas as illustrated by dredging in the Bay of Fundy, *Am. J. Sci.* **41**:449-461.
- Kissling, D. L., 1973, Circumrotary growth form in Recent and Silurian corals, in: *Animal Colonies* (R. S. Boardman, A. H. Cheetham, and W. A. Oliver, Jr., eds.), Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 43-58.
- Knight, A. P., 1988, Ecological and sedimentological studies on china clay waste deposits in Mevagissey Bay, Cornwall, Ph. D. thesis, University of London.
- Knight, A. P., and Bosence, D. W. J., 1988, China clay waste pollution: A giant palaeoecological experiment, in: *Abstracts, Society of Economic Paleontologists and Mineralogists Annual Midyear Meeting*, Volume V, p. 29.
- Knowlton, N., Lang, J. C., Rooney, M. C., and Clifford, P., 1981, Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals, *Nature* **294**:251-252.
- Kobluk, D. R., 1988, Cryptic faunas in reefs: Ecology and geological importance, *Palaios* **3**:379-390.
- Kobluk, D. R., and van Soest, R. W. M., 1989, Cavity-dwelling sponges in a southern Caribbean coral reef and their paleontological implications, *Bull. Mar. Sci.* **44**:1207-1235.
- Koch, C. F., and Sohl, N. F., 1983, Preservation effects in paleoecological studies: Cretaceous mollusc examples, *Paleobiology* **9**:26-34.
- Kondo, Y., 1989, Bivalve orientation analysis as a method of biostratigraphic interpretation of

- shallow sea fossiliferous facies, in: *28th International Geological Congress Abstracts*, Volume 2, Washington, D.C., pp. 2-210.
- Kornicker, L. S., Wise, C. D., and Wise, J. M., 1963, Factors affecting the distribution of opposing mollusk valves, *J. Sediment. Petrol.* **33**:703-712.
- Kranz, P. M., 1974a, The anastrophic burial of bivalves and its palaeoecological significance, *J. Geol.* **82**:237-265.
- Kranz, P. M., 1974b, Computer simulation of fossil assemblage formation under conditions of anastrophic burial, *J. Paleontol.* **48**:800-808.
- Kristensen, I., 1957, Differences in density and growth in a cockle population in the Dutch Wadden Sea, *Arch. Néer. Zool.* **12**:351-453.
- Kurtén, B., 1954, Population dynamics—A new method in paleontology, *J. Paleontol.* **28**:286-292.
- Lambers, P., and Boekschoten, G. J., 1986, On fossil and recent borings produced by acrothoracic cirripeds, *Geol. Mij.* **65**:257-268.
- Lasker, H., 1976, Effects of differential preservation on the measurement of taxonomic diversity, *Paleobiology* **2**:84-93.
- Lavoir, M. E., 1956, How sea stars open bivalves, *Biol. Bull.* **111**:114-122.
- Lawrence, D. R., 1968, Taphonomy and information losses in fossil communities, *Geol. Soc. Am. Bull.* **79**:1315-1330.
- Lawrence, D. R., 1969, The use of clonid sponges in paleoenvironmental analysis, *J. Paleontol.* **43**:539-543.
- Leopold, M. F., Marteiijn, E. C. L., and Swennen, C., 1985, Long-distance transport of prey from the intertidal zone to high-tide roosts by the oystercatcher, *Ardea* **73**:76-82.
- Lessios, H. A., 1988, Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned?, *Annu. Rev. Ecol. Syst.* **19**:371-393.
- Lever, J., 1958, Quantitative beach research. I. The "left-right phenomenon": Sorting of lamellibranch valves on sandy beaches, *Basteria* **22**:21-51.
- Lever, J., and Thijssen, R., 1968, Sorting phenomena during the transport of shell valves on sandy beaches studied with the use of artificial valves, *Symp. Zool. Soc. Lond.* **22**:259-271.
- Lever, J., Kessler, A., van Overbeeke, A. P., and Thijssen, R., 1961, Quantitative beach research. II. The "hole effect": A second mode of sorting of lamellibranch valves on sandy beaches, *Neth. J. Sea Res.* **6**:339-358.
- Levinton, J. S., 1970, The paleoecological significance of opportunistic species, *Lethaia* **3**:69-78.
- Levinton, J. S., and Bambach, R. K., 1970, Some ecological aspects of bivalve mortality patterns, *Am. J. Sci.* **268**:97-112.
- Lewy, Z., 1975, Early diagenesis of calcareous skeletons in the Baltic Sea, western Germany, *Meyniana* **27**:29-33.
- Lewy, Z., 1981, Maceration of calcareous skeletons, *Sedimentology* **28**:893-895.
- Lewy, Z., and Samtleben, C., 1979, Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods, *Lethaia* **12**:341-351.
- Liddell, W. D., and Brett, C. E., 1982, Skeletal overgrowths among epizoa from the Silurian (Wenlockian) Waldron Shale, *Paleobiology* **8**:67-78.
- Liddell, W. D., and Ohlhorst, S. L., 1988, Hard substrata community patterns, 1-120 m, north Jamaica, *Palaios* **3**:413-423.
- Lindberg, D. R., and Kellogg, M. G., 1982, Bathymetric anomalies in the Neogene fossil record: The role of diving marine birds, *Paleobiology* **8**:402-407.
- Lingwood, P. F., 1976, The marine Mollusca of Liverpool Bay (Irish Sea), *J. Conchol.* **29**:51-56.
- Livingstone, R. J., 1987, Field sampling in estuaries: The relationship of scale to variability, *Estuaries* **10**:194-207.
- Lowenstam, H. A., and Weiner, S., 1989, *On Biomineralization*, Oxford University Press, New York.
- Machalski, M., and Walaszczyk, I., 1987, Faunal condensation and mixing in the uppermost Maastrichtian/Danian Greensand (Middle Vistula Valley, central Poland), *Acta Geol. Polon.* **37**:75-91.

- MacDonald, K. B., 1969, Quantitative studies of salt marsh mollusc faunas from the North American Pacific Coast, *Ecol. Monogr.* **39**:33-60.
- MacDonald, K. B., 1976, Paleocommunities: Toward some confidence limits, in: *Structure and Classification of Paleocommunities* (R. W. Scott and R. R. West, eds.), Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 87-106.
- Mah, A. J., and Stearn, C. W., 1986, The effect of Hurricane Allen on the Bellaire fringing reef, Barbados, *Coral Reefs* **4**:169-176.
- Mancini, E. A., 1978, Origin of micromorph faunas in the geologic record, *J. Paleontol.* **52**:321-333.
- Mapes, R. H., Fahrer, T. R., and Babcock, L. B., 1989, Sublethal and lethal injuries of Pennsylvanian conulariids from Oklahoma, *J. Paleontol.* **63**:34-37.
- Marshall, B. A., 1987, Osteopeltidae (Mollusca: Gastropoda): A new family of limpets associated with whale bone in the deep-sea, *J. Molluscan Stud.* **53**:121-127.
- Martin-Kaye, P., 1951, Sorting of lamellibranch valves on beaches in Trinidad, *Geol. Mag.* **288**:432-434.
- Martinell, J., and dePorta, J., 1982, Observations on the molluscan thanatocoenoses from Platja Llarga (Salou, Spain), *Malacologia* **22**:587-591.
- Masse, J.-P., Thomassin, B. A., and Acquaviva, M., 1989, Bioclastic sedimentary environments of coral reefs and lagoon around Mayotte Island (Comoro Archipelago, Mozambique Channel, SW Indian Ocean), *J. Coastal Res.* **5**:419-432.
- Mather, J. A., 1982, Choice and competition: Their effects on occupancy of shell homes by *Octopus joubini*, *Mar. Behav. Physiol.* **8**:285-293.
- McCall, P. L., and Tevesz, M. J. S., 1983, Soft-bottom succession and the fossil record, in: *Biotic Interactions in Recent and Fossil Benthic Communities* (M. J. S. Tevesz and P. L. McCall, eds.), Plenum Press, New York, pp. 157-196.
- McCave, I., 1988, Biological pumping upwards of the coarse fraction of deep-sea sediments, *J. Sediment. Petrol.* **58**:148-158.
- McClintock, T. S., 1985, Effects of shell condition and size upon the shell choice behavior of a hermit crab, *J. Exp. Mar. Biol. Ecol.* **88**:271-285.
- Meldahl, K. H., 1987a, Origin of shell beds and evolution of a shelly sand spit, Bahia la Choya, Northern Gulf of California, *Paleontol. Soc. Spec. Publ.* **2**:189-199.
- Meldahl, K. H., 1987b, Sedimentologic and taphonomic implications of biogenic stratification, *Palaaios* **2**:350-358.
- Meldahl, K. H., and Flessa, K. W., 1990, Taphonomic pathways and comparative biofacies and taphofacies in a Recent intertidal/shallow shelf environment, *Lethaia* **23**:43-60.
- Menard, H. W., and Boucot, A. J., 1951, Experiments on the movement of shells by water, *Am. J. Sci.* **249**:131-151.
- Meyer, D. L., 1971, Post-mortem disarticulation of Recent crinoids and ophiuroids under natural conditions, *Geol. Soc. Am. Abstr. Progr.* **3**:645.
- Meyer, D. L., and Meyer, K. B., 1986, Biostratigraphy of Recent crinoids (Echinodermata) at Lizard Island, Great Barrier Reef, Australia, *Palaaios* **1**:294-302.
- Meyer, D. L., Ausich, W. I., and Terry, R. E., 1989, Comparative taphonomy of echinoderms in carbonate facies: Fort Payne Formation (Lower Mississippian) of Kentucky and Tennessee, *Palaaios* **4**:533-552.
- Middlemiss, F. A., 1962, Brachiopod ecology and lower Greens and palaeogeography, *Palaeontology* **5**:253-267.
- Middleton, G. V., 1967, The orientation of concave-convex particles deposited from experimental turbidity currents, *J. Sediment. Petrol.* **37**:229-32.
- Miller, A. I., 1988, Spatial resolution in subfossil molluscan remains: Implications for paleobiological analysis, *Paleobiology* **14**:91-103.
- Miller, A. I., and Cummins, H., 1989, A numerical model for the formation of fossil assemblages: Estimating the degree of post-mortem transport along environmental gradients, *Geol. Soc. Am. Abstr. Progr.* **21**:A70.
- Miller, A. I., and Cummins, H., 1990, A baseline numerical model for the formation of fossil assemblages: Estimating the amount of post-mortem transport along environmental gradients, *Palaaios* **5**:303-316.

- Miller, K. B., Brett, C. E., and Parsons, K. M., 1988, The paleoecologic significance of storm-generated disturbance within a Middle Devonian muddy epeiric sea, *Palaaios* **3**:35-52.
- Miller, A. I., Llewellyn, G., Parsons, K. M., Cummins, H., Greenstein, B. J., Boardman, M. R., Sloane, G. B., and Jacobs, D. K., 1990, The effect of Hurricane Hugo on molluscan skeletal distributions, Salt River Bay, St. Croix, U.S. Virgin Islands, *Geol. Soc. Am. Abstr.* **22**:A330.
- Miller, W., III, 1983, Survey of the Pyramidellid gastropods in the Wassaw Sound area, coastal Georgia, *Nautilus* **97**:93-98.
- Miller, W., III, and DuBar, J. R., 1988a, Community replacement of a Pleistocene *Crepidula* biostrome, *Lethaia* **21**:67-78.
- Miller, W., III, and DuBar, J. R., 1988b, The use of size frequency distribution in paleoecology: A reply, *Lethaia* **21**:416.
- Milliman, J. D., 1974, *Marine Carbonates*, Springer-Verlag, New York.
- Milliman, J. D., Pilkey, O. H., and Ross, D. R., 1972, Sediments of the continental margin off the eastern United States, *Geol. Soc. Am. Bull.* **83**:1315-1334.
- Mills, E. L., 1969, The community concept in marine zoology, with comments on continua and instability in some marine communities: A review, *J. Fish. Res. Board Can.* **26**:1415-1428.
- Moore, D. G., and Curran, J. R., 1964, Wave-base, marine profile of equilibrium, and wave-built terraces: Discussion, *Geol. Soc. Am. Bull.* **75**:1267-1274.
- Moors, H. T., 1970, Current orientation of graptolites: Its significance and interpretation, *Sediment. Geol.* **4**:117-134.
- Morse, J. W., 1986, The surface chemistry of calcium carbonate minerals in natural waters: An overview, *Mar. Chem.* **20**:91-112.
- Müller, A. H., 1979, Fossilization (taphonomy), in: *Treatise on Invertebrate Paleontology. Part A, Introduction* (R. A. Robison and C. Teichert, eds.), Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas, pp. 2-78.
- Myers, A. C., 1981, Shell hash in the gravel beaches on islands of the central Maine coast, *Geol. Soc. Am. Abstr.* **13**:167.
- Nagle, J. S., 1967, Wave and current orientation of shells, *J. Sediment. Petrol.* **37**:1124-1138.
- Natland, M. L., 1957, Paleoecology of west coast Tertiary sediments, *Geol. Soc. Am. Mem.* **67**(2):543-572.
- Nelson, C. S., 1978, Temperate shelf carbonate sediments in the Cenozoic of New Zealand, *Sedimentology* **25**:737-771.
- Nelson, C. S., 1988, An introductory perspective on non-tropical shelf carbonates, *Sediment. Geol.* **60**:3-12.
- Nelson, C. S., and Hancock, G. E., 1984, Composition and origin of temperate skeletal carbonate sediments on South Maria Ridge, northern New Zealand, *N. Z. J. Mar. Freshwater Res.* **18**:221-239.
- Nelson, C. S., and Young, H. R., 1985, Biodegradation of temperate-water skeletal carbonates by boring sponges on the Scott Shelf, British Columbia, Canada, *Mar. Geol.* **65**:33-45.
- Nichols, F. H., and Thompson, J. K., 1985, Time scales of change in the San Francisco Bay benthos, *Hydrobiologia* **129**:121-138.
- Nichols, J. A., Rowe, G. T., Clifford, C. H., and Young, R. A., 1978, In situ experiments on the burial of marine invertebrates, *J. Sediment. Petrol.* **48**:419-425.
- Noble, J. P. A., and Logan, A., 1981, Size frequency distributions and taphonomy of brachiopods. A recent model, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **36**:87-105.
- Noe-Nygaard, N., Surlyk, F., and Piasecki, S., 1987, Bivalve mass mortality caused by toxic dinoflagellate blooms in a Berriasian-Valanginian lagoon, Bornholm, Denmark, *Palaaios* **2**:263-273.
- Norris, R. D., 1986, Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California, *Palaaios* **1**:256-270.
- Oliver, J. S., Kvitek, R. G., and Slatery, P. N., 1985, Walrus feeding disturbance: Scavenging habits and recolonization of the Bering Sea benthos, *J. Exp. Mar. Biol. Ecol.* **91**:233-246.

- Olson, E. C., 1957, Size-frequency distribution of samples of extinct organisms, *J. Geol.* **65**:309-333.
- Orlov, Yu. A., 1959, *Fundamentals of Paleontology*, Izdatel'stvo Akademii Nauk SSR, p. 482 [translation, Israel Program of Scientific Translations, Jerusalem (1962)].
- Oschmann, W., 1988, Kimmeridge clay sedimentation—A new cyclic model, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **63**:109-140.
- Paine, R. T., 1966, Food web complexity and species diversity, *Am. Nat.* **100**:65-75.
- Paine, R. T., and Levin, S. A., 1981, Intertidal landscapes: Disturbance and the dynamics of pattern, *Ecol. Monogr.* **51**:145-178.
- Palmer, T. J., and Fürsich, F. T., 1974, The ecology of a middle Jurassic hardground and crevice fauna, *Palaeontology* **17**:507-524.
- Papp, A., 1944, Die senkrechte Einregelung von Gastropodengehäusen in Tertiärschichten des Wiener Beckens, *Palaeobiologica* **8**:144-153.
- Parker, R. H., 1960, Ecology and distributional patterns of marine macroinvertebrates, northern Gulf of Mexico, in: *Recent Sediments, Northwest Gulf of Mexico* (F. P. Shepard, F. B. Phleger, and T. H. van Andel, eds.), American Association of Petroleum Geologists, Tulsa, Oklahoma, pp. 307-337.
- Parker, R. H., 1963, Zoogeography and ecology of some macroinvertebrates, particularly mollusks, in the Gulf of California and the continental slope off Mexico, *Vidensk. Medd. Dansk. Naturh. Foren.* **126**:1-178.
- Parsons, K. M., Brett, C. E., and Miller, K. B., 1988, Taphonomy and depositional dynamics of Devonian shell-rich mudstones, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **63**:109-140.
- Pearson, T. H., and Barnett, P. R. O., 1987, Long-term changes in benthic populations in some west European coastal areas, *Estuaries* **10**:220-226.
- Petersen, C. G. J., 1914, Valuation of the sea, II, The animal communities of the sea bottom and their importance for marine zoogeography, *Rep. Dan. Biol. Sta.* **21**:1-44.
- Peterson, C. H., 1975, Stability of species and of community for the benthos of two lagoons, *Ecology* **56**:958-965.
- Peterson, C. H., 1976, Relative abundance of living and dead molluscs in two California lagoons, *Lethaia* **9**:137-148.
- Peterson, C. H., 1977, The paleontological significance of undetected short-term temporal variability, *J. Paleontol.* **51**:976-981.
- Peterson, C. H., 1983, Interactions between two infaunal bivalves, *Chione undatella* (Sowerby) and *Protothaca staminea* (Conrad), and two potential enemies, *Crepidula onyx* Sowerby and *Cancer anthonyi* (Rathburn), *J. Exp. Mar. Biol. Ecol.* **68**:145-158.
- Peterson, C. H., 1985, Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance, *Paleobiology* **11**:139-155.
- Philippon, J., and Plaziat, J.-C., 1975, Roles respectifs de la corrosion et des Cryptogames perforantes dans la destruction des coquilles de Mollusques des mangroves. Conséquences sur la fossilisation, *C. R. Acad. Sci. Paris* **281**:617-620.
- Pickrill, R. A., 1985, Sedimentation in an ebb-tidal delta, Ranganu Harbor, Northland, New Zealand, *N. Z. J. Geol. Geophys.* **28**:531-542.
- Pilkey, O. H., and Curran, H. A., 1986, Molluscan shell transport—You ain't seen nothin' yet, *Palaios* **1**:197.
- Pilkey, O. H., Martin, R. W., and Luternauer, J., 1967, The carbonate fraction of beach and dune sands, *Sedimentology* **8**:311-327.
- Pilkey, O. H., Fierman, E. I., and Trumbull, J. V. A., 1979, Relationship between physical condition of the carbonate fraction and sediment environments: Northern Puerto Rico shelf, *Sed. Geol.* **24**:283-290.
- Pip, E., 1988, Differential attrition of molluscan shells in freshwater sediments, *Can. J. Earth Sci.* **25**:68-73.
- Pisera, A., 1987, Boring and nesting organisms from Upper Jurassic coral colonies from northern Poland, *Acta Palaeontol. Polon.* **32**:83-104.
- Plotnick, R. E., 1986, Taphonomy of a modern shrimp: Implications for the arthropod fossil record, *Palaios* **1**:286-293.

- Poag, C. W., 1969, Dissolution of molluscan calcite by the attached foraminifer *Vasiglobulina*, new genus (*Vasiglobulinae*, new subfamily), *Tulane Stud. Geol. Paleontol.* **7**:45-72.
- Ponder, W. F., 1983, A revision of the Recent Xenophoridae of the world and of the Australian fossil species (Mollusca: Gastropoda), *Mem. Aust. Mus.* **17**:1-126.
- Powell, E. N., and Davies, D., 1989, When is an "old" shell really old? *Donax* on Texas beaches, *Geol. Soc. Am. Abstr. Progr.* **21**:A71.
- Powell, E. N., Stanton, R. J., Jr., Cummins, H., and Staff, G., 1982, Temporal fluctuations in bay environments—The death assemblage as a key to the past, in: *Proceedings Symposium Recent Benthological Investigations in Texas and Adjacent States*, Academy of Science, Austin, Texas.
- Powell, E. N., Cummins, H., Stanton, R. J., and Staff, G., 1984, Estimation of the size of molluscan larval settlement using the death assemblage, *Estuarine Coastal Shelf Sci.* **18**:367-384.
- Powell, E. N., Logan, A., Stanton, R. J., Jr., Davies, D. J., and Hare, P. E., 1989, Estimating time-since-death from the free amino acid content of the mollusc shell: A measure of time averaging in modern death assemblages? Description of the technique, *Palaios* **4**:16-31.
- Pratje, O., 1929, Fazettieren von Molluskenschalen, *Palaeontol. Z.* **11**:151-169.
- Price, A. R. G., 1982, Western Arabian Gulf echinoderms in high salinity waters and the occurrence of dwarfism, *J. Nat. Hist.* **16**:519-527.
- Price, J. H., Irvine, D. E. G., and Farnham, W. F. (eds.), 1980, *The Shore Environment*, Volume 2: Ecosystems (Systematics Association Special Volume 17), Academic Press, London.
- Prince, C. M., Elmore, R. D., Ehrlich, R., and Pilkey, O. H., 1987, Areal and lateral changes in a major trailing margin turbidite—The Black Shell Turbidite, *Geo-Marine Lett.* **7**:103-112.
- Probert, P. K., 1973, The bottom fauna of china clay waste deposits in Mevagissey Bay, Thesis, University of London.
- Probert, P. K., 1984, Disturbance, sediment stability and trophic structure of soft bottom communities, *J. Mar. Res.* **42**:893-921.
- Rasmussen, K. A., and Brett, C. E., 1985, Taphonomy of Holocene cryptic biotas from St. Croix, Virgin Islands: Information loss and preservation biases, *Geology* **13**:551-553.
- Raup, D. M., 1973, Depth inferences from vertically imbedded cephalopods, *Lethaia* **6**:217-226.
- Reaves, C. M., 1986, Organic matter metabolizability and calcium carbonate dissolution in nearshore marine muds, *J. Sediment. Petrol.* **56**:486-494.
- Rees, E. I. S., Nicholaidou, A., and Laskaridou, P., 1977, The effects of storms on the dynamics of shallow water benthic associations, in: *Biology of Benthic Organisms. Proceedings of the 11th European Symposium on Marine Biology* (B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden, eds.), Pergamon Press, Oxford, pp. 465-474.
- Reichelt, R. E., Green, D. G., and Bradbury, R. H., 1985, Discrete simulation of cyclone effects on the spatial patterns and community structure of a coral reef, in: *Proceedings 5th International Coral Reef Congress, Tahiti*, Volume 3, pp. 337-342.
- Reyment, R. A., 1980, Floating orientations of cephalopod shell models, *Palaeontology* **24**:931-936.
- Reyment, R. A., 1986, Nekroplanktonic dispersal of echinoid tests, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **52**:347-349.
- Rhoads, D. C., and Stanley, D. J., 1965, Biogenic graded bedding, *J. Sediment. Petrol.* **35**:956-963.
- Richards, R. P., and Bambach, R. K., 1975, Population dynamics of some Paleozoic brachiopods and their paleoecological significance, *J. Paleontol.* **49**:775-798.
- Richter, R., 1942, Der Einkippungsregel, *Senckenbergiana* **25**:181-206.
- Rosenberg, R., 1977, Benthic macrofaunal dynamics, production and dispersion in an oxygen-deficient estuary of west Sweden, *J. Exp. Mar. Biol. Ecol.* **26**:107-133.
- Rowland, S. M., and Gangloff, R. A., 1988, Structure and paleoecology of Lower Cambrian reefs, *Palaios* **3**:111-135.
- Ruffell, A. H., 1990, The mineralogy and petrology of the Sulphur Band phosphates (Aptian-Albian), at Folkestone, Kent, *Proc. Geol. Assoc.* **101**:79-84.



- Ruhrmann, G., 1971, Riff-nahe Sedimentation paläozoischer Krinoiden-Fragmente, *Neues Jahrb. Geol. Paläontol. Abh.* **138**:56–100.
- Sadler, P. M., 1981, Sediment accumulation rates and the completeness of stratigraphic sections, *J. Geol.* **89**:569–584.
- Saelen, G., 1989, Diagenesis and construction of the belemnite rostrum, *Palaeontology* **32**:765–798.
- Salazar-Jimenez, A., Frey, R. W., and Howard, J. D., 1982, Concavity orientations of bivalve shells in estuarine and nearshore shelf sediments, Georgia, *J. Sediment. Petrol.* **52**:565–586.
- Sammarco, P. W., and Risk, M. J., 1990, Large-scale patterns in internal bioerosion of *Porites*: Cross continental shelf trends on the Great Barrier Reef, *Mar. Ecol. Progr. Ser.* **59**:145–156.
- Samtleben, C., 1981, Die Muschelfauna der Schlei (Westliche Ostsee)—aktuopaläontologische Untersuchungen an einem sterbenden Gewässer, *Meyniana* **33**:6–183.
- Sanders, H. L., 1956, Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities, *Bull. Bingham Oceanogr. Coll.* **15**:345–414.
- Sanderson, D. J., and Donovan, R. N., 1974, The vertical packing of shells and stones on some Recent beaches, *J. Sediment. Petrol.* **44**:680–688.
- Sando, W. J., 1984, Significance of epibionts on horn corals from the Chainman Shale (Upper Mississippian) of Utah, *J. Paleontol.* **58**:185–196.
- Sarnthein, M., 1971, Oberflächensedimente im Persischen Golf und Golf von Oman, II, Quantitative Komponentenanalyse der Grossfraktion, *Meteor. Forsch. Ergebn. Reihe C* **5**:1–113.
- Saunders, W. B., and Spinosa, C., 1979, *Nautilus* movement and distribution in Palau, Western Caroline Islands, *Science* **204**:1199–1201.
- Schäfer, W., 1972, *Ecology and Palaeoecology of Marine Environments*. University of Chicago Press, Chicago.
- Schiffelbein, D. E., 1985, Extracting the benthic mixing impulse response function: A constrained deconvolution technique, *Mar. Geol.* **65**:313–336.
- Schindel, D. E., 1980, Microstratigraphic sampling and the limits of paleontological resolution, *Paleobiology* **6**:408–426.
- Schindel, D. E., 1982, Resolution analysis: A new approach to the gaps in the fossil record, *Paleobiology* **8**:340–353.
- Schopf, T. J. M., 1978, Fossilization potential of an intertidal fauna: Friday Harbor, Washington, *Paleobiology* **4**:261–270.
- Schott, J., Brantley, S., Crerar, D., Guy, C., Borcsik, M., and Willaime, C., 1989, Dissolution kinetics of strained calcite, *Geochim. Cosmochim. Acta* **53**:373–382.
- Schroeder, J., and Zankl, H., 1974, Dynamic reef formation: A sedimentological concept based on studies of Recent Bermuda and Bahama reefs, in: *Proceedings 2nd International Coral Reef Symposium, Brisbane, Volume 3*, pp. 413–428.
- Scoffin, T. P., 1987, *An Introduction to Carbonate Sediments and Rocks*, Chapman and Hall, New York.
- Scoffin, T. P., and Garrett, P., 1974, Processes in the formation and preservation of internal structure in Bermuda patch reefs, in: *Proceedings 2nd International Coral Reef Symposium, Brisbane, Volume 2*, pp. 429–448.
- Scoffin, T. P., and Henry, M. D., 1984, Shallow-water sclerosponges on Jamaican reefs and a criterion for recognition of hurricane deposits, *Nature* **307**:728–729.
- Scoffin, T. P., Alexandersson, E. T., Bowes, G. E., Clokie, J. J., Farrow, G. E., and Milliman, J. D., 1980, Recent, temperate, sub-photic, carbonate accumulation: Rockall Bank, northeast Atlantic, *J. Sediment. Petrol.* **50**:331–356.
- Scott, P. J. B., 1988, Distribution, habitat and morphology of the Caribbean coral- and rock-boring bivalve, *Lithophaga bisulcata* (d'Orbigny), *J. Molluscan Stud.* **54**:83–95.
- Scott, P. J. B., and Risk, M. J., 1988, The effect of *Lithophaga* (Bivalvia: Mytilidae) boreholes on the strength of the coral *Porites lobata*, *Coral Reefs* **7**:145–151.
- Scott, R. W., 1970, Paleocology and paleontology of the Lower Cretaceous Kiowa Formation, Kansas, *Univ. Kansas Paleontol. Contrib. Art.* **52**(Cretaceous 1):1–94.

- Scott, R. W., 1978, Approaches to trophic analysis of paleocommunities, *Lethaia* **11**:1–14.
- Seibold, E., Diester, L., Fütterer, D., Lange, H., Müller, P., and Werner, F., 1973, Holocene sediments and sedimentary processes in the Iranian part of the Persian Gulf, in: *The Persian Gulf* (B. H. Purser, ed.), Springer-Verlag, Berlin, pp. 57–80.
- Seilacher, A., 1963, Umlagerung und Rolltransport von Cephalopoden-Gehäusen, *Neues Jahrb. Geol. Paläontol. Monatsh.* **1963**:593–615.
- Seilacher, A., 1969, Paleocology of boring barnacles, *Am. Zool.* **9**:705–719.
- Seilacher, A., 1973, Biostratigraphy: The sedimentology of biologically standardized particles, in: *Evolving Concepts in Sedimentology* (R. N. Ginsburg, ed.), Johns Hopkins University Press, Baltimore, pp. 159–177.
- Seilacher, A., 1982a, General remarks about event deposits, in: *Cyclic and Event Stratification* (G. Einsele and A. Seilacher, eds.), Springer, Berlin, pp. 161–174.
- Seilacher, A., 1982b, Posidonia shales (Toarcian, S. Germany)—Stagnant basin model revalidated, in: *Paleontology, Essential of Historical Geology* (E. M. Gallitelli, ed.), STEM Mucchi, Modena, Italy, pp. 25–55.
- Seilacher, A., 1984, Constructional morphology of bivalves: Evolutionary pathways in primary versus secondary soft-bottom dwellers, *Palaeontology* **27**:207–237.
- Seilacher, A., 1985, The Jeram model: Event condensation in a modern intertidal environment, in: *Sedimentary and Evolutionary Cycles* (U. Bayer and A. Seilacher, eds.), Springer-Verlag, Berlin, pp. 336–346.
- Seilacher, A., and Meischner, D., 1965, Fazies-Analyse im Paläozoikum des Oslo-Gebietes, *Geol. Rundsch.* **54**:596–619.
- Seilacher, A., and Westphal, F., 1971, Fossil-Lagerstätten, in: *Sedimentology of Parts of Central Europe, Guidebook 8th International Sedimentology Congress* (G. Müller, ed.), W. Kramer, Frankfurt-am-Main, pp. 327–335.
- Seilacher, A., Reif, W.-E., and Westphal, F., 1985, Sedimentological, ecological and temporal patterns of fossil Lagerstätten, *Phil. Trans. R. Soc. Lond. B* **311**:5–23.
- Sheehan, P. M., 1978, The hinging mechanisms of brachiopods—Taphonomic considerations, *J. Paleontol.* **52**:748.
- Shillabeer, N., and Tapp, J. F., 1990, Long-term studies of the benthic biology of the Tees bay and the Tees estuary, *Hydrobiologia* **195**:63–78.
- Shimoyama, S., 1985, Size-frequency distribution of living populations and dead shell assemblages in a marine intertidal sand snail, *Umbonium* (Suchium) *moniliferum* (Lamarck), and their palaeoecological significance, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **49**:327–353.
- Shuto, T., 1973, Molluscan thanatocoenoses in Usuki Bay, East Kyushu, *Tohoku Univ. Sci. Rep. 2nd Ser. Spec. Vol.* **6**:15–27.
- Smith, A. B., 1984, *Echinoid Paleobiology*, Allen and Unwin, London.
- Smith, J. E., 1932, Shell gravel deposits, and the infauna of the Eddystone Grounds, *J. Mar. Biol. Assoc. U. K.* **18**:243–278.
- Smyth, M. J., 1988, The foraminifer *Cymbaloporella tabellaeformis* (Brady) bores into gastropod shells, *J. Foramin. Res.* **18**:277–285.
- Smyth, M. J., 1989, Bioerosion of gastropod shells: With emphasis on effects of coralline algal cover and shell microstructure, *Coral Reefs* **8**:119–125.
- Smyth, M. J., 1990, Incidence of boring organisms in gastropod shells on reefs around Guam, *Bull. Mar. Sci.* **46**:432–449.
- Sokal, R. R., and Rohlf, F. J., 1981, *Biometry*, 2nd ed., W. H. Freeman, San Francisco.
- Sorby, H. C., 1879, Anniversary address of the president: The structure and origin of limestones, *Proc. Geol. Soc. Lond.* **35**:56–95.
- Southward, A. J., 1962, The distribution of some plankton animals in the English Channel and its approaches II. Surveys with the Gulf III high speed sampler, 1958–60, *J. Mar. Biol. Assoc. U. K.* **42**:275–375.
- Southward, A. J., 1980, The western English Channel—An inconsistent system?, *Nature* **285**:361–366.
- Speyer, S. E., and Brett, C. E., 1985, Clustered trilobite assemblages in the Middle Devonian Hamilton Group, *Lethaia* **18**:85–103.

- Speyer, S. E., and Brett, C. E., 1986, Trilobite taphonomy and Middle Devonian taphofacies, *Palaaios* 1:312-327.
- Speyer, S. E., and Brett, C. E., 1988, Taphofacies models for epeiric sea environments: Middle Paleozoic examples, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63:225-262.
- Spjeldnaes, N., 1978, Ecology of selected late and post-glacial marine faunas in the Oslo Fjord area, *Geol. Fören. Stockh. Förh.* 100:189-202.
- Stachowitsch, M., 1980, The epibiotic and endolithic species associated with the gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*, *Mar. Ecol. (Proc. Staz. Zool. Napoli)* 1:73-101.
- Staff, G. M., and Powell, E. N., 1988, The paleoecological significance of diversity: The effect of time averaging and differential preservation on macroinvertebrate species richness in death assemblages, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63:73-89.
- Staff, G. M., and Powell, E. N., 1990, Taphonomic signature and the imprint of taphonomic history: Discriminating between taphofacies of the inner continental shelf and a microtidal inlet, in: *Paleocommunity Temporal Dynamics* (W. Miller, ed.), Paleont. Soc. N. Amer. Spec. Pub., pp. 370-390.
- Staff, G. M., Powell, E. N., Stanton, R. J., and Cummins, H., 1985, Biomass: Is it a useful tool in paleocommunity reconstruction?, *Lethaia* 18:209-232.
- Staff, G. M., Stanton, R. J., Jr., Powell, E. N., and Cummins, H., 1986, Time averaging, taphonomy and their impact on paleocommunity reconstruction: Death assemblages in Texas bays, *Geol. Soc. Am. Bull.* 97:428-443.
- Stanley, S. M., 1970, Relation of shell form to life habits in the Bivalvia (Mollusca), *Geol. Soc. Am. Mem.* 125:1-296.
- Stanton, R. J., Jr., 1976, Relationship of fossil communities to original communities of living organisms, in: *Structure and Classification of Paleocommunities* (R. W. Scott and R. R. West, eds.), Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 107-142.
- Stanton, R. J., and Dodd, J. R., 1976, The application of trophic structure of fossil communities, *Lethaia* 9:327-342.
- Stebbins, T. D., 1987, Mass mortality of the bubble snail *Bulla gouldiana* Pilsbry, 1893 (Gastropoda: Opisthobranchia), *Veliger* 30:95.
- Steimle, F. W., and Sinderman, C. J., 1978, Review of oxygen depletion and associated mass mortality in the Middle Atlantic Bight in 1976, *Mar. Fish. Rev.* 40:17-26.
- Steneck, R. S., 1983, Escalating herbivory and resulting adaptive trends in calcareous algae, *Paleobiology* 9:45-63.
- Steneck, R. S., and Paine, R. T., 1986, Ecological and taxonomic studies of shallow water encrusting Corallinaceae (Rhodophyta) of the boreal northeastern Pacific, *Phycologia* 25:221-240.
- Stephenson, W., Williams, W. T., and Cook, S. G., 1971, Computer analysis of Petersen's original data on bottom communities, *Ecol. Monogr.* 42:387-415.
- Sturrock, S. J., 1982, Foraminifera and carbonate sediments in a temperate water high energy environment, Thesis, University of Exeter.
- Surlyk, F., 1972, Morphological adaptations and population structures of the Danish Chalk brachiopods (Maastrichtian), upper Cretaceous, *K. Dan. Vidensk. Selsk. Biol. Skr.* 19:1-57.
- Swift, D. J. P., 1970, Quaternary shelves and the return to grade, *Mar. Geol.* 8:5-30.
- Swift, D. J. P., 1976, Coastal sedimentation, in: *Marine Sediment Transport and Environmental Management* (D. J. Stanley and D. J. P. Swift, eds.), Wiley, New York, pp. 255-310.
- Taft, W. H., and Harbaugh, J. W., 1964, Modern carbonate sediments of south Florida, Bahamas and Espirito Santo Island, Baja California: A comparison of their mineralogy and chemistry, *Stanford Univ. Publ. Geol. Sci.* 8:1-133.
- Tanabe, K., and Arimura, E., 1987, Ecology of four infaunal bivalve species in the Recent intertidal zone, Shikoku, Japan, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 60:219-230.
- Tanabe, K., Fujiki, T., and Katsuta, T., 1986, Comparative analysis of living and death bivalve assemblages on the Kawarazu Shore, Ehime Prefecture, west Japan, *Bull. Jpn. Assoc. Benthol.* 30:17-30.
- Tasch, P., 1955a, The concept of psephrocrocoenosis applied to "dwarf" fossil faunas, *Am. Midl. Nat.* 53:205-212.

- Tasch, P., 1955b, Paleoeologic observations on the orthoceratid coquina beds of the Maquoketa at Graf, Iowa, *J. Paleontol.* 29:510-518.
- Taylor, J. D., and Layman, M., 1972, The mechanical properties of bivalve (Mollusca) shell structures, *Palaeontology* 15:73-87.
- Taylor, P. D., 1984, Adaptations for spatial competition in Silurian encrusting bryozoans, in: *Autecology of Silurian Organisms* (M. J. Bassett and J. D. Lawson, eds.), *Spec. Pap. Palaeontol.* 32:197-210.
- Taylor, P. D., Schembri, P. J., and Cook, P. L., 1989, Symbiotic associations between hermit crabs and bryozoans from the Otago region, southeastern New Zealand, *J. Nat. Hist.* 23:1059-1085.
- Teichert, C., and Serventy, D. L., 1947, Deposits of shells transported by birds, *Am. J. Sci.* 245:322-328.
- Thorson, G., 1957, Bottom communities (sublittoral or shallow shelf), in: *Treatise on marine ecology and paleoecology* (J. W. Hedgpeth, ed.), *Geol. Soc. Am. Mem.* 67:461-534.
- Toots, H., 1965, Random orientation of fossils and its significance, *Wyoming Univ. Contrib. Geol.* 4:59-62.
- Trewin, N. H., and Welsh, W., 1976, Formation and composition of a graded estuarine shell bed, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 19:219-230.
- Tsuchiya, M., 1983, Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores, *J. Exp. Mar. Biol. Ecol.* 66:101-111.
- Tunnicliffe, V., 1979, The role of boring sponges in coral fracture, *Colloq. Int. CNRS* 291:309-315.
- Turner, H. M., 1985, Parasites of eastern oysters from subtidal reefs in a Louisiana estuary with a note on their use as indicators of water quality, *Estuaries* 8:323-325.
- Urlichs, M., 1975, Über einen Kondensationshorizont im Pliensbachium (Lias) von Franken, *Geol. Blätter NO Bayern* 25:29-38.
- Valentine, J. W., 1989, How good was the fossil record? Clues from the Californian Pleistocene, *Paleobiology* 15:83-94.
- Valentine, J. W., and Mallory, B., 1965, Recurrent groups of bonded species in mixed death assemblages, *J. Geol.* 73:683-701.
- Van Straaten, L. M. J. U., 1952, Biogene textures and the formation of shell beds in the Dutch Wadden Sea, *Proc. K. Ned. Akad. Wet. Amst. B* 55:500-516.
- Van Straaten, L. M. J. U., 1956, Composition of shell beds formed in tidal flat environments in the Netherlands and in the bay of Arachon (France), *Geol. Mij.* 18:209-226.
- Van Straaten, L. M. J. U., 1960, Marine mollusc shell assemblages of the Rhine Delta, *Geol. Mij.* 39:105-129.
- Van Straaten, L. M. J. U., 1967, Turbidite, ash layers and shell beds in the bathyal zone of the southeastern Adriatic Sea, *Rev. Géogr. Phys. Géol. Dynam. Sér. 2* 9(3):219-240.
- Van Tassell, J., 1981, Silver Abyssal Plain carbonate turbidite: Flow characteristics, *J. Geol.* 89:317-333.
- Velbel, M. A., and Brandt, D. S., 1989, Differential preservation of brachiopod valves: Taphonomic bias in *Platystrophia ponderosa*, *Palaaios* 4:193-195.
- Vevers, H. G., 1952, A photographic survey of certain areas of the sea floor near Plymouth, *J. Mar. Biol. Assoc. U. K.* 31:215-222.
- Vogel, K., Golubic, S., and Brett, C. E., 1987, Endolith associations and their relation to facies distribution in the Middle Devonian of New York State, U.S.A., *Lethaia* 20:263-290.
- Vogel, S., 1988, *Life's Devices*, Princeton University Press, Princeton, New Jersey.
- Von Esternhagen, H., and Dethlefsen, V., 1983, North Sea oxygen deficiency and its effects on bottom faunas, *Ambio* 12:264-266.
- Waage, K. M., 1964, Origin of repeated fossiliferous concretion layers in the Fox Hills Formation, *Kansas Geol. Surv. Bull.* 169:541-563.
- Wagner, F. J. E., 1975, Mollusca of the Strait of Canso area, *Geol. Surv. Can. Pap.* 75-23:1-22.
- Walker, B. M., 1979, Shell dissolution: Destructive diagenesis in a meteoric environment, *Scanning Electron Microscopy/1979* 2:463-468.
- Walker, K. R., and Bambach, R. K., 1971, The significance of fossil assemblages from fine grained sediments: Time-averaged communities, *Geol. Soc. Am. Abstr. Progr.* 3:783-784.



- Walker, K. R., and Diehl, W. W., 1985, The role of cementation in the preservation of Lower Palaeozoic assemblages, *Phil. Trans. R. Soc. Lond. B* **311**:143-153.
- Walker, K. R., and Parker, W. C., 1976, Population structure of a pioneer and a later stage species in an Ordovician ecological succession, *Paleobiology* **2**:191-201.
- Walker, S. E., 1988, Taphonomic significance of hermit crabs (Anomura: Pagurida): Epifaunal hermit crab-infaunal gastropod example, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **63**:45-71.
- Walker, S. E., 1989, Hermit crabs as taphonomic agents, *Palaios* **4**:439-452.
- Walker, S. E., Kidwell, S. M., and Powell, E. N., 1989, Molluscan death assemblages on the Texas continental shelf are potentially local, not exotic, accumulations, *Geol. Soc. Am. Abstr. Progr.* **21**:A71.
- Walter, L. M., 1985, Relative reactivity of skeletal carbonates during dissolution: Implications for diagenesis, *Soc. Econ. Paleontol. Mineral. Spec. Publ.* **36**:3-16.
- Walter, L. M., and Burton, E., 1990, Dissolution of Recent platform carbonate sediments in marine pore fluids, *Am. J. Sci.* **290**:601-643.
- Walter, L. M., and Hanor, J. S., 1979, Effect of orthophosphate on the dissolution kinetics of biogenic magnesian calcites, *Geochim. Cosmochim. Acta* **43**:1377-1385.
- Walter, L. M., and Morse, J. W., 1984, Reactive surface area of skeletal carbonates during dissolution: Effect of grain size, *J. Sediment. Petrol.* **54**:1081-1090.
- Walter, L. M., and Morse, J. W., 1985, The dissolution kinetics of shallow marine carbonates in seawater: A laboratory study, *Geochim. Cosmochim. Acta* **49**:1503-1513.
- Walther, J., 1893-1894, *Einleitung in die Geologie als historische Wissenschaft*, Fischer, Jena.
- Wanless, H., Tedesco, L., and Tyrrell, K., 1987, Production of subtidal tubular and surficial tempestites by Hurricane Kate, Caicos Platform British West Indies, *J. Sediment. Petrol.* **58**:739-750.
- Ward, M. A., and Thorpe, J. P., 1989, Assessment of space utilisation in a subtidal temperate bryozoan community, *Mar. Biol.* **103**:215-224.
- Ware, S., 1975, British Lower Greensand Serpulidae, *Palaeontology* **18**:93-116.
- Warne, J. E., 1969, Live and dead molluscs in a coastal lagoon, *J. Paleontol.* **43**:141-150.
- Warne, J. E., 1971, Paleoecological aspects of a modern coastal lagoon, *Univ. Calif. Publ. Geol. Sci.* **87**:1-110.
- Warne, J. E., Ekdale, A. A., Ekdale, S. F., and Peterson, C. H., 1976, Raw material of the fossil record, in: *Structure and Classification of Paleocommunities* (R. W. Scott, and R. R. West, eds.), Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 143-169.
- Warner, G. F., 1971, On the ecology of a dense bed of the brittle star *Ophiothrix fragilis*, *J. Mar. Biol. Assoc. U. K.* **51**:267-282.
- Wasmund, E., 1926, Biocoenose und Thanatocoenose, *Arch. Hydrobiol.* **17**:1-116.
- Watson, M. K., and Flessa, K. W., 1979, Time-averaged molluscan assemblages from Cholla Bay, Gulf of California, *Geol. Soc. Am. Abstr. Progr.* **11**:134.
- Watson, R. L., 1971, Origin of shell beaches, Padre Island, Texas, *J. Sediment. Petrol.* **41**:1105-1111.
- Weigelt, J., 1927, *Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung*, Wax Weg, Leipzig [English translation: *Recent Vertebrate Carcasses and their Paleobiological Implications*, University of Chicago Press, Chicago (1989)].
- Wendt, J., 1970, Fossil-Lagerstätten, Nr. 9: Stratigraphische Kondensation in triadischen und jurassischen Cephalopodenkalken der Tethys, *Neues Jahrb. Geol. Paläontol. Abh.* **135**:171-189.
- Wendt, J., 1988, Condensed carbonate sedimentation in the late Devonian of the eastern Anti-Atlas (Morocco), *Eclogae Geol. Helv.* **81**:155-173.
- Westrop, S. R., 1986, Taphonomic versus ecologic controls on taxonomic abundance patterns in tempestites, *Lethaia* **19**:123-132.
- White, C. A., 1879, Conditions of preservation of invertebrate fossils, *U.S. Geol. Surv. Territorial Bull.* **5**:133-141.
- Whittaker, R. H., 1975, *Communities and Ecosystems*, 2nd ed. Macmillan, New York.
- Whittington, H. B., and Conway Morris, S. (eds.), 1985, Extraordinary fossil biotas: Their ecological and evolutionary significance, *Phil. Trans. R. Soc. Lond. B* **311**:1-192.

- Wiedemann, H. V., 1972, Shell deposits and shell preservation in Quaternary and Tertiary estuarine sediments in Georgia, U.S.A., *Sediment. Geol.* **7**:103-125.
- Wignall, P. B., and Myers, K. J., 1988, Interpreting benthic oxygen levels in mudrocks: A new approach, *Geology* **16**:452-455.
- Wilson, J. B., 1965, The palaeoecological significance of infauna and their associated sediments, Ph. D. thesis, University of Edinburgh.
- Wilson, J. B., 1967, Palaeoecological studies on shellbeds and associated sediments in the Solway Firth, *Scot. J. Geol.* **3**:329-371.
- Wilson, J. B., 1982, Shelly faunas associated with temperate offshore tidal deposits, in: *Offshore Tidal Sands* (A. H. Stride, ed.), Chapman and Hall, London, pp. 126-171.
- Wilson, J. B., 1986, Faunas of tidal current and wave-dominated continental shelves and their use in the recognition of storm deposits, *Can. Soc. Petroleum Geol. Mem.* **11**:313-326.
- Wilson, J. B., 1988, A model for temporal changes in the faunal composition of shell gravels during a transgression on the continental shelf around the British Isles, *Sediment. Geol.* **60**:95-105.
- Wilson, M. A., 1985, Disturbance and ecologic succession in an Upper Ordovician cobble-dwelling hardground fauna, *Science* **228**:575-577.
- Wilson, M. A., 1987, Ecological dynamics on pebbles, cobbles and boulders, *Palaios* **2**:594-599.
- Wilson, M. V. H., 1988, Taphonomic processes: Information loss and information gain, *Geosci. Can.* **15**:131-148.
- Wright, T., and Kornicker, L. S., 1962, Island transport of marine shells by birds on Perez Island Alacran Reef, Campeche Bank, Mexico, *J. Geol.* **70**:616-618.
- Wulff, J. I., 1990, Biostratigraphic utility of *Archimedes* in environmental interpretation, *Palaios* **5**:160-166.
- Yanin, B. T., 1983, *Osnovy Taphonomii*, Nedra, Moscow.
- Yochelson, E. L., and Fraser, G. D., 1973, Interpretation of depositional environment of the Plympton Formation (Permian), southern Pequop Mountains, Nevada, from physical stratigraphy and a faunule, *U. S. Geol. Surv. J. Res.* **1**:19-32.
- Yochelson, E. L., and Lindemann, R. H., 1986, Considerations on systematic placement of the styliolines (Incertae sedis: Devonian), in: *Problematic Fossil Taxa* (A. Hoffman and M. H. Nitecki, eds.), Oxford University Press, Oxford, pp. 45-58.
- Young, H. R., and Nelson, C. S., 1988, Endolithic biodegradation of cool-water skeletal carbonates on Scott shelf, northwestern Vancouver Island, Canada, *Sediment. Geol.* **60**:251-267.
- Zenetos, A., 1990, Discrimination of autochthonous vs. allochthonous assemblages in the Eden Estuary, Fife, Scotland, U.K., *Estuarine Coastal Shelf Sci.* **30**:525-540.
- Ziegelmeier, E., 1963, Das Makrobenthos im Ostteil der Deutschen Bucht nach qualitativen und quantitativen Bodengreifer Untersuchungen in der Zeit von 1949-1960, *Veröff. Inst. Meeresforsch. Bremerhaven Sonderbd.* **1**:101-114.
- Ziegelmeier, E., 1964, Einwirkungen des kalten Winters 1962/63 auf das Makrobenthos im Ostteil der Deutschen Bucht, *Helgol. Wiss. Meeresunters.* **10**:276-282.

Table I. Synonymy of Classifications for Shelly Fossil Assemblages<sup>a</sup>

Classification	Wasmund (1926)	Boucot (1953)	Craig (1953)	Orlov (1959)	Brouwer (1959)	Johnson (1960)	Craig and Hallam (1963)	Fagerstrom (1964)	R.W. Scott (1970)	Hallam (1972)	Fürsich (1975, 1977, 1978)
I. Group of cooccurring live organisms	Biocoenosis	Community	Biocenosis	Life assemblage	Living community						
II. Group of cooccurring dead organisms	Thanatocoenosis	Fossil death assemblage	Fossil assemblage	Orictocenosis	Thanatocoenosis	Death assemblage	Death or fossil assemblage (thanatocoenosis)	Fossil assemblage			Fossil assemblage
... that are thought to represent: A. Production by the local fauna					Autochthonous thanatocoenosis						
... and are thought to provide 1. a nearly perfect record of live shelled taxa with respect to species relative abundances, size-frequency distributions, and life positions		Fossil life assemblage	Fossil community	Thanatocenosis	Autochthonous thanatocoenosis	Model I	Life assemblage (fossil community)	Fossil census (perfect) or fossil community	In-place assemblage	Census (assemblage)	
or 2. a somewhat modified record owing to post-mortem disturbance of shells (disarticulation, re-orientation, loss of fragile taxa and size classes) and/or time-averaging of generations			Fossil assemblage		Autochthonous thanatocoenosis	Model II	Indigenous assemblage	Residual census or residual fossil assemblage	Disturbed neighborhood assemblage	Death assemblage	Fossil association (recurrent assemblage); time-averaged community relic
... or to have been modified by 3. the addition of shells from other habitats			Mixed fossil assemblage		Thanatocoenosis of mixed character	Model II and III		Mixed fossil assemblage	Mixed assemblage		
or by 4. the addition of shells from later, ecologically distinct communities that occupy the site; community change may have been driven by physical environmental changes or by live/dead interactions			Mixed fossil assemblage			Model III		Mixed fossil assemblage			Environmentally or faunally condensed assemblage
or by 5. admixture with shells of significantly greater age						Model III		Mixed fossil assemblage			Faunally condensed assemblage
B. Shells that have been transported out of their life habitat			Assemblage of foreign fossils		Allochthonous thanatocoenosis	Model III	Exotic assemblage	Transported fossil assemblage	Transported assemblage		
C. Shells reworked from significantly older deposits							Remanié				
D. Shells introduced from significantly younger deposits											

<sup>a</sup>Italics indicates term used only for fossil examples.

Brouwer (1959)	Johnson (1960)	Craig and Hallam (1963)	Fagerstrom (1964)	R.W. Scott (1970)	Hallam (1972)	Fürsich (1975, 1977, 1978)	Yanin (1983)	Järvinen <i>et al.</i> (1986)	Kidwell <i>et al.</i> (1986)	Fürsich (1990)	Terms used in this chapter
Biocoenosis	Life assemblage	Living community			Life assemblage		Paleocoenosis	Community		Life assemblage	Community
Thanatocoenosis	Death assemblage	Death or fossil assemblage (thanatocoenosis)	Fossil assemblage			Fossil assemblage	Taphocoenosis, thanatocoenosis, or <i>orictocoenosis</i>	Taphocoenosis (after Quenstedt, 1930)		Fossil assemblage	Death or fossil assemblage
Autochthonous thanatocoenosis							Taphocoenosis or thanatocoenosis	Thanatocoenosis		Death assemblage = thanatocoenosis	Indigenous assemblage
Autochthonous thanatocoenosis	Model I	Life assemblage (fossil community)	Fossil census (perfect) or fossil community	In-place assemblage	Census (assemblage)		Taphocoenosis or thanatocoenosis	Paleocommunity	Autochthonous assemblage		Census assemblage
Autochthonous thanatocoenosis	Model II	Indigenous assemblage	Residual census or residual fossil assemblage	Disturbed neighborhood assemblage	Death assemblage	Fossil association (recurrent assemblage); time-averaged community relic	Taphocoenosis or thanatocoenosis	Paleocommunity = recurrent assemblage	Parautochthonous assemblage	Taphocoenosis	Within-habitat time-averaged assemblage
Thanatocoenosis of mixed character	Model II and III		Mixed fossil assemblage	Mixed assemblage			Taphocoenosis or thanatocoenosis	Symmigy	Mixed (parautoch- allochthonous) assemblage	Taphocoenosis	Mixed (indigenous- exotic) assemblage
	Model III		Mixed fossil assemblage			Environmentally or faunally condensed assemblage		Symmigy		Taphocoenosis	Multi-habitat time-averaged or environmentally condensed assemblage
	Model III		Mixed fossil assemblage			Faunally condensed assemblage		Symmigy			Biostratigraphically condensed assemblage
Allochthonous thanatocoenosis	Model III	Exotic assemblage	Transported fossil assemblage	Transported assemblage					Allochthonous assemblage		Exotic or allochthonous assemblage
		Remanié							Remanié		Remanié assemblage
									Leaked assemblage		Piped assemblage