THE SIZE-FREQUENCY DISTRIBUTION IN PALAEOECOLOGY: EFFECTS OF TAPHONOMIC PROCESSES DURING FORMATION OF MOLLUSCAN DEATH ASSEMBLAGES IN TEXAS BAYS

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ABSTRACT. The size-frequency distributions of the living community and death assemblage at two sites in Texas (Laguna Madre and Copano Bay) were compared to assess the effect of taphonomy on size-frequency distributions and survivorship curves during preservation. Taphonomic processes result in the formation of size-frequency distributions which often bear little resemblance to the size-frequency distributions of the species as they died in the living community. Circumstantial evidence suggests that larger size classes and adults tend to be preserved preferentially in the death assemblage. Consequently, biomass and adult individuals are preserved most accurately and serve as the only basis for assessing the population dynamics of a species. The shape of the entire size-frequency distribution is determined primarily by taphonomy; thus it provides a potentially useful source of information on species-specific and site-specific taphonomic processes in the fossil record. Most size-frequency distributions are unimodal. This is the expected equilibrium condition. Bimodal or multimodal distributions indicate a condition of disequilibrium produced by unique ecologic or taphonomic events.

IN benthic ecology, temporal change in the size-frequency distribution of a population can provide valuable information concerning recruitment, growth, and mortality and has been employed to assess important functional interactions in the community such as competition and predation, and important life history strategies such as *r*-selection and *K*-selection (e.g. Fenchel 1975; Stearns 1976; Vermeij *et al.* 1980). In palaeoecology, similar inferences have been sought from size-frequency distributions of fossil species (e.g. Hallam 1961; Hoffman 1976; Mancini 1978), but the size-frequency distribution provides data only on the size-specific mortality of a fossil species. Thus, all inferences on life history strategy and functional interactions within the community must be inferred from similarities with the size-frequency distributions of living species.

The size-frequency distribution for a fossil species is dependent upon the interplay between growth rate, mortality rate, and taphonomic processes. For the size-frequency distribution accurately to reflect the size-specific mortality of the original living community from which it was derived, all size classes must be equally preserved, or biased preservation must be recognized and considered in the interpretation. Moreover, time averaging can produce a cumulative size-frequency distribution composed of many originally distinct cohorts, each with its own size-specific mortality, that may not provide the data required for inferences on population dynamics because the theoretical basis of population analysis is based on the study of single cohorts. Thus, an understanding of population dynamics in the palaeo-community requires an understanding of how fossil assemblages form.

The formation of a death assemblage is the initial step in the creation of a fossil assemblage. During this step the skeletal components of preservable organisms are subjected to such taphonomic processes as dissolution, breakage, bioerosion, abrasion, and such time averaging processes as shell condensation, all of which may affect the size-frequency distribution. To assess the impact of taphonomy and time-averaging on population dynamics, we followed the preservation of cohorts of living species in the death assemblage at two locations in Texas bays and compared the

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size-frequency distributions of individuals at death with the final taphonomically-altered, time-averaged size-frequency distribution in the death assemblage.

MATERIALS AND METHODS

Study Sites

Two shallow-water, marine benthic communities were studied along the Texas coast. One site in Laguna Madre just offshore of Padre Island near South Bird Island was sampled for 18 months at 6-week intervals. The second site in Copano Bay near the mouth of the Aransas River was sampled for 21 months at 6-week intervals. A general description of the area and its geology and ecology can be found in Hedgepeth (1947), Brown *et al.* (1976), McGowen *et al.* (1976), Ladd *et al.* (1957), Parker (1959), and Calnan (1980).

Ecologic and environmental data for the two study sites were presented by Powell *et al.* (1982, 1984), Staff *et al.* (1985, 1986), and Cummins *et al.* (1986 *a*, *b*). Salinity at the Laguna Madre site was ~ 25–40 ‰ during the study period whereas salinity at the Copano Bay site, which was influenced by heavy rains and subsequent river runoff, was below 20 ‰ during this time. Sediment at the Laguna Madre site was a well-sorted fine to medium sand. The Copano Bay site was muddier, containing ~ 18 % clay and silt by weight.

The sampling locations were approximately 50 m offshore in about 1 m of water. A 100 m sampling line was established at each site. On each 6-week sampling occasion, two locations were chosen randomly along this line, but no location was within 2 m of any previous one. This eliminated the possibility of prior disturbance of the death assemblage by the field crew. During the April–October 1981 period, two box-core samples, 3 m apart, each 176 cm^2 × 17 cm deep, and one surface scrape, 24 cm × 3·0 m × 5 cm deep, were taken along a transect oriented perpendicular to the sampling line at each location. For the rest of the study, four box core samples and a 24 cm × 1·5 × 5 cm scrape were taken per 3 m transect. The samples were sieved in the field using a 500 μm screen and preserved in a buffered formalin solution with Rose Bengal.

Laboratory Procedures

All live and dead bivalves and gastropods were identified, measured, and placed into size classes. Sources for identification are listed by Powell *et al.* (1982). The maximum anterior–posterior length was measured for bivalves; the length from apex to abapical tip for gastropods. For the death assemblage, whole organisms were defined as those for which both maximum length and maximum width (height for bivalves) could be measured. For bivalves, left, right, and articulated valves are enumerated separately. To calculate the total number of valves collected, articulated valves were counted twice, free left or right valves once each (Powell *et al.* 1984). Fragments were counted only if the beak was present for bivalves and the apex for gastropods.

Individuals < 4·64 mm were placed in size classes at 0·48 mm intervals; individuals between 4.64 mm and 12·25 mm were grouped in size classes at 0·96 mm intervals. Individual sizes were recorded for larger specimens. For some analyses, specimens were regrouped in wider size classes depending upon the species' maximum size (e.g. size classes for *Tagelus plebeius* were set at 2·26 mm intervals because of its large maximum size).

Data analysis

Size at death, growth rate, and mortality rate were estimated from data on the living community. Growth rates were calculated using the size increase of cohorts over time, augmented where necessary by Levinton and Bambach's (1970) logarithmic growth equation. Mortality was estimated by determining the size classes that living individuals collected at one sampling period would be expected to occupy at the next succeeding sampling period. The difference between the actual number collected at the succeeding sampling period and the number predicted from the previous sample, if no mortality had occurred, gave an estimate of mortality for that period. Adult individuals were frequently rare enough that their patchy distribution (Cummins *et al.* 1986*a*) might have resulted in spurious results if analysis was limited to just two collecting periods. Consequently, mortality of large individuals having life spans much greater than two sampling periods was estimated similarly but using more collecting periods so that the absence of individuals due to real mortality could be distinguished from their absence due to collection failure produced by spatial patchiness. The individuals that died were allocated to the size class they occupied at the initial sampling occasion, as if they had died shortly after sampling. Consequently, the size-frequency distribution of individuals that died during the study represents a minimal estimate of size at death. The total contribution from the living community to the death assemblage was the sum of the mortality in each size class from all samples collected. This method severely underestimates mortality in the smallest size classes because sampling at 6-week intervals underestimates by 70–95 % the number of individuals that settle (Powell *et al.* 1984). Consequently, the size-frequency distributions generated from these estimates of size at death indicate proportionally fewer individuals in the smallest size classes than actually occurred.

The average size-frequency distribution of each species in the death assemblage was calculated by summing data from all individual samples (unless otherwise stated). These size-frequency distributions were grouped using an unweighted pair-group clustering method. The size data were double standardized to per cent maximum size and per cent individuals collected and similarity indices calculated using Euclidean distance after log-transformation of the standardized data. A computer program, NORMSEP, was used to model the size-frequency distributions as summations of one or more normal distributions (see Abramson 1971; Mundry 1972).

The number of adult individuals in the death assemblage was estimated from the general relation between per cent maximum size and first reproduction (Powell and Stanton 1985). Adult bivalves were $\geqslant 44\,\%$ of maximum size; adult gastropods $\geqslant 51\,\%$ of maximum size. Maximum sizes for the Texas coast were obtained from Odé (1975–1979), Andrews (1977), and our own data.

Biomass was calculated from a relation between biomass and shell dimensions (Powell and Stanton 1985). The equation for bivalves is:

$$\log_{10} \text{Biomass (gm)} = 0{\cdot}9576 \log_{10} L^3 - 4{\cdot}8939,$$

where L is the maximum anterior–posterior length in mm. The equation for gastropods is:

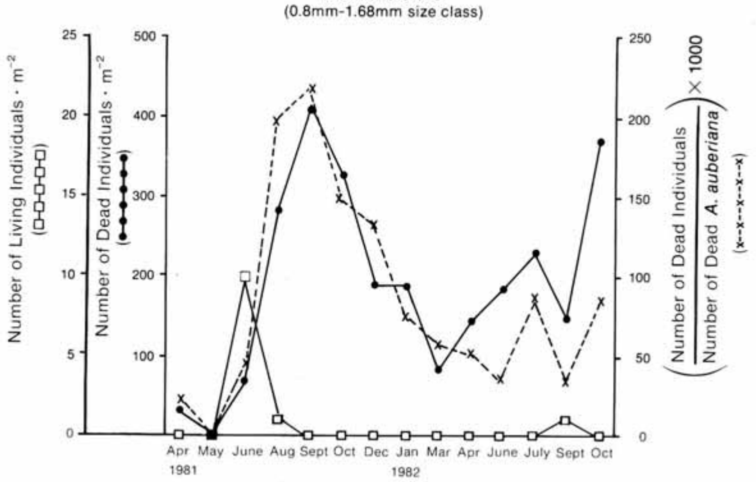
$$\log_{10} \text{Biomass (gm)} = 0{\cdot}7708 \log_{10} V - 3{\cdot}2421.$$

V is an operational equivalent of shell volume derived, in most cases, from the equation for the volume of a cone, $V = \frac{1}{3}\pi\,(W/2)^2 L$, where W (mm) is the maximum width and L (mm) is the maximum length. For a complete discussion of the determination of biomass and its palaeontologic significance, refer to Powell and Stanton (1985) and Staff *et al.* (1985).

Background description of the death assemblage

Individuals of a species were added to the death assemblage in pulses that gradually decayed as taphonomic processes destroyed the constituent individuals (Cummins *et al.* 1986*b*). For example, a pulse of living individuals of the bivalve *Mulinia lateralis* present in June 1981 produced, by their mortality, a pulse in the death assemblage in August, September, and October 1981 that gradually decayed during the next 6 months (text-fig. 1). At both sites, two types of species were present; those that were present as living individuals that died and proceeded through a pulse and decay mode similar to that of *M. lateralis*, and those that were never found alive and so had no input into the death assemblage during the study period. These latter species also did not decay measurably; that is, their continued presence in the death assemblage throughout the study period was due to their relative immunity to taphonomic loss rather than to any input from the living community.

Species, such as *M. lateralis*, which were found alive and which did generate pulses in the death assemblage also comprised individuals of two types (Cummins *et al.* 1986*b*). Some individuals were components of pulses added during the study period. Most of these individuals disappeared from the death assemblage over a period of 4 to 8 months. Other individuals were present at the beginning



TEXT-FIG. 1. Sampling period abundances of *Mulinia lateralis* from Laguna Madre.

of the study and apparently did not decay away. For example, note that for *M. lateralis* (text-fig. 1), the number present in the death assemblage prior to the August–October 1981 pulse is approximately the same as the number present after the pulse had decayed away (March–April 1982). Thus, the death assemblage consisted of a dynamic component comprising individuals added by mortality and destined to decay away and a static component comprising individuals present at the study's inception which decayed little if at all during the study.

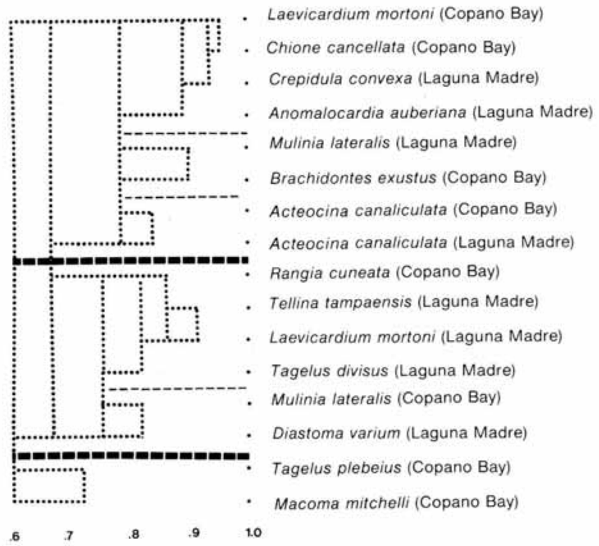
RESULTS

Size frequency distributions

Text-figure 2 shows the three primary groups that were produced by cluster analysis of the average size-frequency distributions of species in the death assemblage (text-figs. 3–7). These groups represent: 1, species with negatively skewed distributions, such as *Tagelus plebeius*; 2, species with moderately positively skewed distributions, such as *Chione cancellata*; and 3, species with highly positively skewed distributions, such as *T. divisus*. Each of the positively skewed groups could be subdivided into a subgroup with unimodal distributions (e.g. *C. cancellata* and *T. divisus*) and a subgroup with bimodal distributions (e.g. *Brachidontes exustus* and *Diastoma varium*). In addition *Acteocina canaliculata* formed a separate subgroup, but its small adult size and the sieve size used during collection precluded collecting individuals in the 10 % maximum size category. This created an artificial difference between this species and the other species with unimodal, moderately positively skewed distributions.

The size-frequency distributions at the two sites were similar except that no species at the Laguna Madre site had a negatively skewed distribution and more distributions were more positively skewed than at the Copano Bay site. No species had a normally distributed size-frequency distribution. NORMSEP was used to approximate the distributions with normal curves. The sum of two or more normal curves was required to get the best fit for all species.

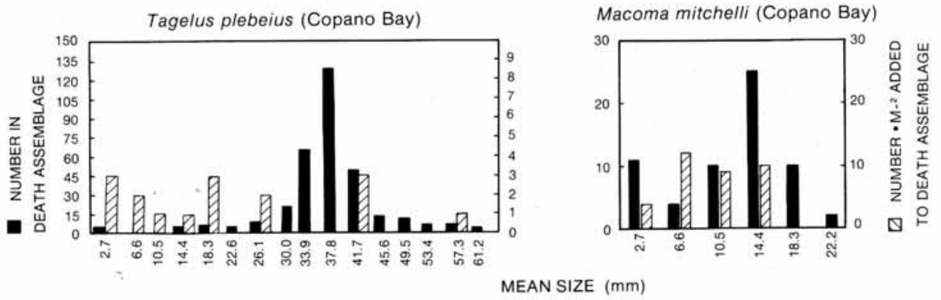
Size at death was determined for each species and the size-frequency distributions compared to the average size-frequency distribution of the species in the death assemblage (text-figs. 3–7). The



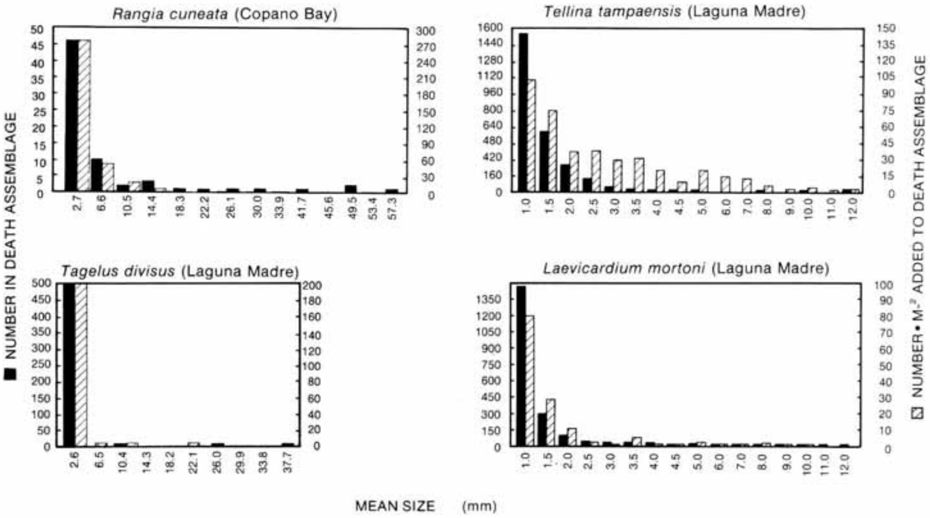
TEXT-FIG. 2. Cluster analysis of species from the Laguna Madre and Copano Bay sites.

two size-frequency distributions were significantly different in all cases except *Crepidula convexa* and *T. divisus* from Laguna Madre ($P < 0{\cdot}05$; Chi-square or Kolmogorov–Smirnov two-sample two-sided tests) (Table 1).

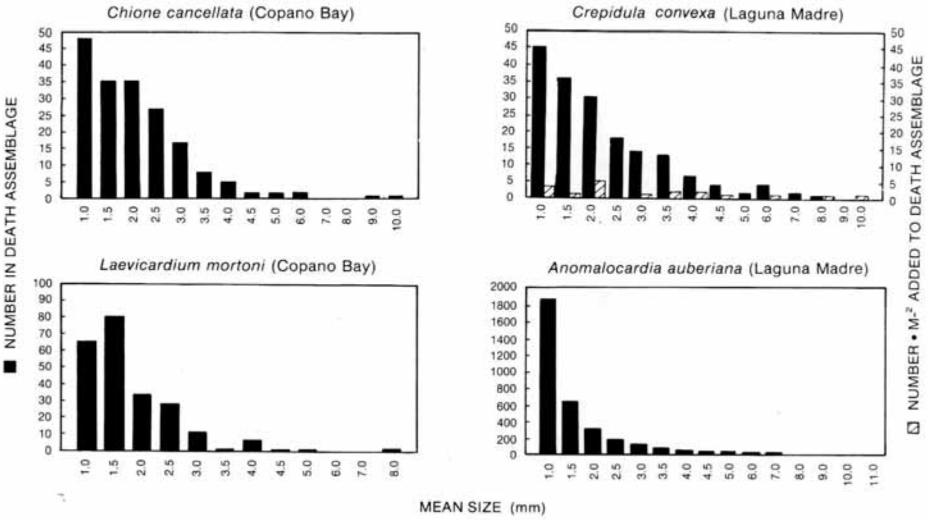
Mortality in the living community resulted in the addition of pulses of individuals into the death assemblage. The size-frequency distribution of a species in the death assemblage immediately after addition of a pulse was compared to the size-frequency distribution after the pulse had decayed (text-figs. 8–10). The size-frequency distributions of most species in the death assemblage were



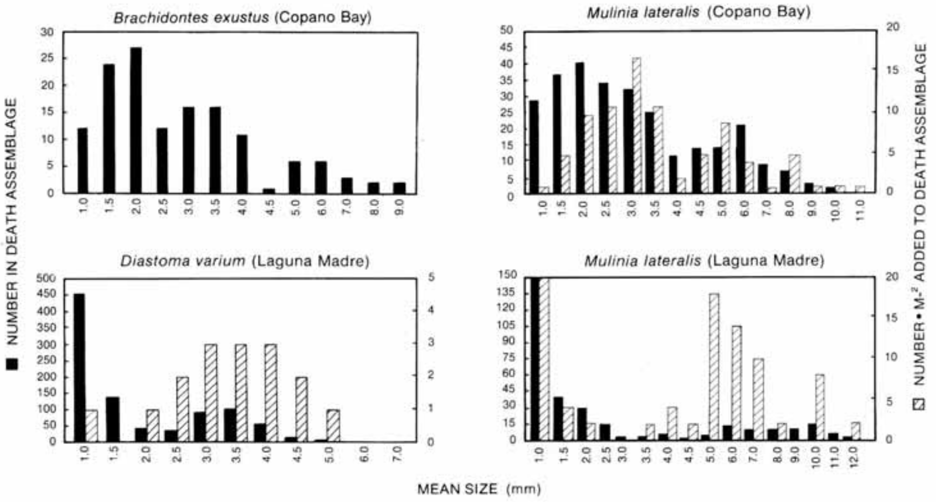
TEXT-FIG. 3. Comparison of the average size-frequency distribution in the death assemblage and the calculated size-frequency distribution of living individuals that died during the study period for taxa with negatively skewed distributions. Number in the death assemblage is the total number actually collected during the study.



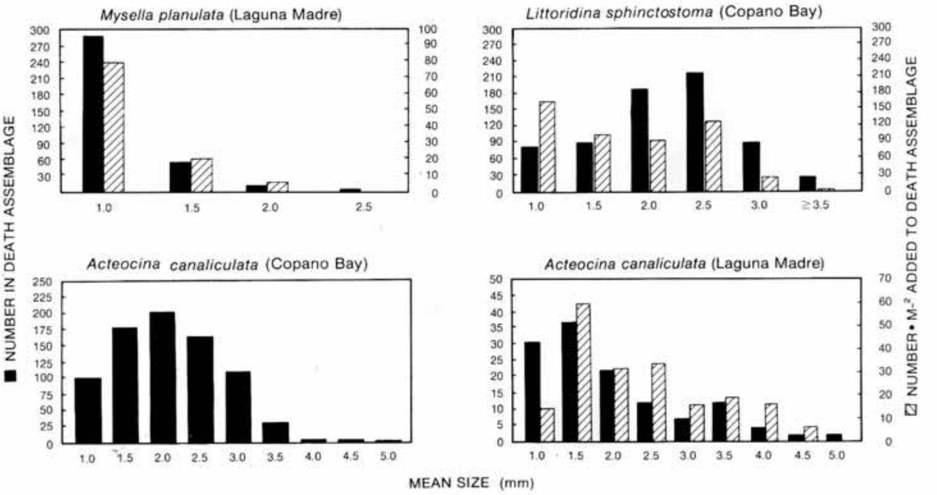
TEXT-FIG. 4. Comparison of the average size-frequency distribution in the death assemblage and the calculated size-frequency distribution of living individuals that died during the study period for taxa with highly positively skewed distributions. Number in the death assemblage is the total number actually collected during the study.



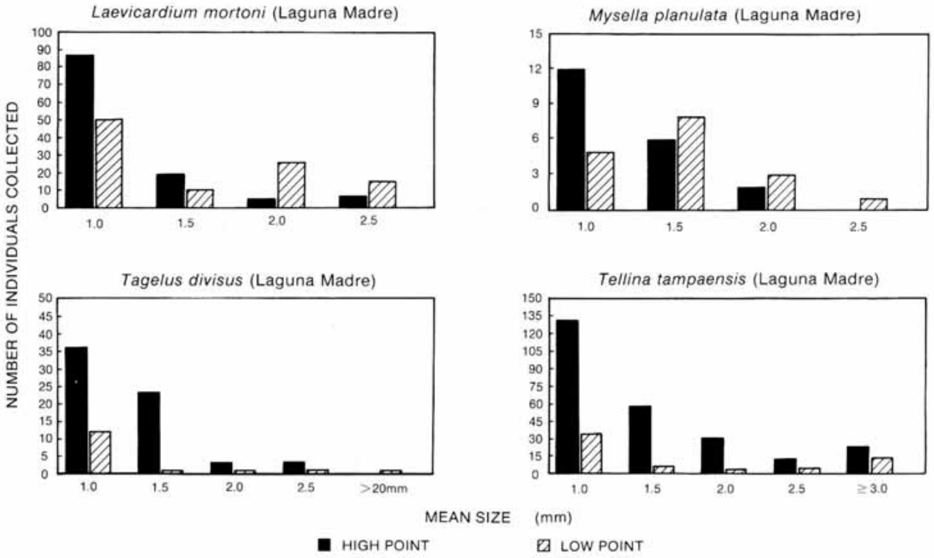
TEXT-FIG. 5. Comparison of the average size-frequency distribution in the death assemblage and the calculated size-frequency distribution of living individuals that died during the study period for taxa with moderately positively skewed distributions. Number in the death assemblage is the total number actually collected during the study.



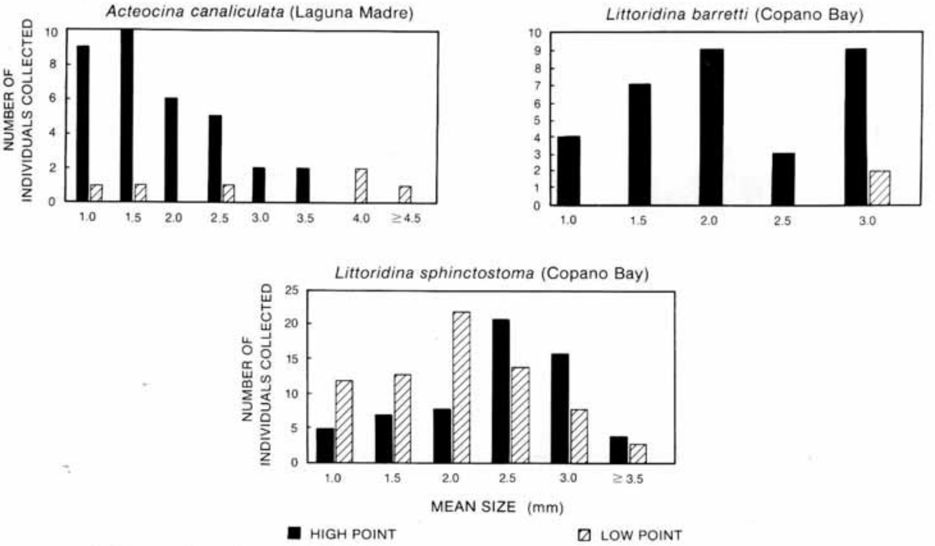
TEXT-FIG. 6. Comparison of the average size-frequency distribution in the death assemblage and the calculated size-frequency distribution of living individuals that died during the study period for taxa with bimodal distributions. Number in the death assemblage is the total number actually collected during the study.



TEXT-FIG. 7. Comparison of the average size-frequency distribution in the death assemblage and the calculated size-frequency distribution of living individuals that died during the study period for miscellaneous taxa. Number in the death assemblage is the total number actually collected during the study.



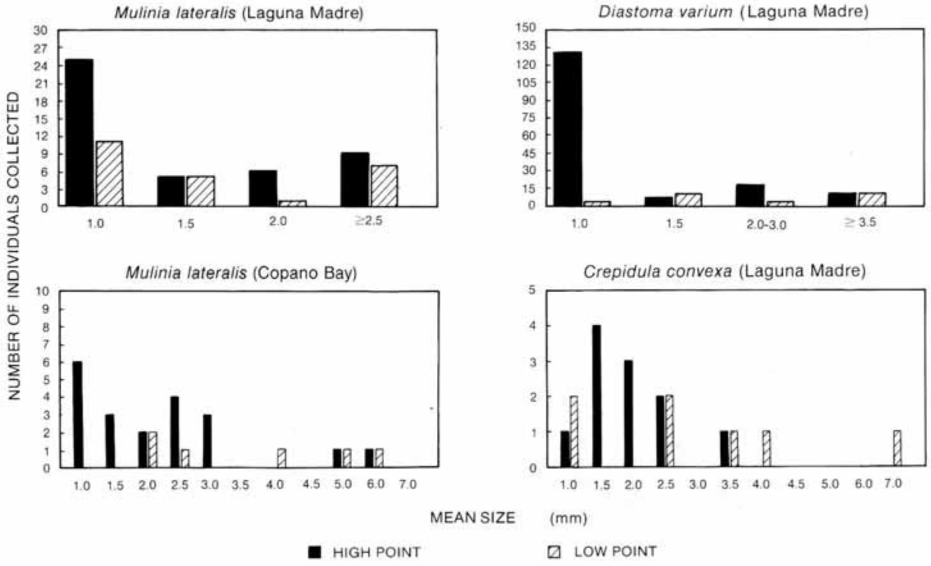
TEXT-FIG. 8. Comparison of the size-frequency distribution in the death assemblage just after an input pulse (the abundance high, see text-fig. 1) with the size-frequency distribution after taphonomic decay (the abundance low, see text-fig. 1) for species with highly positively-skewed distributions.



TEXT-FIG. 9. Comparison of the size-frequency distribution of species in the death assemblage just after an input pulse (the abundance high, see text-fig. 1) with the size-frequency distribution after taphonomic decay (the abundance low, see text-fig. 1).

changed significantly by the addition of individuals and their subsequent decay ($P \leqslant 0{\cdot}10$, Chi-square or Kolmogorov–Smirnov two-sample two-sided tests) (Table 1).

Survivorship curves for species in the death assemblage were calculated and plotted on log paper to approximate age-specific survivorship as suggested by Thayer (1977) (text-fig. 11). Most are concave (Type II of Deevey 1947) or linear (i.e. constant mortality—Type I). A few such as *M. lateralis* and *Rangia cuneata* are sigmoidal. Two, *T. plebeius* and *Macoma mitchelli*, are convex (Type III). The survivorship curves show that species were grouped by the cluster analysis primarily by the proportion of juveniles in the population. Species also can be grouped from the pattern of the adult survivorship by visual inspection of the survivorship curves. These groupings were similar to those derived by the cluster analysis except that *R. cuneata* could be grouped with taxa with moderately positively skewed size-frequency distributions and *Anomalocardia auberiana* with other species from Laguna Madre with highly positively skewed size-frequency distributions. In addition, bimodality was not sufficiently intense to produce an obvious plateau in the survivorship curve for any of the three bimodal species.



TEXT-FIG. 10. Comparison of the size-frequency distributions of species in the death assemblage just after an input pulse (the abundance high, see text-fig. 1) with the size-frequency distribution after taphonomic decay (the abundance low, see text-fig. 1).

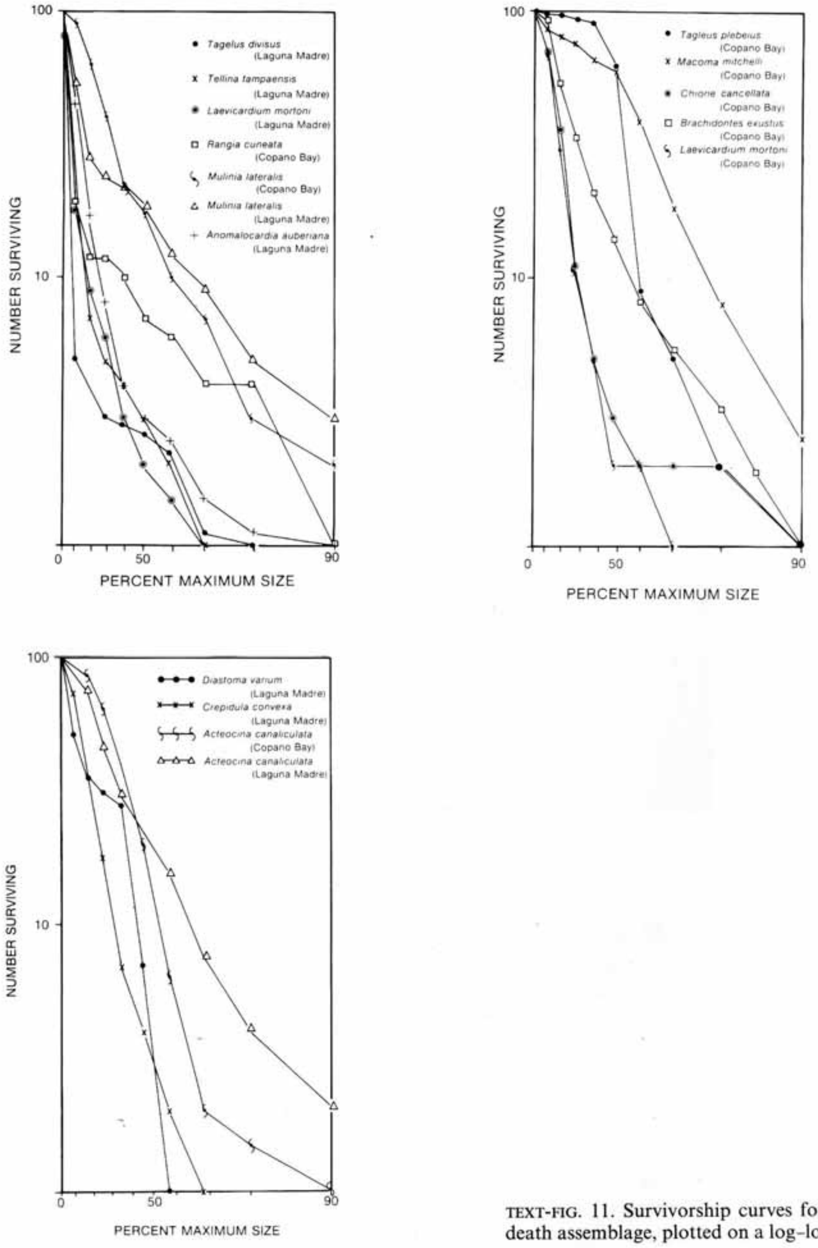
At both sites, about half of the individuals that died during the study (as calculated from size at death data from the living community) were ≥ 30% of the maximum size collected (text-fig. 12; tables 2 and 3). By comparison, in the death assemblage at the Copano Bay site, nearly two-thirds of the individuals collected were in this size range but only 26% of the individuals were as large at Laguna Madre (text-fig. 12). Thus, the two sites differed dramatically in the individual's average size in the death assemblage; most individuals were smaller at the Laguna Madre site, yet the average size at death was similar. In contrast, biomass was distributed similarly at both sites. Individuals $\geqslant 30\%$ of the maximum size collected accounted for over 80% of the biomass in both death assemblages and among the individuals that died during the study.

TABLE 1. Comparisons of the size-frequency distribution for the calculated input pulse into the death assemblage (see methods section) with the total death assemblage and comparisons of the size-frequency distribution of species prior to taphonomic loss (as judged by an abundance peak in the death assemblage following an input pulse) with the size-frequency distribution following taphonomic loss (as judged by a numerical low in the death assemblage). All tests used chi-square except those marked by * in which the Kolmogorov–Smirnov two-sample test was used.

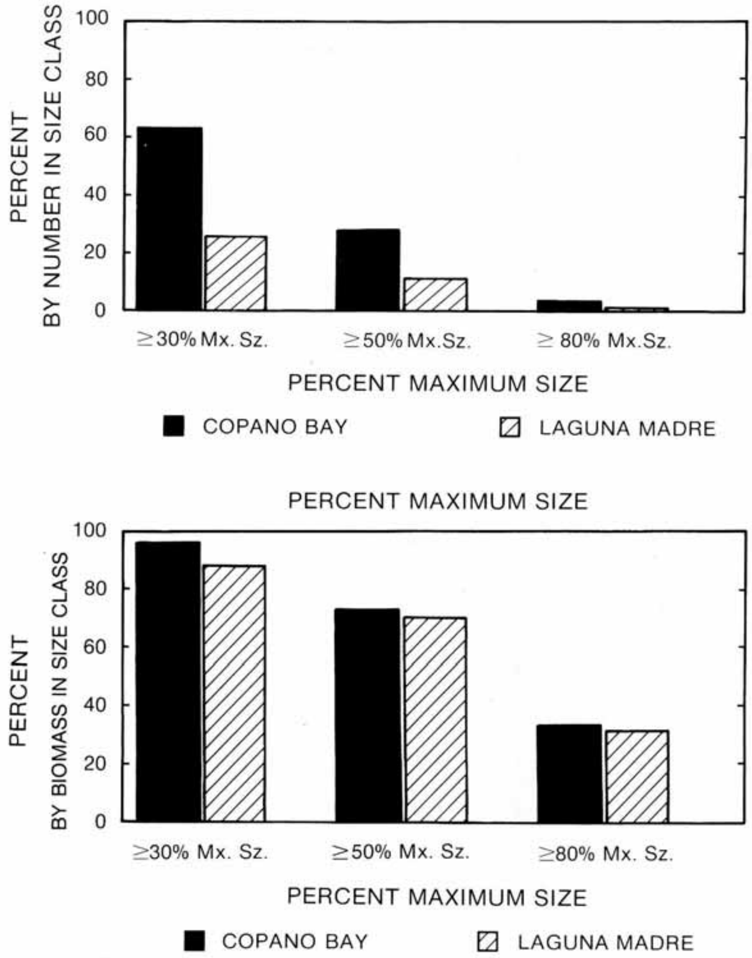
	Calculated input pulse vs Total death assemblage	Pre-taphonomic loss vs Post-taphonomic loss
Laguna Madre		
Diastoma varium	$P < 0{\cdot}001$	$P < 0{\cdot}001$
Crepidula convexa	$P > 0{\cdot}20$*	$P > 0{\cdot}20$*
Tagelus divisus	$P > 0{\cdot}20$	$P > 0{\cdot}20$*
Laevicardium mortoni	$0{\cdot}025 < P < 0{\cdot}05$	$0{\cdot}005 < P < 0{\cdot}010$
Tellina tampaensis	$P < 0{\cdot}001$	$0{\cdot}01 < P < 0{\cdot}025$
Mysella planulata	$0{\cdot}05 < P < 0{\cdot}10$	$P > 0{\cdot}20$*
Mulinia lateralis	$P < 0{\cdot}001$	$P > 0{\cdot}20$*
Acteocina canaliculata	$P < 0{\cdot}001$	$P > 0{\cdot}20$*
Odostoma cf. *teres*	$P < 0{\cdot}001$	—
Copano Bay		
Littoridina barretti	$P < 0{\cdot}001$	$0{\cdot}05 < P < 0{\cdot}1$*
Tagelus plebeius	$P < 0{\cdot}001$	—
Macoma mitchelli	$P < 0{\cdot}001$	—
Rangia cuneata	$P < 0{\cdot}001$	—
Mulinia lateralis	$0{\cdot}005 < P < 0{\cdot}01$	$P > 0{\cdot}20$*
Littoridina sphinctostoma	$P < 0{\cdot}001$	$0{\cdot}01 < P < 0{\cdot}025$

However, considerable variability was present from one species to another in the number of individuals in the death assemblage $\geqslant 30\%$ of the maximum size collected. Less than 10% of the individuals of most species with large input pulses were this large (Table 4). *Acteocina canaliculata* was the atypical member of this group. Over 69% of its individuals were in this size range. Species with small pulses or without input had proportionately more large individuals in the death assemblage (Tables 5 and 6). Furthermore, on the average, for the latter two groups, proportionally more large individuals were present at the Copano Bay site than at the Laguna Madre site. For example, 52% of the individuals of species at Copano Bay with mortality < 10 individuals per m^2 over the study were $\geqslant 30\%$ of the maximum size collected; the corresponding percentage at Laguna Madre was only 16·1%. Eighty per cent of the individuals of species with mortality between 10 and 100 individuals per m^2 over the study were of this size at the Copano Bay site, yet only 34% were as large at Laguna Madre. In contrast, over 80% of the biomass was in individuals $\geqslant 30\%$ of the maximum size collected in nearly all species in both death assemblages (Tables 4–6).

Three abundant species (*Laevicardium mortoni*, *C. cancellata*, and *B. exustus*) in the death assemblage at the Copano Bay site were represented only by juveniles, but adults were present in all



TEXT-FIG. 11. Survivorship curves for taxa in the death assemblage, plotted on a log–log scale.



TEXT-FIG. 12. The average percentage of individuals and biomass of all species in the death assemblage reaching the indicated percentage of the maximum size collected.

abundant species in the death assemblage at Laguna Madre (Table 2). Most individuals (over 90 %) of most species were juveniles in both death assemblages. Of the common species, only three at Copano Bay, *A. canaliculata*, *T. plebeius*, and *M. mitchelli*, had > 45 % of the individuals of adult size. Only one species, again *A. canaliculata*, had such a high proportion of adults at Laguna Madre. As expected, those species with negatively skewed size-frequency distributions had proportionally more adults. Species with moderately or highly positively skewed size-frequency distributions, however, differed little in the proportion of adults present (except *A. canaliculata*).

TABLE 2. The observed maximum size, known maximum size, and the percentage of individuals reaching reproductive maturity for species from Copano Bay and Laguna Madre.

	Maximum size collected in mm	Known maximum size in mm	Maximum size collected as a percentage of known maximum size	Percentage of individuals reaching reproductive maturity
Copano Bay				
Laevicardium mortoni	7·96	23·0	26·0	0·0
Acteocina canaliculata	5.12	5.0	100·2	45·0
Chione cancellata	9·92	38·0	26·0	0·0
Brachidontes exustus	8·96	20·7	43·0	0·0
Tagelus plebeius	65·02	85·0	76·0	65·1
Macoma mitchelli	22·05	29·0	76·0	75·8
Rangia cuneata	57·00	80·0	71·0	0·6
Mulinia lateralis	10·88	16·2	67·0	9·7
Laguna Madre				
Laevicardium mortoni	14·10	23·0	61·0	4·0
Acteocina canaliculata	5·12	5·0	100·2	48·0
Tagelus divisus	36·80	30·0	119·5	3·3
Anomalocardia auberiana	10·88	16·0	67·0	1·0
Diastoma varium	6·80	6·0	113·0	28·8
Crepidula convexa	9·92	12·0	82·7	6·1
Tellina tampaensis	16·25	20·0	81·0	2·8
Mulinia lateralis	12·90	16·2	79·6	18·8

TABLE 3. Comparison of the percentage of individuals and biomass that reached the indicated percentage of maximum size collected (from Table 2) in the size-frequency distribution of living individuals that died during the study (i.e. the cumulative size-frequency distribution of individuals added to the death assemblage during the study).

	Percentage of individuals			Percentage of biomass		
	⩾ 30 % Max. size	⩾ 50 % Max. size	⩾ 80 % Max. size	⩾ 30 % Max. size	⩾ 50 % Max. size	⩾ 80 % Max. size
Copano Bay						
Mulinia lateralis	80·7	25·3	8·4	97·8	73·0	44·4
Rangia cuneata	0·9	0·6	0·0	45·6	42·9	0·0
Macoma mitchelli	79·4	40·0	9·7	99·2	83·5	36·2
Average	53·7	22·0	6·0	80·9	66·5	26·7
Laguna Madre						
Tagelus divisus	4·6	2·8	0·0	81·4	74·7	0·0
Laevicardium mortoni	14·9	4·3	0·0	91·3	67·6	0·0
Crepidula convexa	50·0	22·2	5·6	94·8	75·7	57·6
Tellina tampaensis	32·3	8·2	0·5	84·2	47·0	8·4
Mulinia lateralis	84·4	42·2	13·3	99·5	85·9	52·5
Acteocina canaliculata	92·4	46·0	11·1	98·7	79·0	33·7
Average	46·4	20·9	5·2	89·9	68·8	33·2

TABLE 4. The percentage of individuals and biomass in the death assemblage reaching the indicated percentage of maximum size collected for species whose calculated input into the death assemblage over the study period was > 100 individuals per m².

	Percentage of individuals			Percentage of biomass		
	⩾ 30 % Max. size	⩾ 50 % Max. size	⩾ 80 % Max. size	⩾ 30 % Max. size	⩾ 50 % Max. size	⩾ 80 % Max. size
Copano Bay						
Rangia cuneata	14·0	10·0	4·4	96·5	69·9	26·5
Laguna Madre						
Tagelus divisus	3·8	2·9	1·3	91·7	89·5	62·4
Laevicardium mortoni	9·0	2·9	0·4	90·9	69·4	27·6
Tellina tampaensis	6·4	3·2	0·8	82·9	74·7	40·6
Acteocina canaliculata	69·5	27·7	5·6	95·3	69·9	26·5
Average	22·2	9·2	2·0	92·2	75·9	36·7

TABLE 5. The percentage of individuals and biomass in the death assemblage reaching the indicated percentage of maximum size collected of species whose calculated input into the death assemblage over the study period was < 10 individuals per m².

	Percentage of individuals			Percentage of biomass		
	⩾ 30 % Max. size	⩾ 50 % Max. size	⩾ 80 % Max. size	⩾ 30 % Max. size	⩾ 50 % Max. size	⩾ 80 % Max. size
Copano Bay						
Acteocina canaliculata	87·4	39·7	1·4	97·0	67·0	6·1
Laevicardium mortoni	3·0	4·8	1·8	85·6	53·5	32·0
Brachidontes exustus	54·0	21·0	4·9	96·1	76·2	37·7
Chione cancellata	35·5	4·4	1·1	86·3	43·6	25·0
Average	51·7	17·5	2·3	91·3	60·1	25·2
Laguna Madre						
Anomalocardia auberiana	16·1	2·5	0·5	79·5	43·3	17·4

Table 7 shows the fragment to whole ratios for each site. Species at the Laguna Madre site had far fewer fragments per whole shell than did the species at the Copano Bay site.

DISCUSSION

Size-frequency distributions are an important tool of ecologic study. Comparison of a temporal sequence of size-frequency distributions provides data on recruitment, growth, mortality, and life history strategy of species in the community. Size-frequency distributions also are the primary tool utilized by the palaeontologist in the analysis of a species' population structure. A temporal sequence cannot be collected, however. Consequently, the sole datum provided by a size-frequency distribution of a fossil species normally is the size at death of the preserved individuals, from which all

TABLE 6. The percentage of individuals and biomass in the death assemblage reaching the indicated percentage of maximum size collected for species whose calculated input into the death assemblage over the study period was between 10 and 100 individuals per m^2.

	Percentage of individuals			Percentage of biomass		
	$\geqslant 30\%$ Max. size	$\geqslant 50\%$ Max. size	$\geqslant 80\%$ Max. size	$\geqslant 30\%$ Max. size	$\geqslant 50\%$ Max. size	$\geqslant 80\%$ Max. size
Copano Bay						
Mulinia lateralis	62·3	20·7	5·0	96·9	74·2	34·6
Tagelus plebeius	97·0	91·5	6·3	99·9	98·4	16·7
Macoma mitchelli	80·6	65·8	17·7	99·7	96·1	47·2
Average	80·0	59·3	9·7	98·8	89·6	32·8
Laguna Madre						
Mulinia lateralis	27·0	20·6	7·7	96·2	92·4	57·6
Diastoma varium	36·7	28·8	0·8	84·7	75·7	5·4
Crepidula convexa	36·9	7·4	0·6	82·7	41·0	6·3
Average	33·5	18·9	3·0	87·9	69·7	23·1

TABLE 7. Fragment to whole shell ratios for species at Copano Bay and Laguna Madre.

Copano Bay		Laguna Madre	
Acteocina canaliculata	1·12	*Acteocina canaliculata*	0·32
Littoridina barretti	0·95	*Anomalocardia auberiana*	0·49
Diastoma varium	6·20	*Diastoma varium*	0·49
Brachidontes exustus	11·60	*Mysella planulata*	0·05
Chione cancellata	2·53	*Tellina tampaensis*	0·42
Tagelus plebeius	2·23	*Crepidula convexa*	0·32
Mulinia lateralis	3·35	*Mulinia lateralis*	0·42
Littoridina sphinctostoma	2·37	*Laevicardium mortoni*	0·42
Laevicardium mortoni	3·99		

inferences about population dynamics must be derived. Thus, an understanding of the effects of time averaging and taphonomy on the size-frequency distribution is crucial.

Size-selective preservation

Each cohort of a species produces its own size-specific mortality pattern. Some of these individuals are not preserved and the remainder are mixed with individuals of previous generations to form the final death assemblage (Craig and Oertel 1966; Hallam 1967, 1972). The size-specific mortality pattern of one or a few cohorts of most species in the living community at both sites compared poorly with the size-frequency distributions of species in the death assemblages. For example, no large *M. mitchelli* were added to the death assemblage during the study, proportionally more adult *A. canaliculata* were added at the Laguna Madre site than were already present in the death assemblage, and proportionally fewer large *Mulinia lateralis* were added to the death assemblage at the Copano Bay site than were already present. Either survivorship during our study differed considerably from previous years, or taphonomic processes altered the size-frequency distribution in the death assemblage (Kurten 1964; Olson 1957). The distinction between the two is crucial. If variation in survivorship is more important, then the death assemblage preserves a time-averaged picture of the population dynamics of a species. If size-specific taphonomy is responsible, then its population dynamics cannot be reconstructed from the size-frequency distribution.

If size-selective preservation occurred, then small shells should decay faster (Olson 1957, Hallam 1967). We compared the size-frequency distribution just after the addition of a pulse (at the maximum point of numerical abundance in the death assemblage) with the size-frequency distribution after taphonomic loss (at the point of lowest abundance in the death assemblage). The distributions prior to taphonomic loss were significantly different from the distributions after taphonomic loss in about one-half of the cases. Unfortunately, in our study, instantaneous mortality did not occur, so that larger individuals died later. Taphonomic decay was so rapid (text-fig. 1; Cummins *et al.* 1986*b*) that considerable decay of small shells occurred before the larger shells were added. Thus, the data suggest but do not prove size-selective taphonomic loss. Nevertheless, in all but one case, proportionally more large shells were present, yet the number of small shells added by mortality was large in comparison to the number already present and the number of large shells added was very small. To explain this fact by temporal differences in survivorship would require the extraordinary coincidence of all species at both sites having unusually poor survivorship simultaneously during this study. This is unlikely and provides a strong suggestion of the importance of size-selective taphonomy.

The proportion of large individuals in the death assemblage of species having different population levels in the living community provides additional evidence for size-selective taphonomy. Species having < 100 individuals per m^2 added to the death assemblage during the study consistently had fewer small individuals in the death assemblage than other species. *A. canaliculata* at Laguna Madre, a species with unusually good survivorship (Powell *et al.* 1984), was the only exception. At Laguna Madre, 16–37 % of all individuals of these species were $\geqslant 30$ % of the maximum size collected, whereas only 4–9 % were of similar size in species with mortality > 100 individuals per m^2. The respective numbers for Copano Bay were 30–97 % and 14 %.

There are only three possible reasons for such a dramatic difference. Either, *a*, in the past survivorship was unusually high at both sites only in species which coincidentally had little input into the death assemblage during our study, or, *b*, adults and juveniles live in separate habitats only for those species which coincidentally had low or no input into the death assemblage during our study, or, *c*, size-specific taphonomic loss occurred.

The importance of adult migration for some species is well known (e.g. Beukema 1973; Werner 1956), however the species of interest here recruit primarily by larval settlement (e.g. Fraser 1967; Moore and Lopez 1969; Powell *et al.* 1984) so that adult migration is an unlikely cause.

Temporal variability in the survivorship of cohorts is well described (e.g. Hughes 1980; Brosseau 1978), however, the coincidence of good survivorship at both sites in so many species, but only in those species that occurred rarely or not at all in the living community during this study, is unlikely. Nearly all studies substantially underestimate juvenile mortality, frequently by 80 % or more (Powell *et al.* 1984). Even with such substantial errors, however, few data support low juvenile mortality in gastropod and bivalve molluscs (Cadée 1982*a*). Almost invariably juvenile mortality is high (in addition to Cadée 1982*a*, we checked Dare 1976; Muus 1973; Holland and Dean 1977; Brosseau 1978; Coe and Fitch 1950; Phillips 1981; Seager 1982; Schmidt and Warme 1969; Yamada 1982; and others referenced herein and in Powell and Cummins 1985; see also Doherty 1979 and Cadée 1982*b* for brachiopods). At our two sites, all molluscan species that settled during 1981–1983 had high juvenile mortality (Powell *et al.* 1984). Consequently, most size-frequency distributions of molluscs in death assemblages produced by *in situ* mortality should be highly positively skewed in the absence of taphonomic processes (see also Craig and Oertel 1966; Hallam 1972).

Certainly the available data on molluscan population dynamics imply that the number of species present in this study whose size-frequency distribution might otherwise suggest good survivorship would be unprecedented in bay environments like Copano Bay and Laguna Madre. Juvenile mortality normally is very high in these habitats. The proportion of individuals in the smaller size classes differs from that expected from typical molluscan population dynamics except in species which had juveniles added to the death assemblage during the study. Apparently, without continual input of juveniles, highly positively skewed size-frequency distributions would be absent from both sites because juveniles are poorly preserved.

Two abundant species, *L. mortoni* and *M. lateralis*, were common at both sites. Survivorship for both species was better at Laguna Madre. Proportionally more adults were collected in the death assemblage at this site. Even so, in both cases, proportionally more of the individuals collected were in the larger size classes (even though they were not adults) at the Copano Bay site. Thus, survivorship of both species was better at Laguna Madre, but their size-frequency distribution was more negatively skewed at the Copano Bay site. Clearly, variations in survivorship are an unlikely explanation for the observed differences in survivorship curves and size-frequency distributions of those two species.

Consequently, although the data do not prove unequivocally that size-specific taphonomy occurred, all data strongly suggest the importance of this process in determining the shape of size-frequency distributions in both death assemblages. In nearly all cases the largest size classes became proportionally more important because more individuals in the smallest size classes decayed away.

Site-specific preservation

The paucity of shell material in the smallest size classes at Copano Bay is typical of many fossil and death assemblages (Dodd *et al.* 1985; Broadhurst 1964; Brookfield 1973; Stewart 1981). There are two possible explanations for the lack of small shells in the fossil record which may also apply to Copano Bay (Broadhurst 1964; Craig and Oertel 1966; Boucot 1953).

1. The mortality rate could be much higher for the smallest size classes at Laguna Madre than at Copano Bay. Poor survivorship of the smallest living individuals would result in a buildup of individuals in the smallest size classes in the death assemblage in spite of decay if periodic settlement were predictable. Observations and inferences as previously discussed do not support this hypothesis. Moreover, potential predators were observed more frequently at the Copano Bay site. The Copano Bay site also is more environmentally unstable. In fact, more taxa were present exclusively as juveniles at the Copano Bay site than at the Laguna Madre site. Thus, differential survivorship is an unlikely explanation.

2. Taphonomic processes may be different in kind or extent. Size-specific taphonomic loss may be more extreme at the Copano Bay site or the more constant input of individuals into the death assemblage at the Laguna Madre site might continually maintain a considerable number of small shells in the death assemblage in spite of high taphonomic loss. Although rates of taphonomic loss were similar for most species at both sites (Cummins *et al.* 1986*b*), two species, *R. cuneata* and *Macoma mitchelli*, decayed so rapidly at the Copano Bay site that no decay rate could be measured. Such was not the case at the Laguna Madre site. Fragmentation was much higher at the Copano Bay site as well. Taxa with little or no input into the death assemblage during the study had proportionally more large individuals at the Copano Bay site. On the average, there was more time between input pulses into the death assemblage at the Copano Bay site because species set more regularly, in greater numbers, at the Laguna Madre site. Consequently, there was more time for taphonomic loss between pulses at the Copano Bay site, but more smaller shells were added to the death assemblage at the Laguna Madre site. Thus, variation in taphonomic loss plus differential rates of input of small shells offer the best explanation for the difference in size-frequency distributions between the two sites.

Most taphonomic processes can be size selective. Smaller shells may be more easily transported than larger shells (Boucot 1953; Boucot *et al.* 1958, but see Trewin 1973). At both sites, most shells $\leqslant 1\cdot5$ cm in size were transported, at least locally, but larger shells were transported less (Cummins *et al.* 1986*a*). Predation may be size selective (Dare 1976; Vermeij 1980). If the preyed upon individuals were broken or removed from the area, the size classes involved would be under-represented in the death assemblage. Dissolution and abrasion may be more effective in certain size classes than in others (Flessa and Brown 1983; Chave 1964). Apparently such processes as dissolution and shell breakage must be more intense in Copano Bay, because physical transportation affected the spatial distribution of shells more at Laguna Madre (Cummins *et al.* 1986*a*).

Modality and skewness of frequency distributions

The word 'mode' has been used in several ways by biologists and geologists. The statistical definition of a mode is the measurement which occurs with the highest frequency. In contrast, in fisheries biology, the term is used frequently to designate the size class of highest frequency for a cohort (i.e. a modal class). Many cohorts may be present in a population at any given time yielding a multimodal distribution (Abramson 1971). Such a size-frequency distribution may be visually multimodal if the cohorts are well separated. Frequently, however, they are not, and modes are recognized by fitting normal curves to a size-frequency distribution based on the assumption that the size distribution of organisms, within cohorts, will be normally distributed. In contrast, in geology and palaeontology, modes usually are visually distinctive abundance peaks in a size-frequency distribution (e.g. Sheldon 1965).

Size-frequency distributions of our species were of four types, the first three being unimodal; highly positively skewed (text-fig. 4), moderately positively-skewed (text-fig. 5), negatively skewed (text-fig. 3), and bimodal (text-fig. 6) (with the highest mode highly or moderately postively skewed). Highly postively, moderately positively, and negatively skewed distributions primarily demonstrate the relative effectiveness of size-selective taphonomy and the temporal pattern of larval settlement. No species without substantial and frequent larval settlement had a highly positively skewed size-frequency distribution. In spite of the considerable emphasis on normal or bell-shaped distributions (e.g. Hallam 1972), none of our species had a normal distribution. We attempted to fit the observed distribution pattern to a normal distribution pattern using the NORMSEP computer program without success. We suggest that normal distributions are produced very infrequently in death assemblages from bay environments.

Unimodal distributions

Most distributions were unimodal. The time-averaged death assemblage contains a cumulation of shells produced by yearly patterns of size-specific mortality, each year potentially being different from all others, and taphonomic decay. Nevertheless, each size-frequency distribution should be unimodal initially and highly positively skewed. To check this assumption, we calculated the expected size-frequency distribution for input pulses from size at death data available in the literature (e.g. Brousseau 1978; Phillips 1981; Yamada 1982; Coe and Fitch 1950) and from our data. All were unimodal except *Gemma gemma* (Jackson 1968) and *Mulinia lateralis*, which was bimodal at both our sites (see also Cadée 1982*a*). Thus, the size-frequency distribution of shells obtained from the death of a single cohort usually is unimodal. In addition, each size-frequency distribution should be subjected to taphonomic processes all of which, if size-selective, remove relatively more individuals from the smaller size classes of the size-frequency distribution. Consequently each taphonomically altered distribution should be unimodal. On the average the cumulation of many such distributions should yield a unimodal distribution, because each individual mode will not be sufficiently different from all others to cause the distribution of modes to be anything but unimodal. Thus, unimodality can be considered the standard condition for size-frequency distributions in time-averaged death assemblages.

Bimodality

In textural analysis of sediment the number of modes present often is indicative of the degree of physical sorting which has taken place. Sediments with multimodal grain size distributions are not at equilibrium with the physical environment (Singer and Anderson 1984; Curray 1960; Sonu 1972).

Most bimodal or multimodal size-frequency distributions in palaeontology can probably be ascribed to an analogous condition of disequilibrium, and should be rare. Olson (1957) found bimodal or multimodal distributions in only 15 % of the cases he examined. Only three species had bimodal distributions in our study.

Bimodality could arise for several reasons.

1. In a living population, distinct modes are frequently visible when several cohorts are present. Catastrophic mortality could preserve a cohort's size-frequency distribution intact (Sheldon 1965). Thus, census populations might be modelled as a series of normal curves. Catastrophic mortality in which a series of cohorts died simultaneously did not occur at our two sites during the study; nevertheless, most size-frequency distributions could be modelled by the summation of two or more normal curves (using NORMSEP) as if several cohorts were present. This clearly is false. Thus, a series of normal curves can be fitted to the time-averaged mortality pattern derived from normal cohort mortality in the living community and the mere presence of such a fit cannot be used as an indicator of catastrophic death.

2. If the input into the death assemblage from the living community is visibly multimodal, one would expect the resulting death assemblage also to be multimodal. For this to occur, survivorship would have to be very low for the very young and old and very high for the middle size classes, or sexual dimorphism must be present. Our species were not sexually dimorphic enough to produce a bimodal distribution. Little evidence for bimodal mortality was available in the literature for single cohorts (see previous references). Only *M. lateralis* had a bimodal mortality pattern at our two sites during the study, but more than one cohort was included in this analysis.

3. If shell material is transported into the habitat, then the size-frequency distribution of the transported assemblage would be dependent upon the size-frequency distribution of the source material and the strength of the transporting event. The transporting event might cause the mixing of size-frequency distributions from two different sources which were spatially separated or from one source at two different time periods when the size-frequency distributions were different. For instance, *Diastoma varium* at Laguna Madre was transported into the area on floating seagrass blades (Powell *et al.* 1982). One transporting event may have contained a majority of juvenile specimens whereas the other contained older individuals. The resulting size-frequency distribution for *D. varium* is characterised by visibly distinct modes. At Copano Bay, *Brachidontes exustus* has a bimodal size-frequency distribution. This bivalve generally is found attached to oyster shells and almost certainly was allochthonous. A scenario similar to that of *D. varium* would explain its bimodal distribution.

4. A very large input pulse with a size-frequency distribution different from that already present in the death assemblage, limited time-averaging (i.e. the summation of only a few cohorts), or the addition of juveniles to an assemblage after size-selective taphonomy had removed nearly all of the small individuals, might insert a secondary mode into the size-frequency distribution. At Copano Bay the size-frequency distribution of *Tagelus plebeius* was bimodal during the time of maximum juvenile mortality but before complete taphonomic loss of the small individuals had occurred.

Many bimodal or multimodal size-frequency distributions within one fossil assemblage (with no evidence for physical transportation) might suggest that a catastrophic event resulted in the preservation of the size structure of a living population. On the other hand, a few bimodal size-frequency distributions, as found at both our sites, might suggest either allochthonous input into the assemblage, the presence of species with wildly fluctuating survivorship from cohort to cohort or an unusual population dynamics yielding a bimodal mortality pattern. Discrimination between these three might be difficult without corroborating evidence from other sources. All, however, represent a condition of disequilibrium from the standard unimodal condition.

Biomass

Usually, a small number of large individuals contribute most of the biomass present for a species. At Laguna Madre, for example, over 88 % of the total biomass is found in individuals ⩾ 30 % of the maximum size collected despite the fact that only 27 % of the total number of individuals are in this size range. Biomass is a more effective statement of palaeo-community structure than numerical abundance because larger specimens have a better chance of being preserved (Staff *et al.* 1985, 1986). Consequently, the total biomass of a cohort is probably better preserved than is the cohort's numerical abundance.

Adult abundance

Similarly, adults should be preserved better than juveniles (Cummins *et al.* 1986*b*). The proportion of the total number of individuals that were adults was quite variable among the species in both death assemblages. For instance, only 1 % of the *Anomalocardia auberiana* and only 6 % of the *D. varium* reached reproductive maturity but over 45 % of the *Acteocina canaliculata* and over 65 % of the *T. plebeius* and *Macoma mitchelli* were adults. Four explanations for this variability are possible.

1. Species which died before reaching reproductive maturity might indicate settlement in a marginal habitat even if they are numerically abundant. *Laevicardium mortoni*, for example, reached reproductive size at the Laguna Madre site, but not at the Copano Bay site. *L. mortoni* is a species characteristic of hypersaline lagoons (Parker 1959). Copano Bay is a marginal habitat for this species.

2. Transported individuals may all be small. At both sites, smaller individuals were transported more effectively than larger ones (Cummins et al. 1986*a*). The almost complete absence of adult *B. exustus* at the Copano Bay site might be explained similarly.

3. Size-selective taphonomy may have removed the smaller size classes. On the average, gastropods had more adults than bivalves. Gastropod survivorship may be generally higher or taphonomic loss may be greater for adult bivalves. Except for *D. varium*, the fragment to whole shell ratios tended to be lower for gastropods (i.e. more whole shells were present). Consequently, gastropods may be preserved better.

4. Survivorship may have been high. The one species with better than average survivorship, *A. canaliculata*, also had a higher percentage of adults at both sites. Nevertheless, the number of adult *A. canaliculata* present in the death assemblage is much higher than expected even from this good survivorship. Less than 30 % of the living individuals reached ⩾ 30 % of maximum size (Powell *et al.* 1984), but nearly one-half of all individuals in the death assemblage were adults.

Thus, the two primary factors affecting the number of adults in the death assemblages in Copano Bay and Laguna Madre are low survivorship primarily due to settlement in suboptimal habitat and better preservation of adults. Interestingly, adults are preserved better regardless of size. That is, size-specific taphonomy may be explained at least partially by juvenile-specific taphonomy. Adult *A. canaliculata* are no larger than juvenile *Tellina tampaensis*. Adult *Mulinia lateralis* are about the size of juvenile *Tagelus plebeius*. Nevertheless, in both cases, adults were preserved better. Perhaps changes in shell mineralogy, mode of death, or life and death position offer explanations.

CONCLUSIONS AND RECOMMENDATIONS

Size-frequency distributions and survivorship curves have been used to study differences in population dynamics between species (Thayer 1977; Richards and Bambach 1975; Stanton *et al.* 1981). Size-frequency distributions which are positively skewed yielding survivorship curves of Type I and II might, for example, indicate high juvenile mortality and *r*-selection (Surlyk 1974; Alexander 1977). Size-frequency distributions which are strongly negatively skewed yielding survivorship curves of Type III or sigmoidal in shape might indicate *K*-selection, bet-hedging, or the transport of smaller individuals away from the site of death by physical processes (Stearns 1976; Craig and Hallam 1963; Boucot 1953). In order for size-frequency distributions and survivorship curves to be more than a function of differential taphonomy between size classes, however, all size classes must be affected at an equal rate. Unfortunately, as Samtleben (1973) found for *Mytilus edulis* and Shimoyama (1985) for *Umbonium moniliferum*, most size-frequency distributions are shaped primarily by taphonomic processes. Few distributions from either of our sites could be explained based on the population dynamics of the species. Taphonomic processes consistently offered the better explanation. Therefore, the interpretation of a species' population dynamics, inferences on *r*- and *K*-selection and the like may not be accurate in many cases.

On the other hand, the data suggest that inferences based on certain portions of the size-frequency distribution may be more accurate. The use of adult numbers and biomass are examples. The real problem is the poor preservation of juveniles (Olson 1957). The study of population dynamics, if it is to be successful, must be based primarily on the study of the larger size classes which typically are the adult individuals. Here, good data on a species' success in the community may be available.

In contrast to the bleak prospects for use of the entire size-frequency distribution to assess population dynamics, the data suggest that the size-frequency distribution is an outstanding repository of data about taphonomic processes. Both species- and site-specific effects may be preserved in the fossil record. To be useful, however, a better understanding of the biologic and taphonomic factors causing site- and species-specific differences is required. Moreover, the process by which time averaging cumulates individual cohorts into an overall size frequency is poorly understood. Does the final product represent a long-term average or is it dominated by the infrequent recruitment and mortality of unusually large cohorts? Nevertheless, all evidence points to the ultimate value of the size-frequency distribution as an indicator of taphonomic processes because it is more or less independent of other lines of evidence typically used. In effect, the initial belief in the 1950s of the value of the size-frequency distribution for assessing transportation would appear to be closer to the primary data provided by it than its more recent use to assess a species' population dynamics.

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