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Onshore–Offshore Trends in the Size-Frequency Distribution of Death Assemblages: Northwestern Gulf of Mexico

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The size-frequency distributions of death assemblages were compared at three sites on the inner continental shelf of Texas by means of three descriptor variables, numerical abundance, paleoproduction (biomass at death), and paleoingestion (lifetime ingestion, a measure of energy flow). These death assemblages were then compared with six other death assemblages covering a transect from the estuary (Copano Bay, TX) to the continental slope. Typically, size-frequency distributions are based on abundance and size classes are set proportional to the largest individual in the collection. Restriction to this one analysis would have identified few of the important trends observed in this study. The evaluation of size frequency on the basis of species' maximum size as well as assemblage maximum size and the comparison of a suite of assemblages on the basis of the largest maximum size provide important new inferences into community dynamics. The distribution of measures of energy flow across the size-frequency spectrum provided an additional, valuable source of information on community structure and habitat optimality. Within-habitat variability was consistently less than between-habitat variability. The autochthonous continental slope assemblages were the most diverse in their size-frequency spectra. Comparison between habitats showed that the continental slope assemblages had the largest proportion of adult individuals. The continental shelf assemblages were dominated by juveniles. The chemoautotrophic and heterotrophic assemblages in Copano Bay and on the continental slope were similar in most respects despite substantial differences in their trophic structure. Similarity existed in the proportion of adults, in the tendency toward bimodality, and in the degree to which species reached maximum size. The shapes of the size-frequency spectra were controlled in large measure by (a) the relative loss of juveniles through taphonomy, (b) the degree of survivorship to adulthood, probably predominately determined by predation, (c) the food and space resources present that control species size, and (d) the optimality of the habitat that allowed animals to approach maximum size. The habitats on the continental slope had the highest proportion of individuals near maximum size. The Copano Bay assemblages were also characterized by a large proportion of adult individuals; however, these normally did not reach sizes above 70% of species' maximum size. The largest individuals were found at the petroleum seeps and in the heterotrophic assemblages from Copano Bay. Continental slope habitats should be temporally most stable, and our information supports that expectation. Food supply should be greatest in estuaries and in cold seeps where chemosynthetic processes dominate. Our data support this expectation.

In spite of the efforts of a great many paleontologists and ecologists, it is still a difficult and uncertain task to reconstruct even the preservable portion of communities from their fossil or death assemblages. Difficulties arise from two sources: the degradation or loss of data from the original assemblage/community and the limited knowledge of how autecologic attributes of the community are interred. Increasingly, efforts have been directed at examining the taphonomic processes in modern environments in order to determine the degree and kind of alteration of the preservable fauna that can be expected in various habitats (Brett and Baird, 1986; Staff et al., 1986; Miller, 1988; Meldahl and Flessa, 1990; Russell, 1991; Callender and Powell, 1992; Powell et al., 1992; Bartley, 1996). These studies notwithstanding, relatively few modern benthic environments and their assemblages have been described quantitatively with regard to the important taphonomic processes and the impact of those processes on death assemblage formation (e.g., Aller, 1995; Greenstein and Moffat, 1996; Springer and Flessa, 1996; Martin et al., 1996; and see Powell et al., 1989) and even fewer have attempted to relate taphonomic process and autecologic structure within environmen-

tal gradients to obtain a more holistic view of assemblage formation (e.g., Callender and Powell, 1992, 1997). Conceptual models, however, provide the underpinnings for such an approach (Speyer and Brett, 1988; Brandt, 1989; Meldahl and Flessa, 1990; Aberhan and Fürsich, 1991).

In this paper, we examine a primary attribute of death and fossil assemblages, the size-frequency distribution of the constituent species. We focus first on the death assemblages at three stations on the shallow continental shelf of Texas. Previous studies described the taphonomic condition of these death assemblages (Staff and Powell, 1990a), observed distinct taphonomic signatures related to sediment type and water depth, and described the guild and tier structure (Staff and Powell, 1999). Here we expand the analysis to examine the influence of autecologic and taphonomic processes in establishing the characteristics of the size-frequency distribution by comparing these assemblages with those from the nearby continental slope and a nearby coastal embayment, Copano Bay. These assemblages were chosen because their guild, tier, and size-frequency structure had been well studied and because the autecologic and taphonomic processes functioning in their formation had been previously considered (Powell et al., 1998). In addition, the assemblages cover a broad range of assemblage types including assemblages dominated by species harboring chemoautotrophic symbiotic bacteria and by a more normal heterotrophic fauna.[1] With this larger set of assemblages, we then examine variability in the size-frequency distribution at the alpha (within habitat) and beta (between habitats) levels of ecosystem structure (e.g., Harrison et al., 1992). We consider (1) whether within-habitat variability exceeds between-habitats variability in the size-frequency spectra, (2) whether chemoautotrophically based assemblages can be consistently discriminated from heterotrophic assemblages, (3) whether onshore–offshore trends are present in the size-frequency

distribution of assemblages and whether they can be related to trends in tier and guild structure and taphonomy, and (4) whether unique combinations of size-frequency, tier, and guild structure are present that could permit discrimination of these assemblage types in the stratigraphic record. Finally, we consider the concept of habitat optimality and the curiosity of bimodal adult sizes in some of the size-frequency spectra.

METHODS

Field collection.—Three sites (stations 1, 2, and 3) were located in water depths of 15, 19, and 22 m at distances of 5 km (27°32.55'N, 97°10.23'W), 7 km (27°32.58'N, 97°9.75'W), and 9 km (27°32.97'N, 97°8.61'W), respectively, offshore of Corpus Christi Bay, TX, on the inner continental shelf (Staff and Powell, 1990a:fig. 1).[2] All three locations were below normal wave base but above storm wave base. Substrate was composed predominately of sand and silt with various amounts of gravel and clay. All three stations were south of the coastal area influenced by the Mississippi River plume (e.g., Cochrane and Kelly, 1986; Walker and Rouse, 1993; Sahl et al., 1997); thus, salinities and oxygen contents remained at levels typical of open continental shelves. Curray (1960), Berryhill et al. (1976), and Brown et al. (1976) described the geology of the region. Staff and Powell (1990a, 1990b) and Callender et al. (1992) discussed the taphonomy at these sites.

Shelf fauna were collected with a 30-cm-square, 1-m-deep box core. Each station was sampled about every 6 wk over a 14-mo period during 1986–87. Normally, four box cores were taken per station per sampling occasion. The entire upper 15 cm of each box core sample was sieved onboard ship through a 1-mm-mesh sieve immediately after collection. Each sample, therefore, represented four 0.09-m² box cores, each representing about 0.01 m³. For this contribution, we consider the cumulative assemblage sampled over the 14-mo period. Hence, the assemblage was described from a total sample of 2.88, 2.52, and 3.24 m² to a depth of 15 cm for stations 1, 2, and 3, respectively.

Data analysis.—Individuals were sorted and identified to species. Taxonomic authorities in-

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[1] For simplicity, we use the term chemoautotrophic for species harboring chemoautotrophic symbiotic bacteria. We differentiate two primary assemblage types, an assemblage dominated by a chemoautotrophic fauna and an assemblage dominated by a heterotrophic fauna, by the proportion of paleoingestion or paleoproduction supplied by species with chemoautotrophic bacterial symbionts. In the chemoautotrophic assemblages, the chemoautotrophic species contribute ≥50% of the assemblage's paleoingestion or paleoproduction.

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[2] For comparison, depths for the Copano Bay stations were all 1 m; depths for the slope stations varied between 513 and 754 m.

cluded Abbott (1974), Defenbaugh (1976), and Andrews (1977). All whole specimens were tallied. Molluscan fragments were tallied if beaks (for bivalves) and apexes (for gastropods) were present. The maximum anterior–posterior length for each bivalve and the apex-to-adapical tip length for each gastropod were measured to the nearest 0.1 mm. For bivalves, each disarticulated valve was counted. In environments where taphonomic loss rates or biological predation rates are high, little chance exists for both valves of a disarticulated bivalve to survive (Powell and Stanton, 1996; Callender and Powell, 1997). Powell (1992) suggested that rates of taphonomic loss might be relatively low on the continental shelf. Evidence from taphonomic signatures of this shelf assemblage support this surmise (Staff and Powell, 1990a, 1990b), as does the information to be presented here. Accordingly, the contribution of bivalves to community attributes might be somewhat overestimated, in the extreme by a factor of two, if both valves are consistently preserved. Larger species and individuals will likely be the most biased because the likelihood of their preservation is highest (Powell et al., 1989; Callender and Powell, 1997).

Paleoenergetics.—We examined the assemblages by using the basic community attribute of abundance of the constituent species and also using two attributes indicative of community energetics, paleoingestion, and paleoproduction. Living communities can be defined in terms of the abundance and biomass of the constituent species and the contribution of each species to the community's energy budget. Paleoproduction and paleoingestion are the paleoecological analogues of biomass and energy flow through the consumer food chain in living communities (Powell and Stanton, 1995). We use the prefix "paleo" to distinguish time-averaged attributes from ecological attributes. Because the individuals in a fossil or death assemblage have completed their life spans, measures of community energetics must be integrated over animal life spans (Staff et al., 1986; Powell et al., 1989). Paleoproduction is the net production of somatic tissue over the animal's life span rather than the standing crop at any one time. Paleoingestion is the estimated minimal amount of energy required to have sustained the preserved individual over its life span rather than the amount of energy processed during a discrete time interval as generally used in ecological studies. For heterotrophs, paleoingestion is equivalent to the amount of food ingested.

Paleoingestion, as described by Powell and Stanton (1995), is calculated by:

$$I_{lt} = \frac{A_{lt}}{\alpha} = \frac{P_{g_{lt}} + P_{r_{lt}} + R_{lt}}{\alpha} \quad (1)$$

where A_{lt} is the energy assimilated (in joules) over the individual's life span, $P_{g_{lt}}$, paleoproduction, is the portion of net production devoted to somatic growth over the individual's life span, $P_{r_{lt}}$ is the portion of net production devoted to reproduction over the individual's life span, R_{lt} is the amount of energy respired over the individual's life span, and I_{lt}, paleoingestion, is the amount of energy consumed (in joules) over the animal's life span or the assimilated energy over the assimilation efficiency, α. Methods of calculation of the terms in Equation 1 are presented in Powell and Stanton (1995). Of necessity, only whole individuals from the death assemblage were used, there being no way to measure the original size of fragmented specimens. Staff and Powell (1999) discussed the possible error associated with this approach.

Size-frequency distributions.—We examined the size-frequency distribution in three ways depending upon how an individual's size was standardized with respect to the remainder of the assemblage. (1) In one case, we standardized individual size relative to the known maximum size of the species (Powell and Stanton, 1996). In this case, all adults, regardless of size, are relatively large, but some juveniles, classified as small by this definition, may be of the same size as adults of another species, themselves considered large. The absence of adults indicates a suboptimal environment for that species (Cummins et al., 1986b). Accordingly, "large," by this criterion, is an important population attribute. (2) In the second case, we standardized size relative to the size of the largest shell found in the assemblage. By this definition, some adults are small. (3) In a final set of comparisons, we standardized size to the size of the largest shell found in a series of study sites on the onshore–offshore transect from Copano Bay, TX, to the continental slope. An assemblage comprised exclusively of small individuals may indicate a generalized impoverishment in food supply (Hallam, 1965; Hofmann et al., 1994).

The size-frequency distribution of each assemblage was divided into 10 equal size classes computed as the 10th percentiles of the chosen maximum size. We also calculated the fraction of the species' paleoproduction and paleoingestion contributed by the members of

each size class. These plots are not frequency distributions for which the size classes have been redefined in terms of the biomass or energy flow parameter plotted. Rather, we retained the size classes defined by linear dimension to show the relative importance of each linear size class in the total paleoproduction or paleoingestion of the species or assemblage. Accordingly, the frequency spectra for paleoproduction and paleoingestion show the contribution by members of a given linear size class to the whole assemblage. This follows the convention of Stanton et al. (1981) and Powell and Stanton (1985).

Maximum size was obtained from Odé (1975–1988) and our unpublished data. Maximum ages were obtained from Comfort (1957), Powell and Cummins (1985), Powell and Stanton (l985), Heller (1990), and Callender and Powell (1997). Maximum age for Veneridae was obtained from $T_\infty = 10^{1.588\log_{10}(L_\infty)-1.75}$, derived from maximum age–maximum size pairs for *Phacosoma japonicum, Dosinia hepatica, Dosinia exoleta, Mercenaria mercenaria, Phacosoma staminea, Callista chione, Tapes philippinarum,* and *Anomalocardia squamosa.* In cases where a maximum age could not be obtained from the literature, through reference either to the species in question or to a closely related taxon, we assigned a maximum age of 2 yr. Consequently, paleoenergetics was underestimated for these species. No dominant species were so assigned. Newly obtained information on Lucinidae permitted a maximum age to be set at 7 yr (Berg and Alatalo, 1982) rather than the default condition of 2 yr as used in previous treatments (e.g., Powell and Stanton, 1996; Callender and Powell, 1997).

Human intervention.—Human activities affect nearly all present-day assemblages in some way (Frey et al., 1987; Aitken et al., 1988; Aronson, 1990; Walker, 1995), and these effects potentially compromise application of findings to the stratigraphic record. Fishing activities are particularly significant in their effect on the present-day structure of benthic communities (e.g., Ismail, 1985; Cadée et al., 1995; Beukema and Cadée, 1996) and are particularly pervasive on the continental shelf (Rumohr and Krost, 1991; Hall, 1994; Witbaard and Klein, 1994; Morton, 1996). The Texas continental shelf is particularly impacted by the shrimp fishery, a bottom trawl fishery (Flint and Rabalais, 1981; Larson et al., 1989), and by the erection of oil and gas production platforms (Fucik and El-Sayed, 1979; Kennicutt et al., 1996; Peterson et al., 1996). Nearshore hyp-

oxia, a persistent problem off Louisiana and north Texas, does not extend southward into this area (Rabalais et al., 1993, 1995). Shrimping can be expected to negatively impact the larger and longer-lived species, particularly shallow infauna and semi-infauna (see, e.g., Rumohr and Krost, 1991; Eleftheriou and Robertson, 1992). Shrimping activities are normally less intense near oil and gas production platforms, which were within several kilometers of our shallowest station (station 1). Thus, the deeper stations, stations 2 and 3, were likely more impacted by this activity. The frequency of impact is uncertain. We never observed shrimping on our sites; however, shrimping likely impacts much of the inner Texas continental shelf at least once per year. Given the sedimentation rate on the Texas shelf (Siringan and Anderson, 1994) and the depth of the box core samples, it is unlikely that shrimping activities have significantly impacted the community attributes averaged over the 25-cm sampling depth. Powell et al. (1992) and Callender and Powell (1997) considered the same issues for the Copano Bay and continental slope assemblages, respectively.

RESULTS AND COMPARISONS

We first examine the size-frequency distributions from the three continental shelf assemblages in detail because these assemblages have not been previously described. We then compare them to previously described assemblages from Copano Bay and the continental slope.

The continental shelf assemblages.—Size-frequency distribution by species' maximum size: The individuals were distributed into 10th percentiles of the species' maximum size. Viewed in this way, adults are always large and juveniles are always small, regardless of their actual size. Adulthood occurs at about 50% of maximum size (Powell and Stanton, 1985), although considerable variability exists around this average. Consequently, the size-frequency distribution based on species' maximum size can be used to evaluate the proportion of adults in the assemblage.

The three stations were very similar in their size-frequency distributions based on species' maximum size (Fig. 1a). The vast majority of individuals were newly settled juveniles, 10–20% of maximum size. All three assemblages preserved the typical condition for living communities, that juvenile bivalve survivorship is low, normally below 10% (Thorson, 1966; Brousseau et al., 1982; Powell et al., 1984), de-

Figure 1a - Numerical abundance by assemblage

Figure 1b - Paleoproduction by assemblage

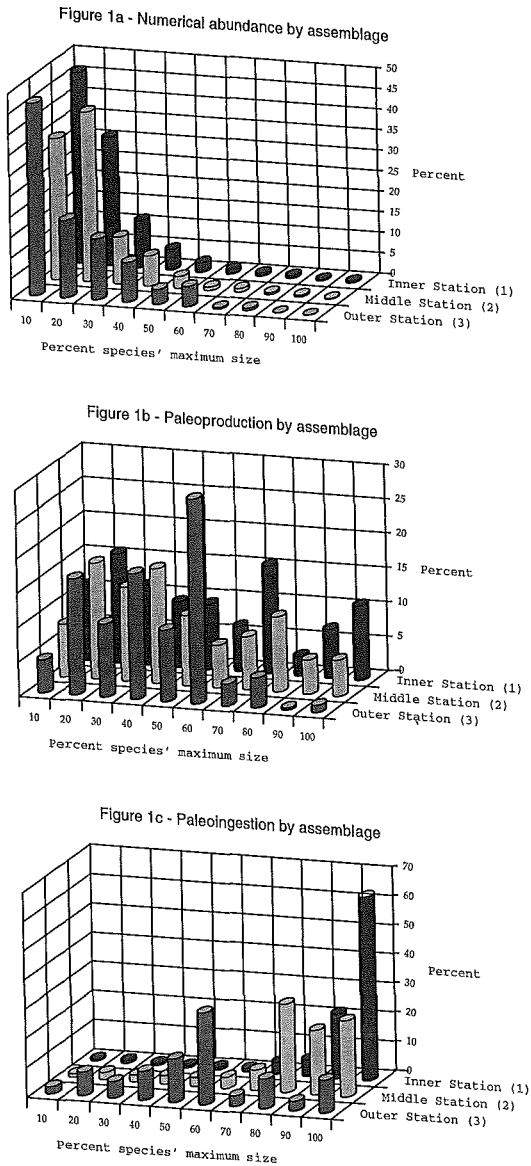Figure 1c - Paleoingestion by assemblage

Fig. 1. The size-frequency distribution of all individuals in each continental shelf assemblage. Size classes defined on the x-axis are the 10th percentiles of species' maximum size, with the listed values being the upper boundaries of each size class. Numerical abundance is represented as the fraction of the total number of individuals in the assemblage in each size class. Paleoproduction and paleoingestion represent the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

spite the well-documented taphonomic bias against these smallest size classes (Samtleben, 1973; Cummins et al., 1986a; Powell et al., 1986; Callender and Powell, 1997).

Essentially all species at the three stations were characterized by a small maximum size, possibly a community-level response to the relatively oligohaline waters of this part of the Gulf of Mexico (El-Sayed, 1972; Biggs and Sanchez, 1997). Defining size classes as a fraction of the species' maximum size permits the identification of individuals living in suboptimal habitats on the basis of the presumption that some individuals of a species should approach maximum size in optimal habitats (Hallam, 1965; Ansell, 1968; Hofmann et al., 1994). Stunting, for example, frequently results from local shortages in food supply (Hallam, 1965; Stańczykowska, 1977; Bowen, 1979); such individuals fail to reach the species' maximum size. Heavy predation pressure on adults likewise would limit the number of individuals approaching maximum size. Very few adults reached near-maximum size in these three assemblages even though these maximum sizes were small. In fact, very few reached 70% of maximum size. None of the three stations was characterized by near-optimum habitat for the vast majority of species.

Paleoproduction was distributed more or less evenly across the size-frequency spectrum in all three assemblages (Fig. 1b). Modes were not easy to discern and not consistent among the stations, although the proportion of paleoproduction contributed by the largest individuals declined with depth (from Station 1 to Station 3). Paleoingestion was distributed primarily in the largest size classes. Adults normally contribute the bulk of population energy flow because they are relatively large and have lived a relatively long time. The same decline in proportional contribution of the largest size classes with depth noted for paleoproduction was present for paleoingestion. In fact, at the deepest station (Station 3), more than half of the paleoingestion was present in animals no larger than 60% of maximum size, whereas, at the shallowest station (Station 1), nearly all paleoingestion was contributed by species >80% of maximum size. Adults were more common in shallower water. The possibility that this is an artifact produced by the presumably lesser influence of commercial fishing at the shallowest station is considered unlikely but cannot be completely excluded.

Size-frequency distribution by assemblage maximum size: Maximum size was also defined as

the size of the largest shell found in the assemblage. By this definition, some adults are small and some juveniles are large, but shells of the same measured size would fall in the same size class regardless of their developmental stage. All three assemblages were characterized by a preponderance of small (≤20% of assemblage maximum size) individuals (Fig. 2a). The distributions of paleoproduction and paleoingestion confirm that most adults were adults of small species and, so, fell within the lowermost four percentile classes of the size-frequency distribution (Fig. 2b,c). In other words, these three assemblages were characterized by a preponderance of juveniles and adults of small species. Few relatively large individuals were collected in any of the three assemblages. Large individuals are typically less common, so their minor contribution might be a sampling artifact produced by the chance failure to collect the largest individuals. However, all three stations were evaluated from total samples of 2.5–3.2 m² (Staff and Powell, 1999), an area significantly larger than sampled for the other assemblages discussed in the next section in which large individuals were much more common; consequently, sampling should have been adequate to obtain any but the rarest large species.

The bay-to-slope transect.—Perspective: Powell and Stanton (1996) described the size-frequency distributions for death assemblages from an estuarine site in Copano Bay, TX. Two assemblages were present at that site, one dominated by heterotrophic filter feeders and one dominated by bivalves (lucinids) with chemoautotrophic bacterial symbionts. Callender and Powell (1997) described a series of continental slope assemblages off Texas and Louisiana. Some assemblages associated with petroleum seeps were dominated by lucinids and thyasirids, each bearing chemoautotrophic bacterial symbionts. One assemblage, characteristic of the typical continental slope, was dominated by heterotrophic species. All of the assemblages were sampled with equivalent methodology: box core and a 1-mm sieve. Together, these assemblages, plus the three described here, cover a transect from a variable salinity estuary to the upper continental slope, representing a diversity of assemblage types.

Staff and Powell (1999) compared the species composition and guild and tier structures of these diverse assemblages. The assemblage types were each unique in a combination of key abundance, paleoproduction, and paleo-ingestion-derived community attributes. At

Figure 2a - Numerical abundance by assemblage

Figure 2b - Paleoproduction by assemblage

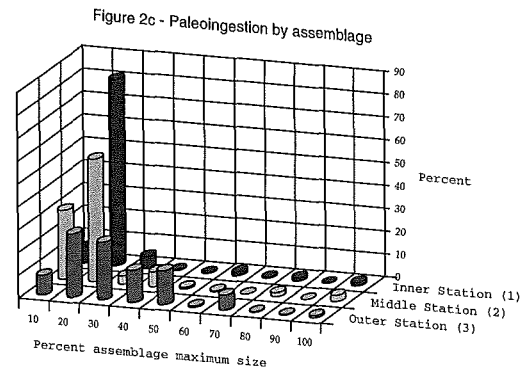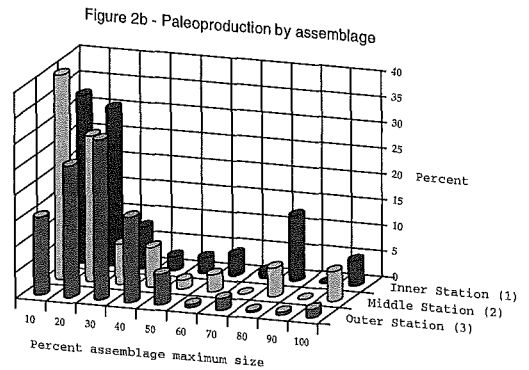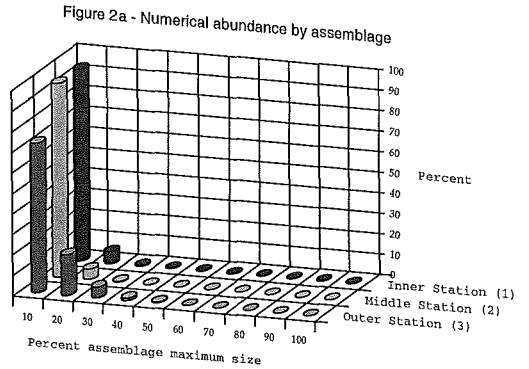Figure 2c - Paleoingestion by assemblage

Fig. 2. The size-frequency distribution of all individuals in each continental shelf assemblage. Size classes defined on the x-axis are the 10th percentiles of assemblage maximum size (the largest individual collected in the assemblage), with the listed values being the upper boundaries of each size class. Note that the maximum size collected varied between assemblages, and, therefore, the linear dimension represented by each size class varies between assemblages. Numerical abundance represents the fraction of the total number of individuals in each assemblage in each size class. Paleoproduction and paleoingestion represent the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

Figure 3a - Numerical abundance by assemblage

Figure 3b - Numerical abundance by assemblage

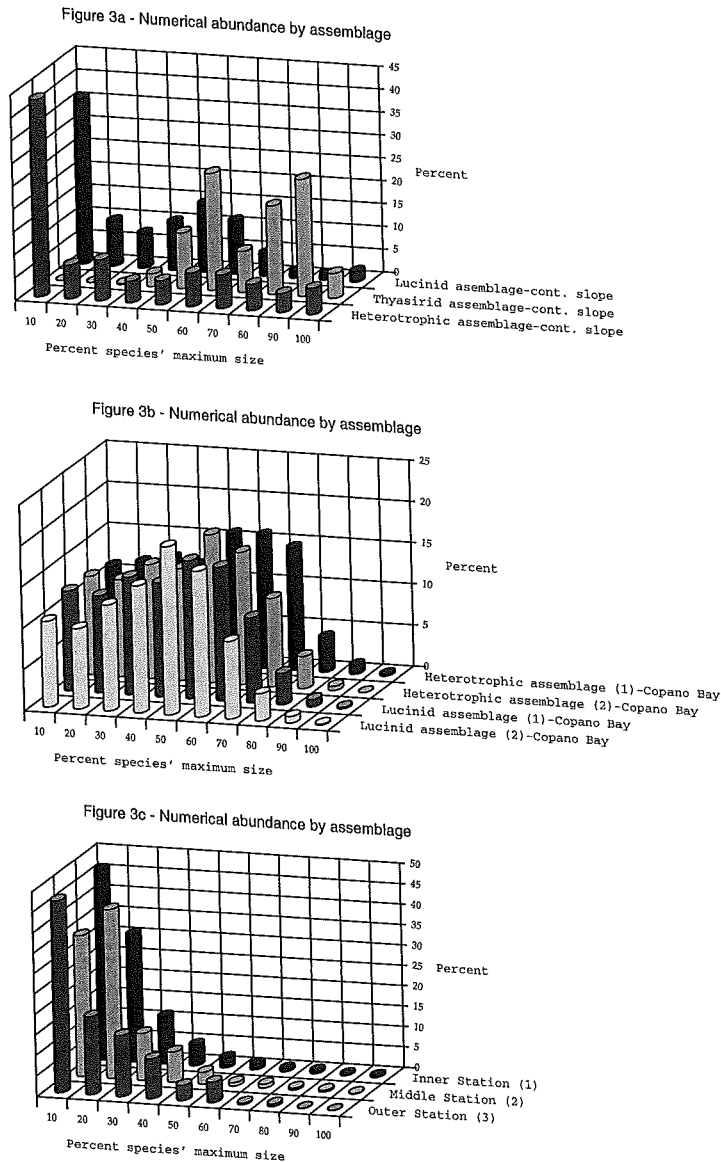Figure 3c - Numerical abundance by assemblage

Fig. 3. The size-frequency distribution of all individuals in each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes defined on the x-axis are the 10th percentiles of species' maximum size, with the listed values being the upper boundaries of each size class. Numerical abundance represents the fraction of the total number of individuals in each assemblage in each size class. Note that the range of the y-axis scale varies between figures.

least as important, however, were the resemblances between certain assemblages. All continental shelf and heterotrophic slope assemblages were characterized by predator dominance of paleoingestion. Deposit feeders and chemoautotrophs increased in importance numerically offshore but not when evaluated by energy flow. All offshore assemblages were characterized by 40% or more of the individuals being infaunal. On the whole, tier structure was more variable than guild structure within habitat. On the whole, paleoingestion was more variable than numerical abundance or paleoproduction within habitat, probably because of the reliance of paleoingestion on long-lived taxa that are normally relatively rare.

The bay-to-slope transect—species maximum size: Most individuals in the three shelf assemblages were juveniles (Fig. 3a). In contrast, the
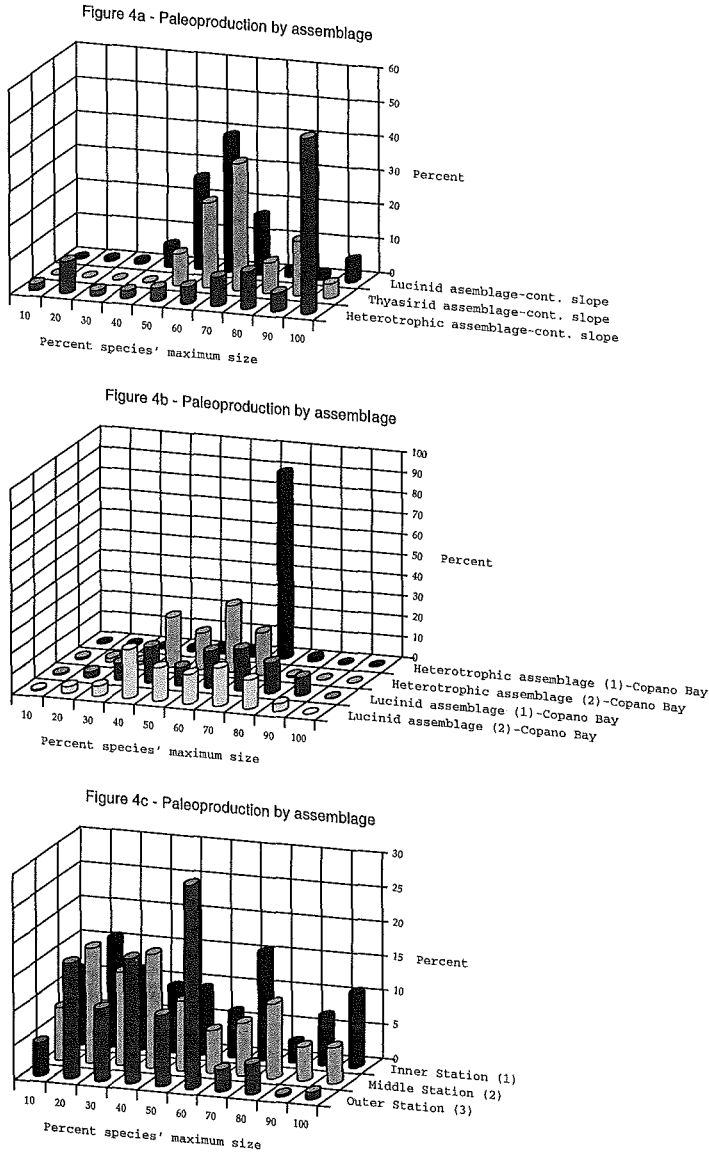
Fig. 4. The distribution of paleoproduction among the 10 size-frequency categories defined in Figure 3 for each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes on the x-axis are defined as the 10th percentiles of species' maximum size, with the listed values being the upper boundaries of each size class. Paleoproduction represents the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

four Copano Bay assemblages, heterotrophic and chemoautotrophic, contained a broad distribution of juveniles and adults (Fig. 3b). On the continental slope, the assemblages tended to contain predominately adult individuals; however, two of three assemblages had a second strong mode in the lowermost size category ($\leq 10\%$ of species maximum size), which contained recent additions of juveniles that had not yet succumbed to taphonomic pro-

cesses (Fig. 3c). The third assemblage, the thyasirid assemblage, was not so characterized and, in fact, was no longer recruiting living individuals, supporting the interpretation for the former two assemblages (Callender and Powell, 1997).

Most paleoproduction was contributed by adults on the continental slope and in Copano Bay (Fig. 4a,b), regardless of the chemoautotrophic or heterotrophic nature of the assem-
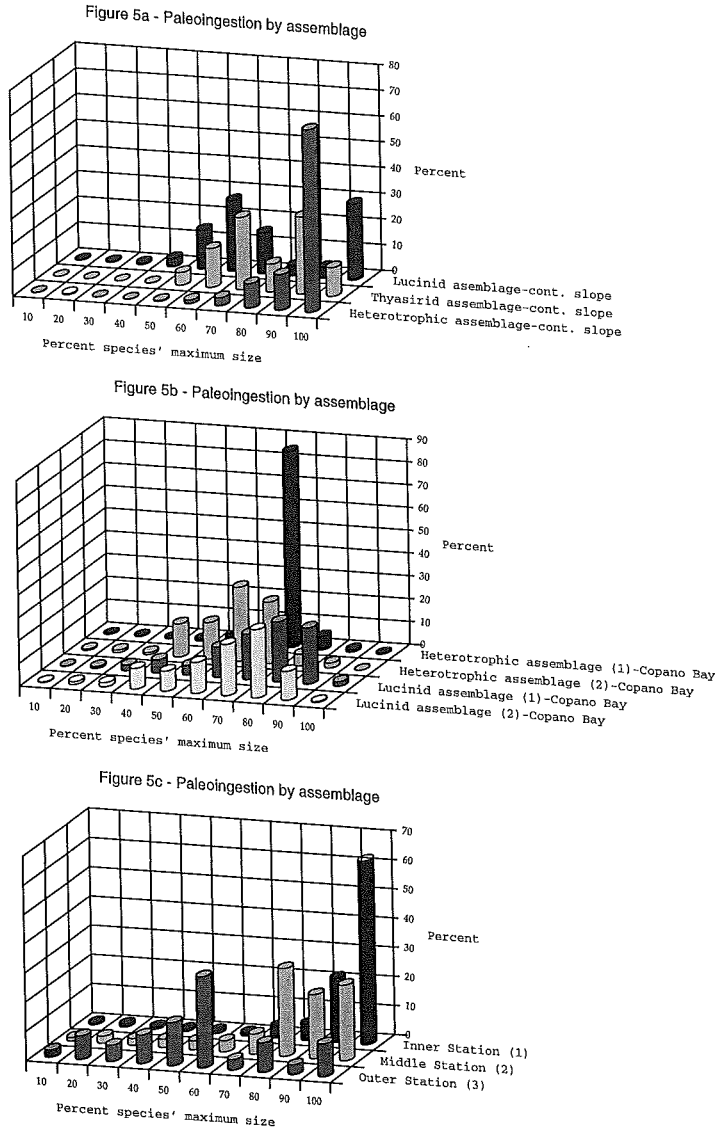
Fig. 5.   The distribution of paleoingestion among the 10 size-frequency categories defined in Figure 3 for each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes on the x-axis are defined as the 10th percentiles of species' maximum size, with the listed values being the upper boundaries of each size class. Paleoingestion represents the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

blage. Not so on the continental shelf, where most individuals were juveniles and, so, juveniles contributed substantially to paleoproduction (Fig. 4c). Likewise, most paleoingestion was contributed by adults on the continental slope and in Copano Bay (Fig. 5a,b). A lesser share, but still the majority, was also contributed by adults at the continental shelf stations (Fig. 5c). Life span, rather than size, is most important in determining energy flow and, so, paleoingestion emphasized the few adults that

were present in the continental shelf assemblages.

The bay-to-slope transect—assemblage maximum size: The distribution of sizes in each assemblage was distinctive in all three continental slope communities, chemoautotrophic and heterotrophic, when compared with the other, shallower, assemblages (Fig. 6a–c). The preponderance of individuals were found in the lowermost two size classes in the Copano Bay
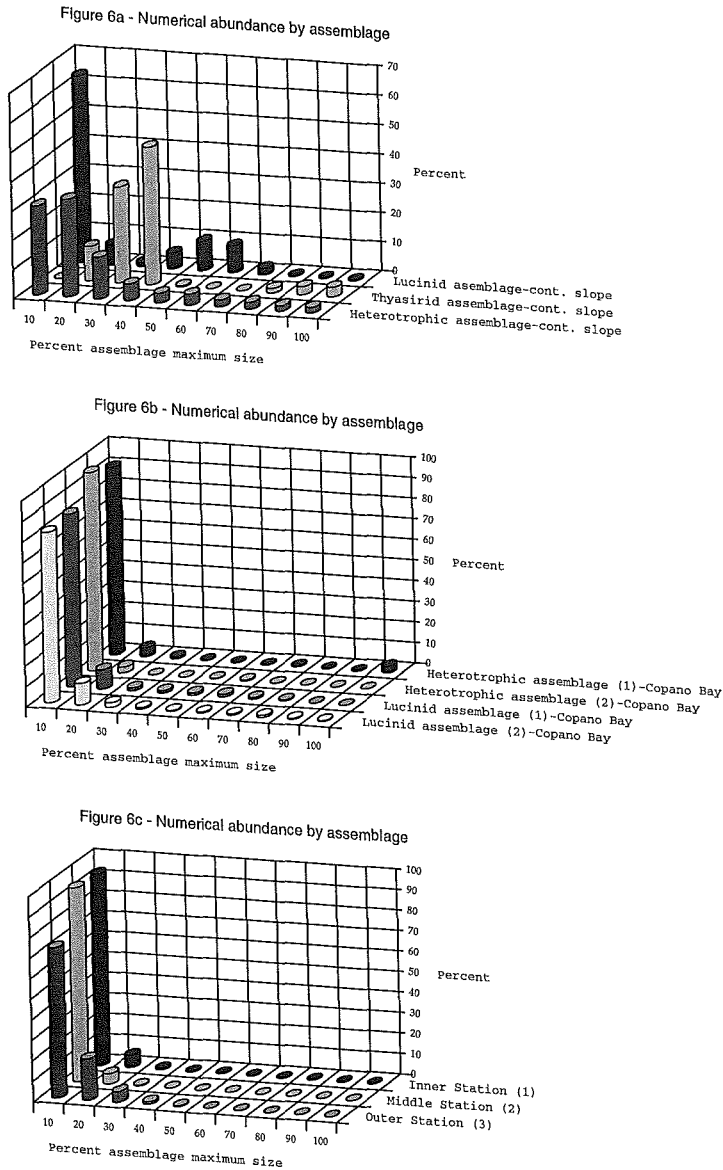
Fig. 6.   The size-frequency distribution of all individuals in each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes defined on the x-axis are the 10th percentiles of assemblage maximum size (the largest individual collected in the assemblage), with the listed values being the upper boundaries of each size class. Note that the maximum size collected varied between assemblages, and, therefore, the linear dimension represented by each size class varies between assemblages. Numerical abundance represents the fraction of the total number of individuals in each assemblage in each size class. Note that the range of the y-axis scale varies between figures.

and continental shelf assemblages, regardless of their chemoautotrophic or heterotrophic character (Fig. 6b,c). On the continental slope, a much larger number of individuals were ≥40% of assemblage maximum size, regardless of their chemoautotrophic or heterotrophic character (Fig. 6a).

The majority of paleoproduction was in the smaller five size classes in the continental shelf assemblages (Fig. 7c). In contrast, in the Copano Bay and continental slope assemblages, the majority of paleoproduction was in the highest five size classes (Fig. 7a,b). Most of the biomass in these assemblages resided in the larger animals. A strong tendency also existed toward bimodality in the frequency spectra,

Figure 7a - Paleoproduction by assemblage

Figure 7b - Paleoproduction by assemblage
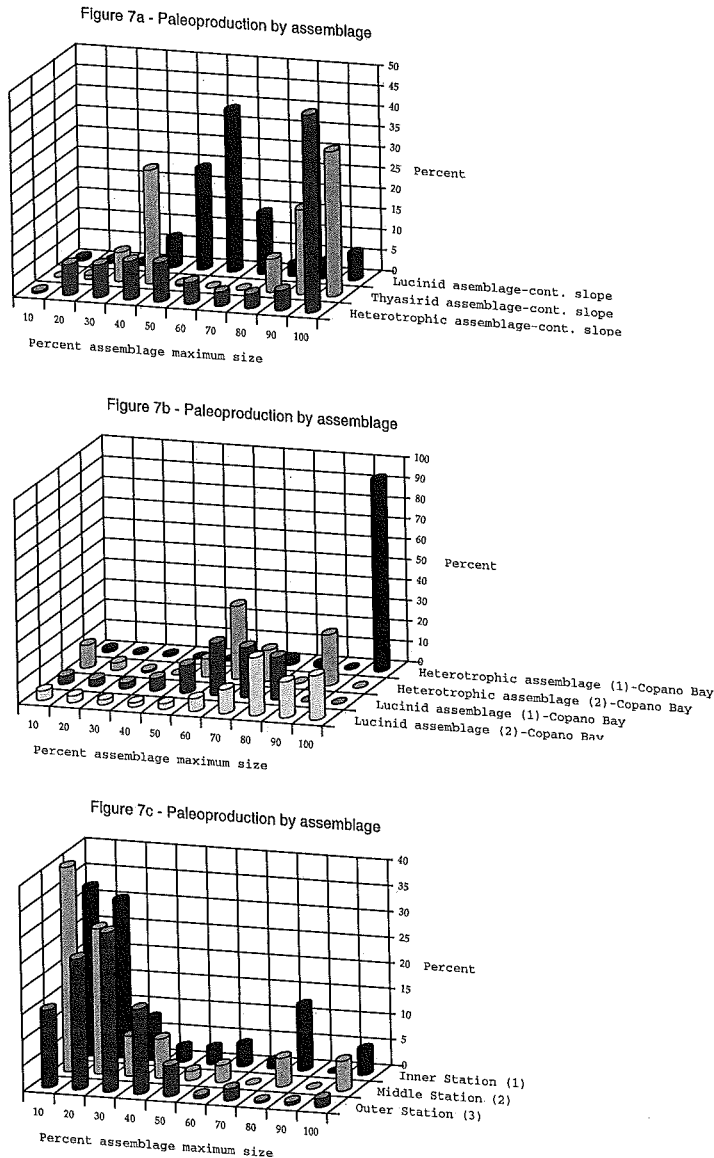

Figure 7c - Paleoproduction by assemblage

Fig. 7.   The distribution of paleoproduction among the 10 size-frequency categories defined in Figure 6 for each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes on the x-axis are defined as the 10th percentiles of assemblage maximum size, with the listed values being the upper boundaries of each size class. Note that the maximum size collected varied between assemblages, and, therefore, the linear dimension represented by each size class varies between assemblages. Paleoproduction represents the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

particularly on the continental slope, where two of the three assemblages were strongly bimodal (Fig. 7a). That is, the assemblage was composed of biomass peaks in the lower five and upper five size classes. In these cases, the assemblage consisted of adults of small and large species that both contributed significantly to paleoproduction.

Bimodality became even more obvious when paleoingestion was distributed across the size-frequency spectra (Fig. 8a–c), confirming that bimodality was due to adults of species of disparate sizes rather than to an uncommon number of juveniles. On the continental slope, the lowermost mode was near 50% of assemblage maximum size (Fig. 8a). In Copano Bay, the
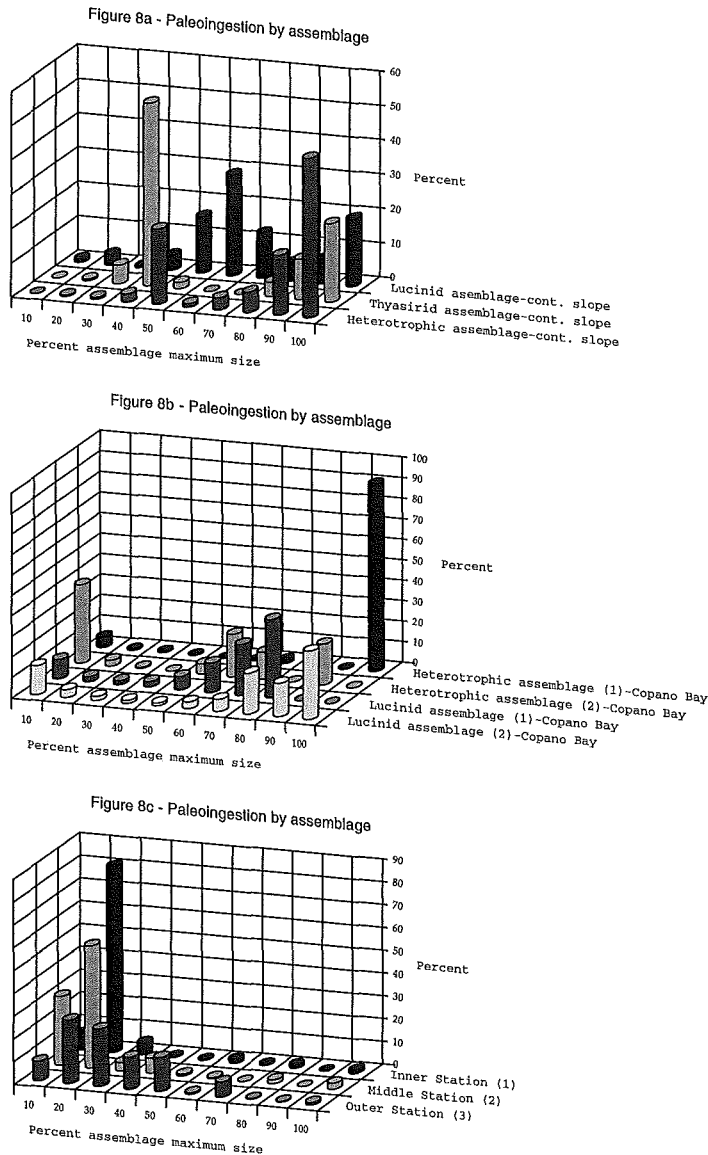
Fig. 8.   The distribution of paleoingestion among the 10 size-frequency categories defined in Figure 6 for each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes on the x-axis are defined as the 10th percentiles of assemblage maximum size, with the listed values being the upper boundaries of each size class. Note that the maximum size collected varied between assemblages, and, therefore, the linear dimension represented by each size class varies between assemblages. Paleoingestion represents the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

lowermost mode was in the 10% category (Fig. 8b). The upper mode in both cases tended to fall at ≥80% of maximum size. Once again, the continental shelf assemblages were unique in having few individuals in the upper five size classes (Fig. 8c). Most of these individuals were juveniles.

The bay-to-slope transect—study maximum size: We classified individuals in 10th percentiles of maximum size established by the largest specimen obtained in any of the study areas. In this way, the relative sizes of individuals in the 10 assemblages could be compared. The Copano Bay assemblages contain taxa that rou-

Figure 9a - Numerical abundance by assemblage

Figure 9b - Numerical abundance by assemblage

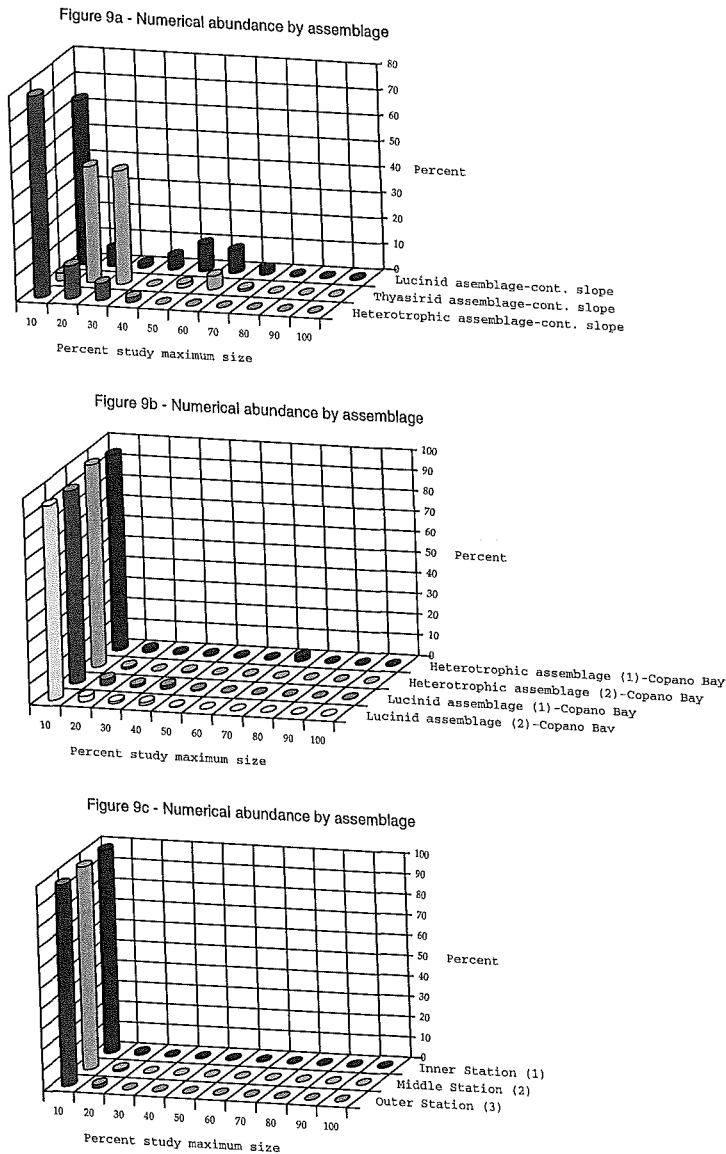Figure 9c - Numerical abundance by assemblage

Fig. 9.   The size-frequency distribution of all individuals in each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes defined on the x-axis are the 10th percentiles of study maximum size (the largest individual collected among all ten of the assemblages), with the listed values being the upper boundaries of each size class. Numerical abundance represents the fraction of the total number of individuals in each assemblage in each size class. Note that the range of the y-axis scale varies between figures.

tinely exceed 50 mm in size, whereas few of the heterotrophic continental slope taxa exceed 25 mm in size, with the exception, of course, of the deep-water petroleum seep communities that have an independent trophic source, chemosynthesis, that permits the presence of taxa of larger size.

Comparison of the size-frequency spectra (Fig. 9a–c) for the 10 assemblages shows that the continental slope assemblages contained significant numbers of individuals much larger than those found in any of the other assemblages. Particularly noteworthy are the two chemoautotrophic faunas, the lucinid and thyasirid assemblages, which contain far and away the largest fraction of large animals. In comparison, the Copano Bay and continental shelf assemblages overwhelmingly consist of small in-

dividuals (Fig. 9b,c). Of the two, the continental shelf assemblages are proportionately smaller in average size. Of interest is the similarity of the chemoautotrophic and heterotrophic assemblages in Copano Bay. In both assemblages, most of the individuals are small, heterotrophic bivalves and gastropods. However, both assemblages contain some larger individuals of about the same size as found in the continental slope assemblages: filter-feeding bivalves in one case and chemoautotrophic bivalves in the other (Powell and Stanton, 1996). Particularly noteworthy is the proportionately greater contribution of relatively large individuals in the heterotrophic continental slope assemblage than in any of the heterotrophic assemblages from Copano Bay or the continental shelf. Although the largest size was smallest in this assemblage (about 25 mm), a considerable number of individuals approached that size.

The larger individuals in the continental slope petroleum seep assemblages contributed most of the paleoproduction to these assemblages (Fig. 10a). In contrast to numerical abundance, however, paleoproduction in the Copano Bay assemblages was also distributed well up into the size-frequency spectra (Fig. 10b). The lowermost size-frequency classes contributed most paleoproduction to the continental shelf assemblages (Fig. 10c). In contrast to numerical abundance, the distribution of paleoproduction in the Copano Bay assemblages more closely compared with the distribution in the continental slope assemblages than with the distribution in the continental shelf assemblages. Bimodality was present in the thyasirid assemblage (Fig. 10a) but was not obvious in any other assemblage, although some tendency toward bimodality was present in two of the continental shelf assemblages and three of four of the Copano Bay assemblages.

The distribution of paleoingestion among the size categories was similar to that for paleoproduction with one exception. Bimodality in the frequency spectra was much more obvious. On the continental slope, both chemoautotrophic assemblages, lucinid and thyasirid, had distinctly bimodal spectra (Fig. 11a). Three of four Copano Bay assemblages were distinctly bimodal (Fig. 11b). Only on the continental shelf was bimodality no more distinctive than it had been with paleoproduction (Fig. 11c). Bimodality was a distinct attribute of all chemoautotrophic assemblages, whether from Copano Bay or the continental slope. Only one heterotrophic assemblage, from Copano Bay, was distinctly bimodal.

DISCUSSION

Alpha and beta-level variability.—Size-frequency distributions might be used to aid discrimination between habitat types in the stratigraphic record. To do so, within-habitat (alpha) variability must be much less than between-habitats (beta) variability. The three continental shelf assemblages were very similar in all respects, whether evaluated by numerical abundance, paleoproduction, or paleoingestion or by species' maximum size, assemblage maximum size, or study maximum size. The Copano Bay assemblages were somewhat more variable, but, still, variability between these assemblages was limited. Both of these groups of assemblages are parautochthonous.[3] The autochthonous continental slope assemblages, by contrast, are relatively diverse in their size-frequency spectra if evaluated by assemblage or study maximum size. The distribution of adult sizes varies considerably in the three continental slope assemblages, although the assemblages are more similar by species' maximum size. The two chemoautotrophic assemblages on the continental slope, the thyasirid and lucinid assemblages, are clearly more similar to each other than to the heterotrophic continental slope assemblage; nevertheless, distinctive differences exist between the two chemoautotrophic assemblages, particularly with the use of paleoproduction or paleoingestion, which emphasize the fact that these two communities differ considerably in the modal size of the adult chemoautotrophic species.

The variability in size-frequency spectra on the continental slope is consistent with the variability in taphonomic signature among these same assemblages (Callender et al., 1990; Callender and Powell, 1992). The similarity in the taphonomic signature of the three continental shelf assemblages (Staff and Powell, 1990b; Callender et al., 1992) mirrors their similarity in size-frequency distribution. The difference in within-habitat transport between the parautochthonous and autochthonous assemblages might be responsible for the lesser within-habitat variability in the parautochthonous assemblages. An alternate possibility is that the degree of microhabitat variability is far larger on the continental slope. The environment is more homogeneous spatially on the continental shelf, somewhat less homogeneous in Copano Bay, and very much less so on the conti-

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[3] These assemblages are considered parautochthonous because they are above hurricane wave base yet do not contain a significant component of exotic species.

Figure 10a - Paleoproduction by assemblage

Figure 10b - Paleoproduction by assemblage
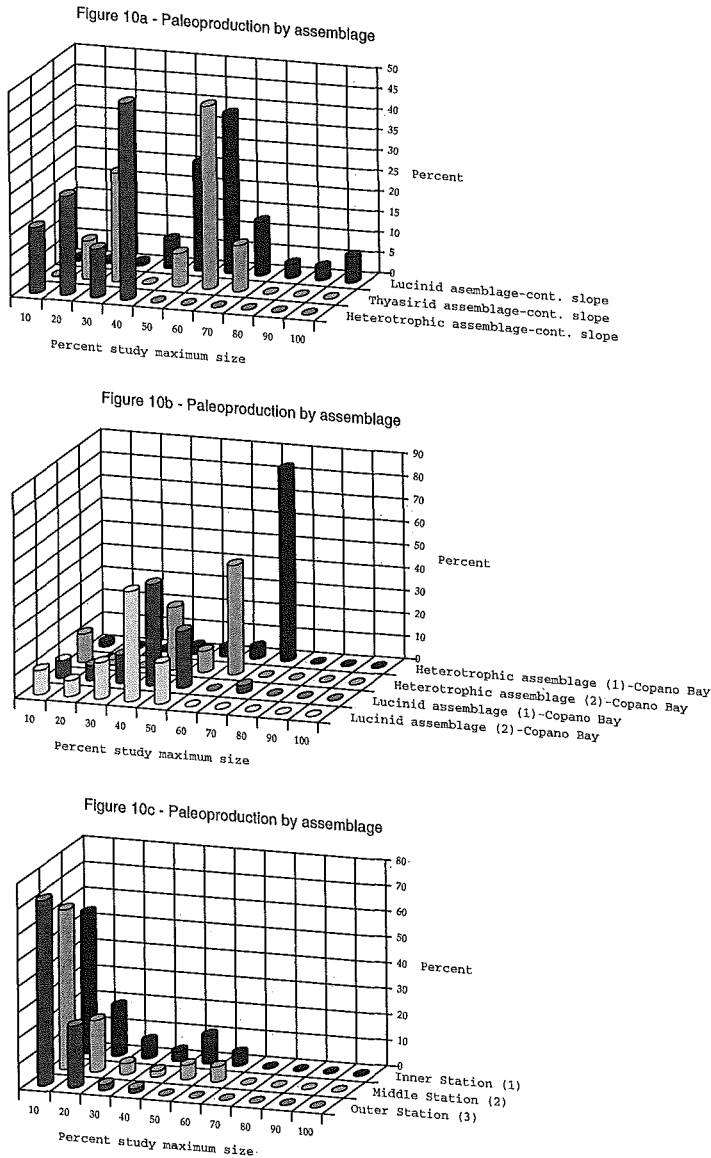

Figure 10c - Paleoproduction by assemblage

Fig. 10.   The distribution of paleoproduction among the 10 size-frequency categories defined in Figure 9 for each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes on the x-axis are defined as the 10th percentiles of study maximum size, with the listed values being the upper boundaries of each size class. Paleoproduction represents the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

nental slope. This trend follows the trend in within-habitat variability in the size-frequency distribution. The present analysis does not permit discriminating the two possible factors, transport and habitat variability, in determining alpha-level variation in assemblage structure.

Regardless of the degree of similarity within-habitat, the really large differences between assemblages were observed when comparing assemblages from one habitat to assemblages from another. The continental slope assemblages were distinctive; they had the largest proportion of adult individuals. The continental shelf assemblages were distinctive; they were overwhelmingly dominated by juveniles. The trends in the proportion of adult individuals determined the overall structure of the size-frequency distribution, regardless, for the most part, of how the distribution was evaluated. A
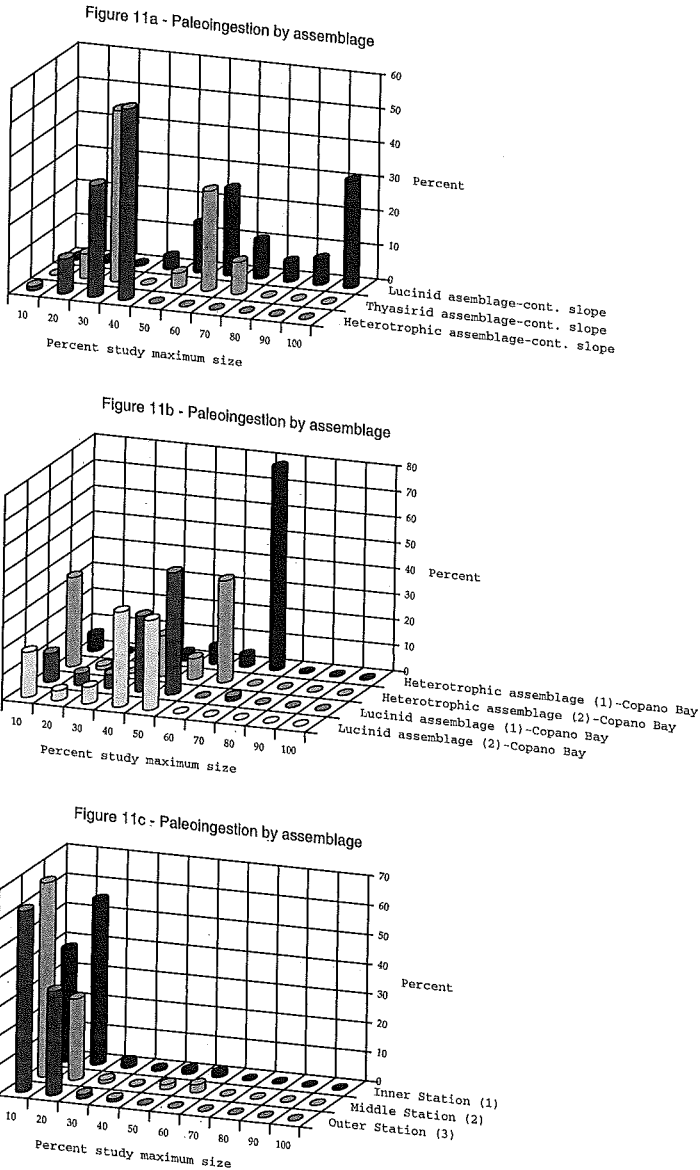
Fig. 11.   The distribution of paleoingestion among the 10 size-frequency categories defined in Figure 9 for each of the 10 continental shelf, continental slope, and Copano Bay assemblages. Size classes are defined as the 10th percentiles of study maximum size, with the listed values being the upper boundaries of each size class. Paleoingestion represents the fraction of the assemblage total contributed by the individuals in each size class. Note that the range of the y-axis scale varies between figures.

singular exception was the similarity in the Copano Bay and continental shelf assemblages evaluated by assemblage or study maximum size with the use of numerical abundance (Figs. 6, 9). In both cases, modes were in the lowermost two size classes. In one case (Copano Bay), many of these individuals were adults of small species; in the other case (the continental shelf), the individuals were nearly all juveniles. Thus, the use of energy flow measures and species' maximum size was necessary to document the differences in the size-frequency composition within this suite of assemblage types. Measures of energy flow permitted the identification of the larger, older individuals, which were important components of the Copano Bay assemblages and which were distinctly lacking on the continental shelf. Species'

maximum size permitted discrimination of adults and juveniles.

The influence of chemoautotrophy.—It is noteworthy that, both in Copano Bay and on the continental slope, the chemoautotrophic and heterotrophic assemblages were similar in most respects despite substantial differences in their trophic structure. Similarity existed in the proportion of adults, in the tendency toward bimodality, and in the degree to which species reached maximum size. The only real distinction was on the continental slope, where the chemoautotrophic and heterotrophic assemblages were distinctive in the size of their largest individuals (relative to study maximum size). It is not intuitively obvious why the chemoautotrophic and heterotrophic assemblages should bear such remarkable resemblances within the two distinctively different habitats. The obvious inference is that, at the ecosystem level, communities have a certain conservatism in the processes of recruitment and survivorship that dictate adult proportional contribution and in the suite of available food and space resources that dictate species size. Regardless, the study dramatically shows the limited use of the size-frequency distributions in identifying ancient chemoautotrophic faunas. Only in an oligohaline setting, such as the continental slope, can any consistent distinction be obtained [Staff and Powell (1999) discussed the discrimination of chemoautotrophic and heterotrophic assemblages in more detail].

Processes determining beta-level variation.—The shape of the size-frequency spectra was controlled in large measure by (a) the relative loss of juveniles through taphonomy, (b) the degree of survivorship to adulthood, probably predominately determined by predation, (c) the food and space resources present that control species size, and (d) the optimality of the habitat that allowed animals to approach maximum size.

Taphonomy: Taphonomic studies suggest that the cold-seep habitats are characterized by higher rates of taphonomic loss than other locations covered by this study (e.g., Cummins et al., 1986a; Staff et al., 1986; Staff and Powell, 1990a; Callender et al., 1994; Callender and Powell, 1997). Very likely, at these sites, a significant component of assemblage structure is determined by taphonomic processes rather than the ecology of the living communities, and this bias is directed not only against juveniles but also against adults of small species. A

greater taphonomic loss of small species and individuals at the Copano Bay and continental shelf sites would have moved the size-frequency distributions of these assemblages toward the pattern shown on the continental slope (see, e.g., Staff and Powell, 1999).

In contrast to the petroleum seeps, the evidence is less strong for high rates of taphonomic loss on the normal (heterotrophic) slope; nevertheless, the size-frequency distribution of the assemblage from the heterotrophic continental slope was not too dissimilar to that found in the petroleum seep assemblages. Thus, an increase in survivorship brought on by a possible reduction in predation rate on the continental slope cannot be discounted as a second factor limiting juvenile abundance (Callender and Powell, 1999).

Food supply: The onshore–offshore transect is characterized by a reduction in the size of the largest taxa that follows the offshore reduction in primary productivity characteristic of this part of the Gulf of Mexico (El-Sayed, 1972; Biggs and Sanchez, 1997). The exceptional cases are the petroleum seeps on the continental slope, which are characterized by an independent food resource. Paleoproduction or biomass-at-death is a good indicator of the daily food supply in the environment and offers an indirect way to compare food richness. Nearly all mollusks have indeterminate growth (Wilbur and Owen, 1964; Levinton and Bambach, 1969), and size varies, although in a complex way, with food supply (Hallam, 1965; Vermeij, 1990; Powell et al., 1995). Growth efficiency declines with size because, typically, maintenance processes scale at a higher power to biomass than does food acquisition (Bauer, 1992; Powell et al., 1992). As a consequence, maximum size is determined by the daily limits on food resources (Condrey, 1982; Powell et al., 1995), normally for bivalves when condition index is highest [condition index varies during the year with food supply and other processes such as spawning (Engle and Chapman, 1953; Soniat and Ray, 1985; Rheault and Rice, 1996)]. Typically, this restriction will result in a proportional increase in the number of small species as well as a limitation on the number of individuals of larger species that attain near-maximum size in oligohaline areas.

Examination of the distribution of paleoproduction across the size-frequency distribution of these 10 assemblages (Fig. 10a–c) reveals evidence of food limitation restricting size in the heterotrophic continental slope assemblages, a somewhat lesser degree of food

limitation in the continental shelf assemblages, and lesser still in the heterotrophic assemblages from Copano Bay. This is the anticipated offshore decline in food availability produced by changes in primary production and the loss of usable substrate as food sinks through an ever deepening water column (Rowe, 1983; Rowe et al., 1991). The chemoautotrophic assemblages of the slope, in contrast, have a larger fraction of large animals. The Copano Bay chemoautotrophic communities are smaller than those on the continental slope, and this is possibly the result of restricted reduced substrate availability in comparison with the continental slope, where sulfide production rates are relatively high, but is more likely ascribed to increased temporal variability in the estuarine habitat, as discussed later.

Predation pressure: Paleoingestion is a function of age and size and so integrates the long-term food supply with other factors, such as predation, that limit life spans. Although the importance of predation in the mortality of populations is not well understood, predators likely account for over 50% of yearly mortality (e.g., Menzel et al., 1957; Vermeij, 1980; Vermeij and Zipser, 1986). The basic trends in paleoingestion follow those for paleoproduction (Fig. 11a–c) in the continental slope assemblages and for those from Copano Bay, indicating that food supply is predominately determining the number of large and old animals. Not so on the continental shelf, where most of the paleoingestion is restricted to the two lowermost size classes, in comparison with paleoproduction. Although some individuals grew to a relatively large size, very few lived to a relatively old age. Increased predation on the continental shelf would seem a likely explanation (see also Callender and Powell, 1999). Indeed, the nearshore continental shelf off Texas is characterized by a high abundance of bivalve predators such as crabs (Ellis et al., 1996), and the death assemblages, themselves, contain an uncommon abundance of predatory snails (Staff and Powell, 1999). Thus, juvenile mortality by predation would seem to be a predominant biological process determining assemblage size frequency in this habitat. However, a predation refuge at large size is characteristic of many prey species (Woodin, 1978; McArdle et al., 1990; Powell et al., 1997), yet little evidence for such a phenomenon exists at this site (Powell et al., unpubl.).

The relative proportions of predators in the continental shelf and slope heterotrophic assemblages are striking (Staff and Powell, 1999). Comparison of predator lifetime ingestion (paleoingestion) with prey lifetime production (paleoproduction) reveals that the continental slope cold-seep assemblages and Copano Bay assemblages have a large surplus of primary consumers, whereas the heterotrophic continental slope assemblage and the three inner continental shelf assemblages are overrepresented by predators. Assuming that the proportions of predator and prey indicate the relative importance of nonpreservable prey, nonpreservable prey were relatively more abundant on the continental shelf and heterotrophic slope. The obvious expectation is that the size frequency of the two assemblage types showing more than the expected number of predators should be skewed toward the juvenile size classes; survivorship should be relatively lower at these sites. The continental shelf assemblages meet this expectation; the heterotrophic continental slope assemblage does not. The paucity of juveniles in the heterotrophic continental slope assemblage is not easily explained by present evidence on predation rate or taphonomy.

Habitat optimality: Defining size classes as a fraction of the species' maximum size permits the identification of individuals living in suboptimal habitats on the basis of the presumption that some individuals of a species should approach maximum size in optimal habitats (Hallam, 1965; Ansell, 1968; Hofmann et al., 1994). Presentation of the size-frequency distribution in terms of the species' maximum size also permits the discrimination of the relative abundances of adults and juveniles, the boundary of which generally falls in the range of 50% of maximum size (Powell and Stanton, 1985). The absence of adults can indicate a suboptimal environment (Cummins et al., 1986b).

Use of the size-frequency distribution to assess habitat optimality assumes that changes in characteristic (local maximum) size indicate variations in scope for growth (Hofmann et al., 1994; Powell and Stanton, 1995; Powell et al., 1995) or temporal stability. Maximum size is normally determined in bivalves by a balance between the rate of food acquisition and the rate of energy expenditure in body maintenance and reproduction and the temporal stability of the environmental processes controlling growth and survivorship. As size increases, the energy needed for maintenance and reproduction increases faster than the increase in energy acquisition so that growth decreases and finally stops at some maximum size, and

this process takes a species-dependent period of time. Of course, predation and other processes of mortality might also restrict local maximum size. Species represented nearly or solely by juveniles are a common occurrence in communities and their death assemblages (e.g., Wells and Gray, 1960; Holland et al., 1977; Zarkanellas, 1979; Cummins et al., 1986b). However, if a significant number of adults exist in the assemblage, then their size is likely a good estimator of optimality. Although predation could be effective in limiting species size, species generally have a large-size refuge (e.g., Woodin, 1978; Coull and Wells, 1983; Holt, 1987; Cohen et al., 1993; Sousa, 1993), and predation should not be completely successful in minimizing adult size even where no size refuge exists.

An important caveat exists with this approach. The degree to which maximum size for the species can be reached in any local environment is dependent on food supply and environmental conditions (Hofmann et al., 1992; Powell et al., 1995). However, a species' maximum size may vary latitudinally over its range (Nicol, 1964; Ansell, 1968; Hofmann et al., 1994) because the division of assimilated energy into reproductive and somatic growth varies with temperature, and higher yearly temperatures at lower latitudes divert more of the assimilated energy into reproductive growth. Smaller individuals produced in this way may be misinterpreted as stunted, as the term is usually defined. In oysters, for example, latitudinal effects produce at least a 20% variation in characteristic adult size (Hofmann et al., 1994). Most of the maximum sizes used in this study were obtained for the latitude of the study. Nevertheless, some of these species reaching 70% of maximum size may have been closer to the maximum size for this latitude than is apparent from the figures.

The adults of some species are bigger than others, and, on the average, within a habitat, the larger species are characterized by longer life spans (scallops more often than not are key exceptions). Thus, for some species, habitat optimality is also associated with habitat stability over extended time periods. Referencing the size classes in a size-frequency distribution to the largest individuals from a group of sites permits identification of regional variations in habitat optimality and habitat stability. The restriction in the size of individuals in specific assemblages, when compared with other assemblages in a study, might normally be explained by a decrease in food resources because the amount of energy required for main-

tenance is a relatively conservative function of biomass. Within a restricted latitudinal range, as food resources decrease, the maximum size of individuals is also reduced, and this will restrict the habitat to small species or stunted individuals of normally larger ones (e.g., Shirayama and Horikoshi, 1989; Vermeij, 1990; Hofmann et al., 1994).

The habitats on the continental slope had the highest proportion of individuals near maximum size. The Copano Bay assemblages were also characterized by a large proportion of adult individuals; however, these normally did not reach sizes above 70% of the species' maximum size. The continental shelf assemblages had few adult individuals. The largest individuals were found at the petroleum seeps and the heterotrophic assemblages from Copano Bay. Individuals were smaller on the heterotrophic continental slope and the chemoautotrophic assemblages from Copano Bay. Recourse to energy flow criteria reveals that the individuals in the former two types of assemblages not only grew to large size but lived relatively long. Continental slope habitats should be temporally most stable, and our information supports that expectation. Food supply should be greatest in estuaries and in cold seeps where chemosynthetic processes dominate. Our data support this expectation.

Copano Bay is characterized by a changing salinity regime that seems to have a 3–5-yr periodicity (Powell et al., 1992). This limits habitat stability as revealed by adult size in both the heterotrophic and chemoautotrophic assemblages in comparison with the continental slope and probably best explains the smaller size of the chemoautotrophic species there. The heterotrophic continental slope, although generating many adult individuals, was restricted to adults of small species. Food restriction is an obvious explanatory factor. What is surprising is the inability of the continental shelf to generate adult individuals in any numbers, despite what would appear to be a relatively stable environment. Predation would seem the likely explanation, although we cannot rule out the importance of commercial fishing in limiting survival to adulthood.

Habitat stability is often related to increased species richness (Sanders, 1968; Staff and Powell, 1988; but see Armonies, 1986). However, Staff and Powell (1988) showed that stability had precisely the opposite effect in death assemblages because time averaging enriched the death assemblage in species in unstable environments. Optimality as judged by the size-frequency distribution is quite distinctive. Pe-

troleum seeps are not species-rich communities (Callender and Powell, 1997; Powell et al., 1998). However, the species living there routinely achieve near-maximum size. Taxon richness was highest on the continental shelf (Powell et al., 1998). The tendency for taxon richness to increase in deeper water (Flint and Holland, 1980) was not observed in the death assemblages on this transect, as might be anticipated from Staff and Powell's (1988) review of a large body of estuarine and continental shelf data. Among the heterotrophic assemblages, taxon richness was about twice as high in Copano Bay as on the continental slope and another factor of two higher on the continental shelf. Accordingly, habitat optimality as inferred from species richness should not be confused with the concept as applied here to size-frequency data. Staff and Powell (1988) proposed that the size-frequency distribution was a much better indicator than species richness of habitat stability. The comparison of the estuarine and continental slope assemblages presented here corroborates that view.

Modal adult size.—Assemblages were often bimodal, with the small and large size classes accounting for significant paleoproduction and paleoingestion. A dichotomy of size classes is a frequent characteristic of benthic communities (e.g., Schwinghamer, 1983; Warwick, 1984) and is believed to exist because significantly different strategies for exploiting available food resources generally require significantly different sizes. However, the size dichotomy in our assemblages existed regardless of whether the larger mode comprised filter-feeding species or chemoautotrophic species, and, in one case, the thyasirid community, both modes were produced by chemoautotrophic species. This suggests that a further aspect of this size dichotomy rests in allocation of living space. Bivalves do compete for space in some habitats (Peterson and Andre, 1980; Peterson, 1982), and larger size is a necessary concomitant of dwelling deeper in the sediment. The frequency of size dichotomies in the size-frequency distribution of death and fossil assemblages is unknown, but we predict that it will be a common feature of fossil and death assemblages and, in the end, be shown to indicate a basic division of food and space resources in the community just as Warwick (1984) has shown for meiofauna and macrofauna.

Paleoingestion is a function of size and age. Had the lowermost mode been represented by juveniles, bimodality would not exist. Juveniles, even if abundant, rarely contribute much paleoingestion because their life span is short. On the other hand, small adults with relatively long life spans contribute proportionately more to paleoingestion than to paleoproduction. Consequently, paleoproduction, if plotted on the size-frequency diagram defined by assemblage maximum size, was more often unimodal or only slightly bimodal. If paleoingestion is plotted on the size-frequency diagram defined by the largest individual in the study, the bimodality is partially obscured. In assemblages where the largest individuals were small, the two modes tended to merge. Nevertheless, the basic bimodality of the energy flow spectrum remained, indicating that the dichotomy in the size-frequency spectrum produced by large and small species was a persistent feature of the community even while the absolute size of the higher mode varied over a wide size range. The singular absence of bimodality on the continental shelf is another indication of the unusually poorly developed adult fauna at these sites.

Comparison with trends in guild and tier structure.—Staff and Powell (1999) examined the guild and tier structure of this same group of assemblages. The assemblage types were each unique in a combination of key abundance, paleoproduction, and paleoingestion-described community attributes. Use of the three approaches simultaneously significantly enriched the evaluation of these assemblages and provided important discriminating characteristics. The same was true in this study. At least as important, however, were the resemblances between assemblages in guild and tier structure. All continental shelf and heterotrophic continental slope assemblages were similar in their predator dominance of paleoingestion. All offshore assemblages were characterized by 40% or more of the individuals being infaunal. All chemoautotrophic assemblages were similar (this being preordained by their designation in this case). The assemblages also grouped together by size frequency. However, in this case, the Copano Bay assemblages bore a greater resemblance to those on the continental slope. The chemoautotrophic and heterotrophic communities were very similar within habitat, but the chemoautotrophic assemblages were different in many respects between habitats. Clearly, the influences determining tier and guild were not those determining size frequency.

Taphonomic signatures constructed in previous studies indicated large within-habitat variability between nearby locations on the conti-

nental shelf and slope (Staff and Powell, 1990a; Callender and Powell, 1992; Callender et al., 1992). With a few exceptions, notably among the petroleum seep assemblages evaluated numerically, within-habitat variability was low in comparison with variability between habitats in tier and guild structures and taxon composition (Staff and Powell, 1999). The size-frequency spectra followed the same pattern. Within-habitat variability was far less than the differences observed between assemblages from different geographic regions. Moreover, within-habitat variability was greatest on the continental slope. The degree of within-habitat variability in taphonomic processes in Copano Bay and on the continental shelf was not adequate to significantly modify assemblage structure on the small scale (and, of course, the life assemblages must have been similar). Not so in the cold-seep habitats, where rates of taphonomic loss are likely the highest of any location covered by this study (e.g., Cummins et al., 1986a; Staff et al., 1986; Staff and Powell, 1990a; Callender et al., 1994; Callender and Powell, 1997). At the petroleum seeps, assemblage differences in guild, tier, and size-frequency structure were substantially determined by the degree to which the smaller size classes were represented in the assemblage, and this attribute was principally controlled by taphonomic processes.

Uniqueness of the transect.—This bay-to-slope transect is characterized by a small and mostly juvenile fauna on the continental shelf, larger and mostly adult animals on the continental slope, and a strong tendency toward bimodality in the size-frequency spectra, particularly with paleoproduction and paleoingestion as measures of energy flow. No data permit the determination of how typical this transect is; however, certain exceptions will exist. Off the coast of New Jersey and Long Island, the Mid-Atlantic Bight is characterized by assemblages containing extremely large clams (≥150 mm) (Weinberg, 1999). Deep-water cold seeps apparently do not exist in this area. The Mid-Atlantic Bight, also characterized by frequent upwelling events and considerably greater rates of primary production than in the northwestern Gulf of Mexico (Neuman, 1996), will likely produce a substantially different trend from that observed off Texas in size-frequency distribution from the bay to the continental slope. Therefore, the comparisons shown here are likely to be most instructive in the identification of the biological and physical processes that produce certain size-frequency distribu-

tions rather than providing identifying traits of bay, continental shelf, and continental slope assemblages. Data from many more such transects are needed before general rules defining onshore–offshore (depth-dependent) processes can be discriminated from the sure-to-be-present exceptions determined by regional variability in environmental processes.

Application of the size-frequency distribution as an assemblage descriptor.—The size-frequency distributions and several indices of energy flow, paleoproduction and paleoingestion, based on them provide valuable information about significant temporal changes and temporal stabilities in community structure. Community structure is controlled by, and in turn records, changes in environmental optimality such as changes in food supply and the division of resources among small and large species, both of which accounted for significant paleoingestion in many of these assemblages. Most assemblages contained species of large and small maximum sizes. Most assemblages contained species living in optimal and suboptimal habitats. The proportions of these varied considerably. Most assemblages contained adults and juveniles, the proportions of which also varied considerably. Utilization of the size-frequency distribution helped identify key similarities and differences among these assemblages that originated from basic processes of community dynamics, food availability, predation, and environmental stability.

However, the size-frequency distribution provided this window into community dynamics only if evaluated in a diverse set of ways. Typically, size-frequency distributions are based on abundance, and size classes are set proportional to the largest individual in the collection (the assemblage in this case) (Craig, 1966; Craig and Oertel, 1966). Restriction to this one analysis would have identified few of the most important trends observed in this study. Although the basic approach of distributing abundance among assemblage-determined size classes has yielded a wealth of information on assemblage structure and population dynamics (e.g., Buss, 1980; Stanton et al., 1981; Cummins et al., 1986b; Cadée, 1988), the evaluation of size frequency based on species' maximum size as well as assemblage maximum size and the comparison of a suite of assemblages based on the largest maximum size provide important, and often dramatic, new inferences into community dynamics. The distribution of energy flow measures, paleoproduction and paleoingestion, across the size-frequency spec-

tra permits an additional important set of inferences. Only by these measures, for example, could the basic bimodality in adult size distributions, so common in these assemblages, be observed. Only in this way could basic inferences on habitat optimality be obtained. The analysis suggests that a rich, but as yet little tapped, information resource on community structures in the stratigraphic record is contained within the size-frequency distribution simply awaiting an increased breadth of analysis and experimental design.

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