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A sea change in Smuggler's Cove? Detection of decadal-scale compositional transitions in the subfossil record

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Abstract

Molluscan death assemblages in coastal marine settings are compositionally dynamic in time and space. Here, we describe a significant temporal faunal transition recorded over some two decades in the upper sedimentary veneer of a currently accumulating shell bed in Smuggler's Cove, St. Croix, US Virgin Islands. It had been demonstrated previously that molluscan death assemblages in the study area reflect the living assemblages from which they were derived. Further, a gradient among these assemblages reflects an environmental gradient of decreasing seagrass cover and increasing bioturbation, transitioning from lucinid bivalves and grazing gastropods inhabiting dense seagrass to other bivalves and predatory gastropods in bioturbated areas. More than two decades after initial sampling, the study area was resampled to investigate whether the environment and assemblages had changed relative to those reported in the earlier investigation. Results demonstrate that, while the general faunal gradient has remained intact, a notable area-wide biotic transition occurred among the living molluscan assemblages, during the intervening period, and is reflected in the accumulated death assemblage. This change is characterized by a major decline in the previously prolific grazing gastropod, *Cerithium litteratum*, and a similarly dramatic increase in the abundance of another grazing gastropod, *Eulithidium affine*. While the cause of this transition is not yet known, it demonstrates the compositional dynamism of this time-averaged assemblage on a decadal time-scale.

Keywords: Taphonomy; Seagrass; Faunal gradient; Death assemblage; Mollusca; Paleoecology

1. Introduction

Because of time-averaging, fossil or subfossil accumulations within changing environments may contain a mixture of temporally distinct faunal elements from different environments. Short-term compositional fluctuations may be overprinted by long-term ecological trends (Walker and Bambach, 1971) and the extent to which time-averaging affects the fidelity of the record is thought to be influenced, in part, by the degree of environmental change during the period of skeletal accumulation (Peterson, 1976; Kidwell and Bosence, 1991). The zone of accumulation and mixing in the upper sedimentary veneer may contain shells up to several thousands of years old (Meldahl et al., 1997; Kowalewski et al., 2000; Carroll et al., 2003) and environmental perturbation should increase the likelihood that a single time-averaged shell bed would combine non-contemporaneous death assemblages (Peterson, 1977).

In a classic study, Peterson (1976) compared molluscan life and death assemblages from two California

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lagoons and showed that death assemblages exhibited a good degree of compositional fidelity to the corresponding life assemblage. Observed differences between life and death assemblages were attributed to population variability and local environmental volatility, and a sizable fraction of species, recorded in the death assemblage in Peterson's study localities were not represented among the live biota during the 37-month study. A taphonomic interpretation of this result suggests that the full range of possible environmental conditions, reflected in the molluscan death assemblages, were not observed at this site during Peterson's investigations and that the resulting death assemblages were comprised of multiple, non-contemporaneous biotas (Olszewski, 1999) rather than a single, large, yet heterogeneous, biota.

To this end, the present study considers directly, via resampling, compositional changes in a suite of death assemblages from Smuggler's Cove, St. Croix, U.S. Virgin Islands over a span of 22 years. Here, we address three fundamental questions: (1) Were subenvironments defined by benthic vegetation zones spatially stable over the 22-year interval between investigations, or were they ephemeral, with significant migration of subenvironmental patches? (2) Did the compositions of subfossil samples collected in 2002 resemble those collected from the same study area in 1980? (3) Were changes, if any, in subfossil compositions also reflected in the present-day live assemblages?

2. Study area

Smuggler's Cove (Fig. 1), a lagoon situated between a bank barrier reef to the north and the island of St. Croix to the south, is located along the northeast shore of St. Croix. The seafloor of Smuggler's Cove is covered by zones of mixed benthic vegetation and bare carbonate sand. Seagrasses comprise the predominant vegetation and include *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*. Macroalgae are also important components of the benthic flora, represented primarily by the genus *Halimeda*.

The study area is characterized by a gently sloping seafloor with depths ranging from 3 m on the southeastern end to 6 m toward the northwestern end. Shoreward subenvironments are dominated by thick, blanketing beds of *T. testudinum*with a dense root-rhizome mat. Vegetation farther offshore consists of a mixture of the three seagrass species, as well as macroalgae. In areas where seagrass is patchy, *Callianassa rathbunae*, a burrowing ghost shrimp, produces mounds and valleys with relief of up to a half meter (Suchanek, 1985). These mounds dominate the landscape of the seafloor in areas where seagrass cover is patchy, as it is in the northwestern portion of the study area.

3. Methods

3.1. Field methods

This study focuses on the same sampling area investigated by Miller (1988; sampling conducted in 1979–1980). Miller's original 360 m sampling transect, trending SE–NW through Smuggler's Cove, was reestablished as closely as possible to its original position using global positioning, in conjunction with aerial photographs of the transect taken in 1980. During

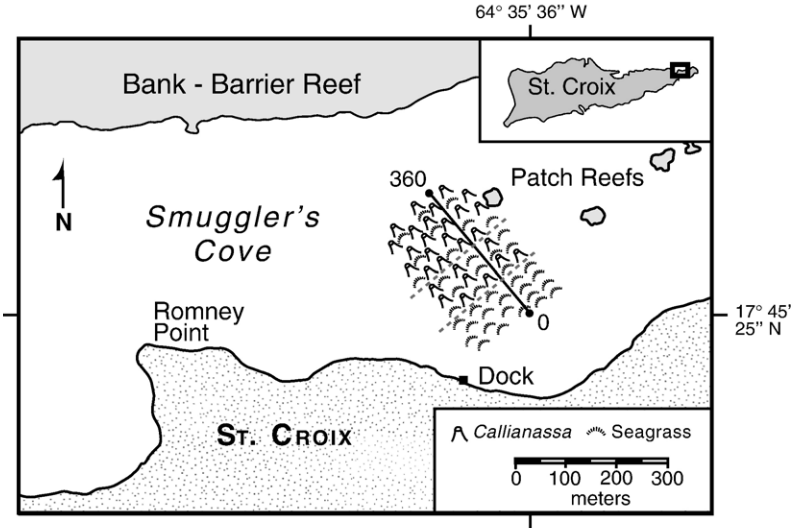

Fig. 1. Map of Smuggler's Cove, modified from Miller (1988), illustrating the location of the study area and general environmental zonations.

the present investigation, the transect was sampled at 30-m intervals for both molluscan assemblages and vegetation census data in contrast to Miller's original study, in which subfossil assemblages were sampled at 10 m intervals and vegetation censuses conducted at 20 m intervals. The subfossil gradient described by Miller was found to be robust in multivariate analysis at 30-m intervals permitting direct comparison with the 2002 samples. The location of each sampling station was determined by extending a 30-m transect tape along the seafloor and assigning the locations of sampling stations by their distance, in meters, from the southeast end of the transect (i.e. from station 0). Bulk samples of subfossil molluscan material were collected from the upper 50 cm of sediment using an airlift (i.e. an underwater suction device) with an attached 4 mm mesh bag, limiting the contribution of juvenile and recently-settled molluscs to this study, the same protocol used previously by Miller. A 20-cm cylindrical template was used to maintain consistent sample volume of approximately 15 l. During this collection procedure, a limited number of live molluscs were obtained and recognized by the presence of intact soft tissues. These individuals were a useful proxy for comparing the life assemblage with the accumulated death assemblage air-lifted from the seafloor, as discussed later. Molluscan subfossils were identified using standard references (e.g., Abbott, 1974; samples from Miller, 1988; Redfern, 2001) and counted as "individuals" if they were (1) identifiable, (2) had a maximum dimension > 4 mm and (3) possessed distinguishable morphologic features that would preclude the counting of skeletal material from the same shell or valve more than once (for detailed description of this methodology see Gilinsky and Bennington, 1994).

Two samples were taken within a few meters of each other at all established sampling stations. In zones with little or no bioturbation and, hence little topographic variation, sampling points were chosen haphazardly. Within *Callianassa*-bioturbated settings, the first sample was taken at a local high point, the top of a mound, and the second taken from a local low point, the bottom of a valley (Miller, 1988); burrow chambers housing large quantities of shell material are typically penetrated during sampling in the valleys but not during sampling on top of mounds (Suchanek, 1983).

Vegetation censuses were conducted eight times at each station by dropping a 10 × 20 cm quadrat haphazardly on the seafloor (Miller, 1988; Tomasko and Hall, 1999). During this censusing, the number of individual seagrass blades of each species and the number of benthic macroalgae rooted in a quadrat were counted. Data for the eight vegetation counts at each station were averaged to obtain a mean characterization of vegetative cover at each station.

3.2. Data analyses

The data used for this study consisted of the 26 most abundant species common to the subfossil assemblages collected in 1979–1980 and the present study. This constraint introduces some bias in favor of finding similarities between the data sets by restricting analyses to the taxa that define the subfossil-environmental gradient, but these taxa account for the vast majority of individuals in both datasets: 85.3% of all individuals counted during the present sampling and 96.4% of individuals in the 1979–1980 sampling. Following Miller (1988), raw bivalve counts were halved to generate a minimum individual count, and data from sample pairs along the transect were averaged to obtain a mean abundance for each taxon per station. Percent transformation of samples was performed on the samples in data matrices to control for variations in sample size; a second, percent-maximum transformation, where the abundance values of a species were converted to a percentage of their maximum abundance achieved in samples within the study area, was conducted in the case of R-mode comparison of species. The purpose of this second transformation is to emphasize differences in species distributions among samples, while mitigating differences in overall species abundances (Miller, 1988). Detrended Correspondence Analysis (DCA; settings included: rescaling axes with a threshold of zero in 26 segments; Hill and Gauch, 1980; McCune and Mefford, 1999) and two-way cluster analysis (UPGMA method; Bray-Curtis Similarity coefficient; Bray and Curtis, 1957) were used to assess spatial and compositional patterns within and between data suites. Detrended Correspondence Analysis (DCA) was conducted using the PC-Ord for Windows version 4.10 (McCune and Mefford, 1999); cluster analyses were performed using PRIMER v.5 for Windows (PRIMER-E, Ltd.; Plymouth, United Kingdom; Clarke and Warwick, 2001). To assess the merits of applying DCA to this dataset, results were compared with a Multidimensional Scaling (MDS) ordination (Scarponi and Kowalewski, 2004). Comparison of these analyses demonstrated that the patterns illustrated were essentially interchangeable and we concur with the findings reported by Miller et al. (2001) and Scarponi and Kowalewski (2004), that DCA is an appropriate method for strongly ordered ecological data.

Vegetation census data were used to assess variation in benthic habitats along the transect. Mean values of raw census counts (individual blades for seagrass species and individual plants for macroalgae) helped to characterize the vegetative coverage at each station, as did the *seagrass coefficient* (Miller, 1988). The equation for the coefficient (C_{sg}) is:$C_{sg} = 0.25(T) + 0.07(S) + 0.02(H)$, where T (*Thalassia testudinum*), S (*Syringodium filiforme*) and H (*Halodule wrightii*) represent the number of blades of each species. The numerical constants represent empirically-derived average surface areas per seagrass blade (in square centimeters) of each species, and the coefficient, therefore, quantifies aggregate seagrass surface area at each station.

4. Results and discussion

4.1. Environmental patterns

Vegetation census data from the 2002 sampling (Fig. 2A) illustrate the primary environmental transitions in Smuggler's Cove. Nearshore environments on the southeast end of the transect are dominated by *Thalassia*, progressing offshore (northwest) to zones comprised of more abundant *Syringodium* and *Halodule*. The 1980 vegetation census data (Fig. 2B) illustrate a broadly similar pattern, indicating that general environmental trends and subenvironmental zonations were uniform, despite the 22-year gap separating the studies. The disparity in sample spacing for the vegetation censuses, discussed earlier, contributes to the greater "smoothness" displayed in the 2002 curves. Associated with the spatial transitions among vegetation zones is a southeast-to-northwest decrease in the aggregate coverage by seagrass blades (Fig. 2C). This decrease was less abrupt in 2002 than it was in 1980, a difference that appears to transcend the differences in sample spacing. Based on vegetation census data, there was an overall increase in seagrass density over the 22-year span (Fig. 2C), driven primarily by an increase in the relative abundance of *Thalassia* throughout the study area. Whether this increase was a response to an area-wide environmental transition or reflects continued successional development (Williams, 1987; Fourqurean et al., 1995) over more than two decades could not be determined.

While subenvironments along the transect and the transitions among them appear to have been maintained over more than two decades here are notable differences at finer scales. In particular, the precise locations of zones in the northwestern half of the transect, dominated by *Syringodium* and *Halodule*, appear to differ between the two studies. It is unclear whether these differences reflect: (a) the more ephemeral, patchy nature of zones covered by *Syringodium* and *Halodule* relative to the more uniform carpets of dense *Thalassia* to the southeast; (b) differences in the precise geographic placements of the two transects; or (c) both. In any case, the comparison of the two censuses suggest that the nearshore

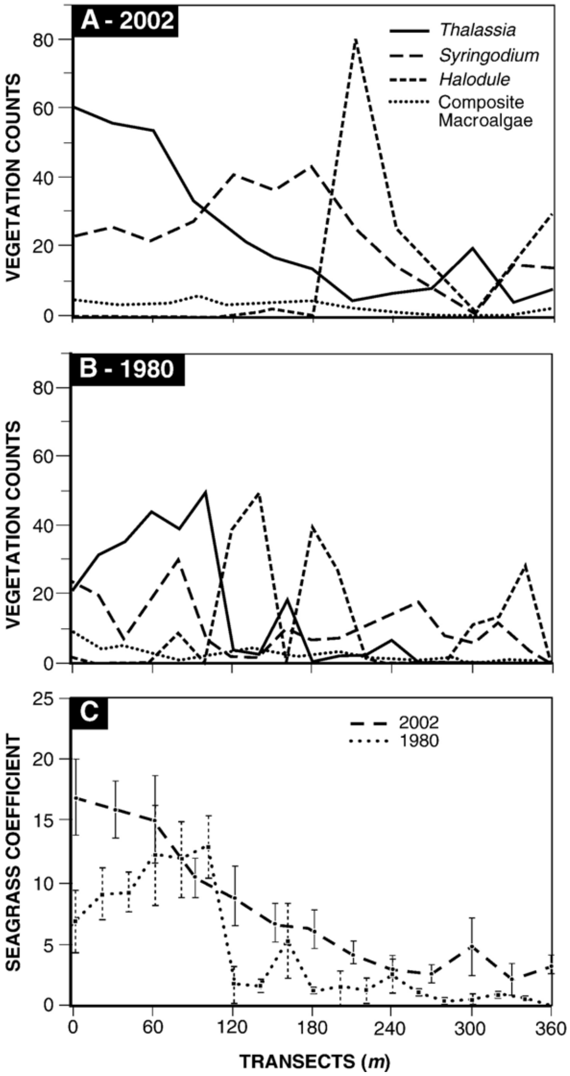

Fig. 2. Transitions in vegetation across the study area. (A) Mean 2002 vegetation census counts per sampling station along the transect from the current investigation. (B) Mean vegetation counts per sampling station from 1980. Census counts represent individual blades of seagrass and whole plants for macroalgae. (C) The seagrass coefficient, used as a proxy for the aerial coverage of benthic vegetation. Error bars represent 95% confidence intervals about the mean, calculated for the seagrass coefficient data. While the overall trend of decreasing seagrass coverage away from shore persists, there appears to have been an overall increase in seagrass coverage throughout Smuggler's Cove relative to 1980. This was related to an overall increase in the density of the wide-bladed seagrass, *Thalassia*, throughout the study area. Different lateral sampling intensities were employed for 1980 and 2002 census data, with 1980 censuses conducted at 20-m intervals and 2002 at 30-m intervals along the sampling transect.

zone of dense *Thalassia* was spatially stable, while the offshore zone of mixed seagrass and *Callianassa* burrows was more varied, spatially and/or temporally.

4.2. Analysis of subfossil assemblages

Two-way cluster analysis of the 2002 subfossil data (Fig. 3) illustrates the spatial distribution and abundances of taxa (R-mode) among the samples (Q-mode), and is rather similar to that illustrated by Miller (1988; Fig. 4). Grazing gastropods and lucinid bivalves (Fig. 3, R-mode Clusters I & II), which are well known to live infaunally in low oxygen seagrass bed sediments (Jackson, 1973; Gros et al., 2003), dominate the southeastern, seagrass covered, portion of the transect (Fig. 3, Q-mode cluster A). R-mode cluster III (Fig. 3) is comprised of species, of various life habits, which occur throughout the study area. These taxa display an

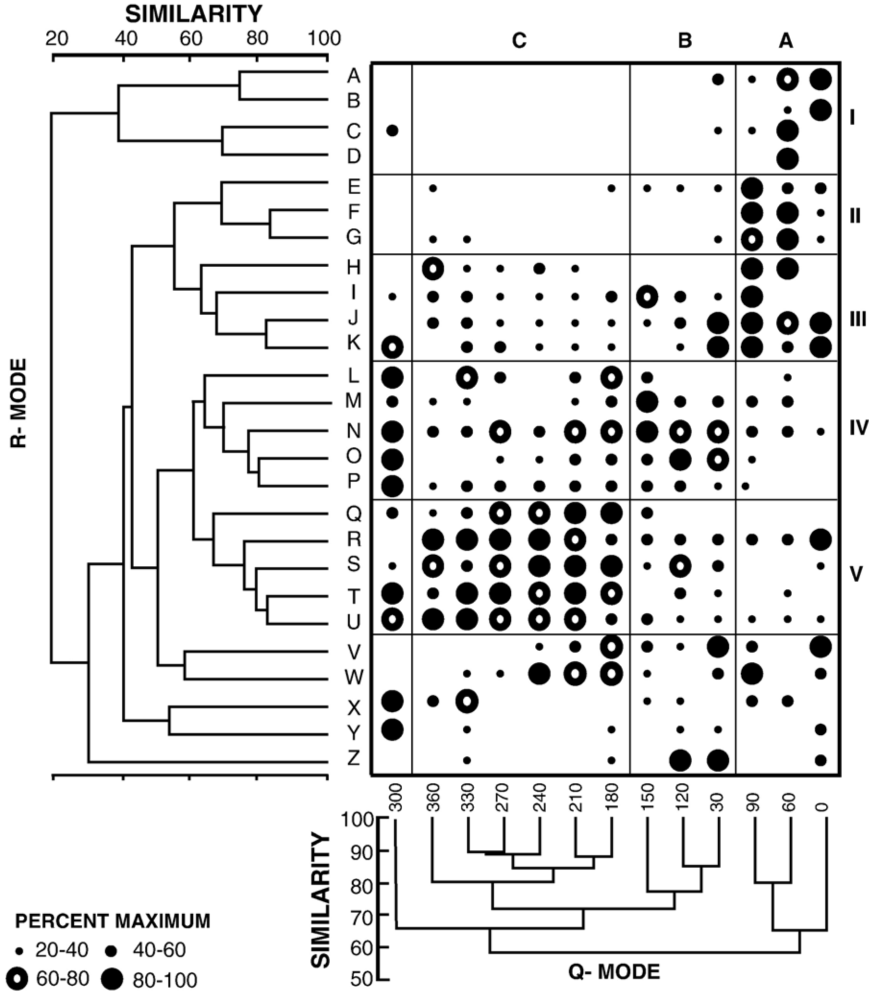

Fig. 3. Two-way cluster analysis of the 2002 death assemblage data. Q- and R-mode dendrograms are oriented at right angles to one another to express faunal distribution and abundance patterns. Species are coded alphabetically (see below). Percentage of maximum abundance for each species is illustrated by the dot matrix. Q-mode clusters are based on similarities of death assemblages from each station while R-mode clusters are based on similarity of species distribution and abundance. Stations 30 and 300 are the only exceptions to the clear geographic ordering of samples along the transect. Station 30 contains the aberrantly large replicate, discussed in the text, and Station 300 was environmentally unique as it occurred near a hard-ground along the edge of a patch reef in Smuggler's Cove. Species codes: A — *Tegula fasciata*; B — *Codakia orbicularis*; C — *Conus jaspideus*; D — *Turbo castanea*; E — *Cerithium eburneum*; F — *Jaspidella jaspidea*; G — *Parvilucina costata*; H — *Columbella mercatoria*; I — *Callucina keenae*; J — *Smaragdia viridis*; K — *Modulus modulus*; L — *Laevicardium laevigatum*; M — *Transennella stimpsoni*; N — *Chione cancellata*; O — *Olivella dealbata*; P — *Americardia guppyi*; Q — *Diplodonta* sp.; R — *Eulithidium affine*; S — *Bulla striata*; T — *Atys caribaea*; U — *Nassarius albus*; V — *Cerithium litteratum*; W — *Tellina mera*; X — *Divalinga quadrisulcata*; Y — *Lucina pensylvanica*; Z — *Astralium phoebium*.

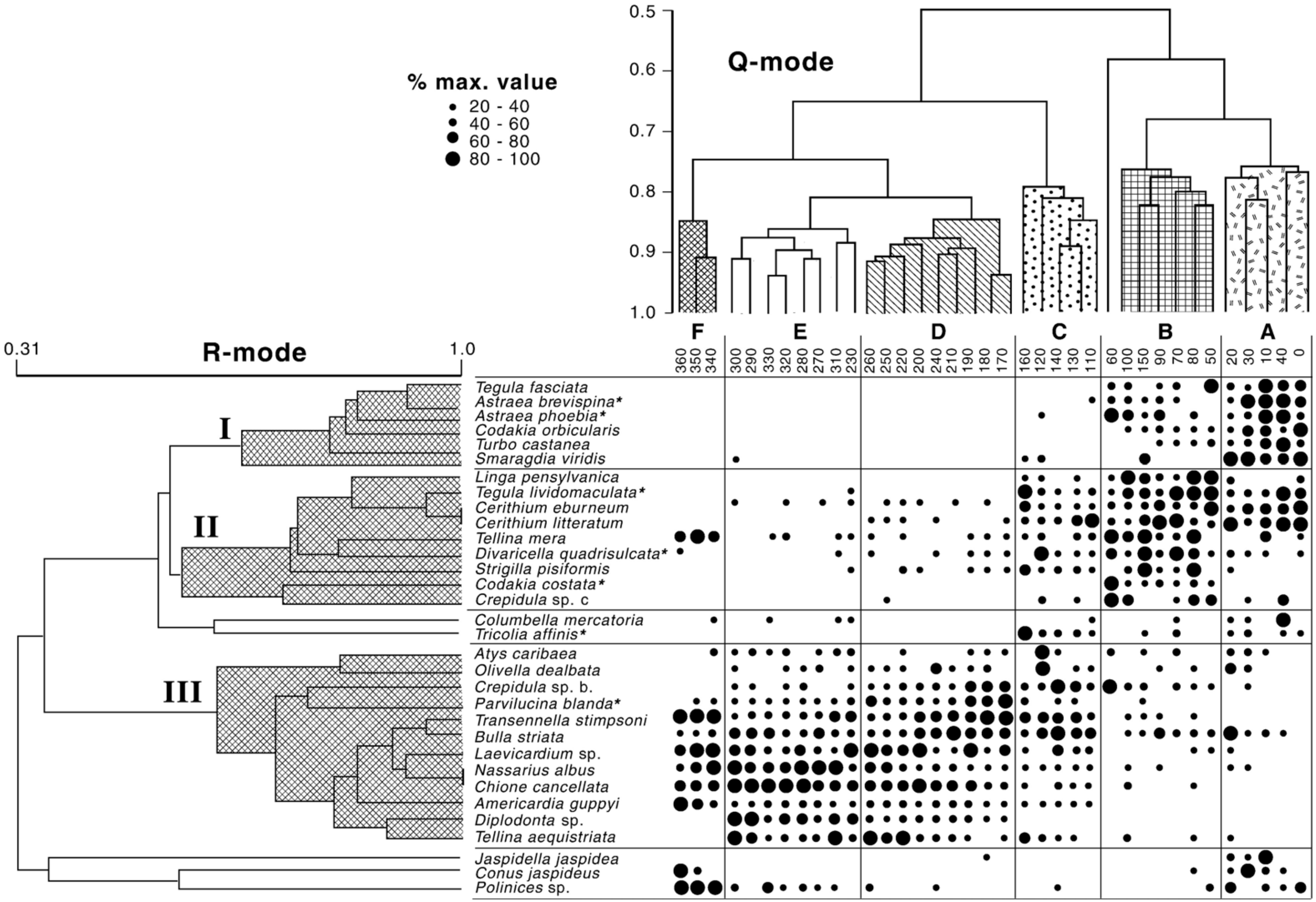

Fig. 4. Two-way cluster analysis of 1980 death-assemblage data from Smuggler's Cove (redrafted from Fig. 4 of Miller, 1988). Miller analyzed the 32 most abundant species (as opposed to the top 26 taxa common to both 1980 and 2002 analyzed during the current investigation; Fig. 3). Southeastern samples are comprised mainly of grazing gastropods and lucinid bivalves, at sites dominated by *Thalassia* (both in 1980 and 2002), whereas samples in the less vegetated, more highly bioturbated sites characterized by a more diverse array of infaunal bivalves and predatory gastropods. The environmental-subfossil gradient described by Miller is maintained in the two-way cluster analysis of 2002 data (Fig. 3) and, while minor differences exist because of ecological changes and small deviations from Miller's methodologies, spatial trends in the molluscan death assemblage were generally maintained during the 22-year sampling hiatus. Species in R-mode analysis that have been reidentified or have undergone taxonomic revision since Miller's investigation are marked with an asterisk (∗). Updated names, from top to bottom, are as follows: *Astraea brevispina* to *Astralium brevispina*, *Astraea phoebia* to *Astralium phoebium*, *Tegula lividomaculata* to *Modulus modulus*, *Divaricella quadrisulcata* to *Divalinga quadrisulcata*, *Codakia costata* to *Parvilucina costata*, *Tricolia affinis* to *Eulithidium affine*, and *Parvilucina blanda* to *Callucina keenae*.

affinity for *Thalassia*-dominated localities (similar to those of R-mode cluster II) but cross the transitional zone into he heavily bioturbated sediments of Q-mode cluster C (Fig. 3) indicating a degree of habitat elasticity. The transitional and northwestern portions of the transect (Fig. 3, Q-mode clusters B & C, respectively) are dominated by species from R-mode clusters IV and V, including a diverse set of infaunal bivalves and

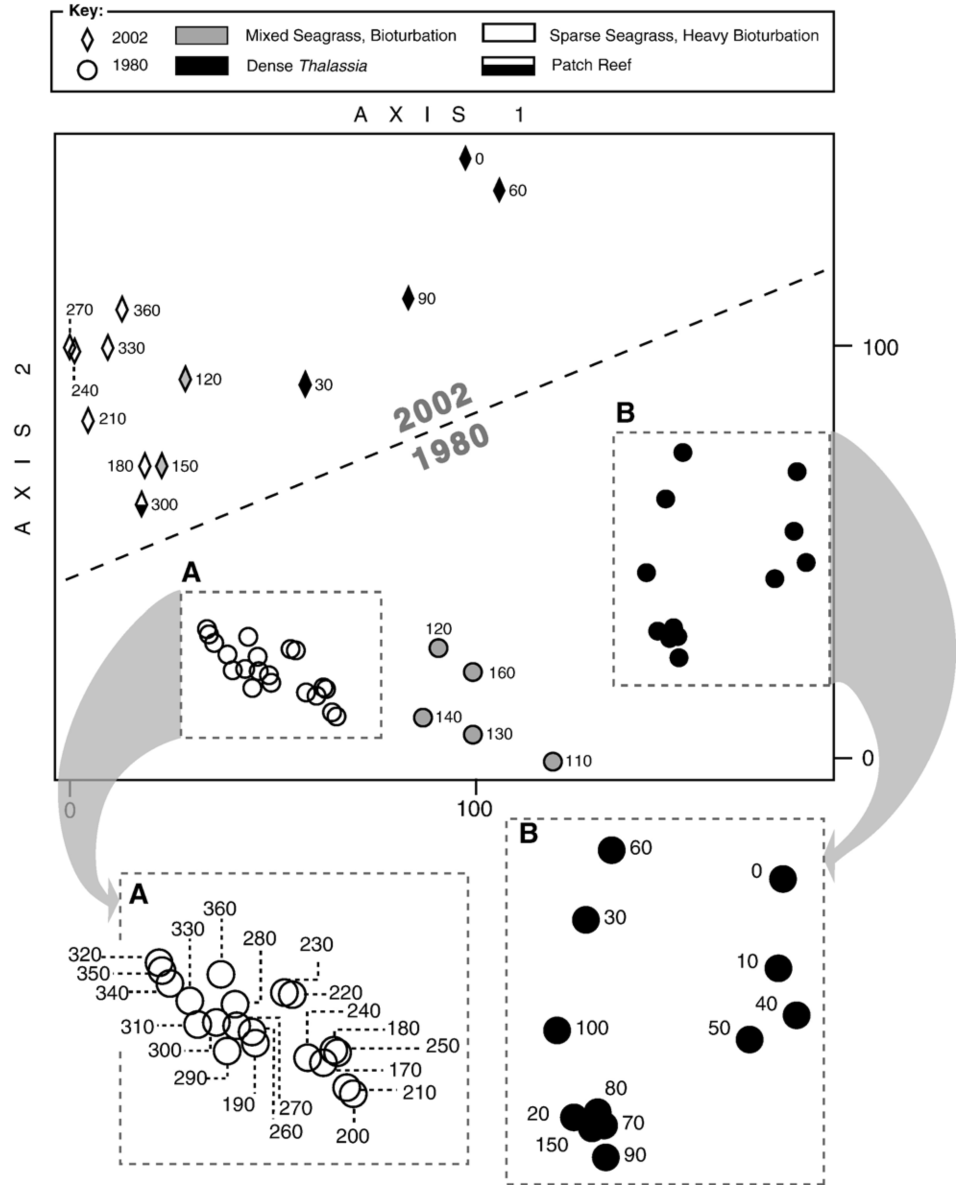

Fig. 5. DCA of the combined top-26 data from 1980 and 2002. Stations are numbered (meters along transect) and coded by environment, with diamonds representing 2002 stations and circles representing 1980 stations. Note the geographic ordering of sampling stations along axis 1 and the division of stations between 1980 and 2002, mainly on Axis 2. Axis 1 relates clearly to environmental and geographic transitions and explains 62.2% of variation in the data, whereas Axis 2, which accounts for 27% of the variation in this data, manifests a consistent faunal difference between 1980 and 2002 data suites: a decrease in *Cerithium litteratum* and increase in *Eulithidium affine*. If *C. litteratum* and *E. affine* are removed from the analysis, the gap along Axis 2 between 1980 and 2002 samples decreases and, along Axis 1, the offset of 2002 samples towards lower ordination scores and away from the southeastern-most samples from 1980 disappears. Clearly, then, the offset on Axis 1, which might otherwise suggest geographic differences in sampling regimes, reflects the particularly high abundance of *C. litteratum* in the 1980 samples from the dense-*Thalassia* (southeastern) portion of the transect. In all, some 89.2% of the variation in these data are expressed by these two DCA axes. Insets are magnifications of tightly-grouped samples from the 1980 data.

carnivorous gastropods (these is only a single grazing gastropod in this group, *Eulithidium affine*). Overall, the spatial transitions in subfossil composition correspond with the change from stable, *Thalassia* beds to bioturbated sand interspersed with patches of all three seagrasses moving towards the northwest (Fig. 2A). A spatially constrained, transitional zone, also noted by Miller (1988) was located between end member environments (Fig. 3, Q-mode cluster B) during both sampling intervals, and was characterized by variable seagrass cover, moderate bioturbation, increased abundance of skeletal material relative to stations in the southeastern region, and a unique combination of faunal assemblages from both end-member environments. However, the inclusion of station 30 in Q-mode cluster B indicates that geographic faunal zonation is not the sole factor governing cluster patterns. One of the replicate samples at station 30 was abnormally rich in skeletal material, which elevated specimen abundance and species richness well above that of geographically adjacent samples. This larger sample size relative to those from other *Thalassia*-dominated sample stations was likely responsible for the anomalous position of the aggregate sample from station 30 on the dendrogram.

When the top-26 species from both studies are compared directly to one another in DCA, the primary feature of both subfossil datasets (Fig. 4) is the faunal gradient represented mainly on DCA Axis 1, with stations arrayed along the axis in an order nearly identical to their geographic positions along the transect. Clearly, this positioning along Axis 1 reflects compositional responses to environmental characteristics, particularly seagrass coverage and bottom stability. In all, more than 62% of the variation in the top-26 data matrix was explained along Axis 1 of the DCA ordination.

Despite this long-term persistence of the faunal gradient in Smuggler's Cove over more than two decades, there was a striking difference between the faunas sampled during the respective investigations, as evidenced by the nearly complete segregation of data points from the two intervals on Axis 2 (Fig. 5). The pattern on axis 2, which accounts for 27% of the variation in these data, can be attributed to a major change in the relative abundances of two important gastropod species, *Cerithium litteratum* and *E. affine*. Both of these species exhibit an herbivorous life habit; at the genus level, *Cerithium* is classified as a generalized grazer, whereas *Eulithidium* is restricted to plant or algal substrates (Todd, 2001). *C. litteratum* was the most numerically dominant subfossil gastropod across all sampling stations in 1980 and was significantly reduced, by a factor of four, in 2002 collections. *E. affine* was uncommon in 1980 collections but became the most numerically dominant gastropod among all sample sites by 2002. Moreover, this pattern in the death assemblages is mirrored by the live species collected in both 1980 and 2002. The most common live species collected in 2002 was *E. affine* (38 individuals; Table 1), which was also the most abundant gastropod in the death assemblage. In 1980, only one specimen of *E. affine* was collected live. In contrast to the 2002 investigation, the most abundant species collected live in 1980 was *C. litteratum*(308 individuals), which was only found live once during the 2002 investigation. Despite these differences, many other species were present at comparable abundances in both studies, although sampling was three times more intense in 1980. The comparison of sample suites from 1980 and 2002 demonstrates, therefore, that there was a transect-wide compositional shift in subfossil assemblages, responding to a change in the living molluscan community during the intervening period. Clearly, then, the subfossil assemblages are compositionally dynamic on a decadal time scale, responding rapidly to changes in the life assemblage from which they were derived.

Table 1
Rank abundances and counts of live collected species

2002		1980	
Eulithidium affine	38	*Cerithium litteratum*	308
Nassarius albus	22	*Cerithium eburneum*	56
Modulus modulus	18	*Tegula fasciata*	34
Parvilucina costata	15	*Parvilucina costata*	28
Smaragdia viridis	14	*Nassarius albus*	25
Cerithium eburneum	10	*Chione cancellata*	11
Jaspidella jaspidea	10	*Astralium phoebium*	11
Columbella mercatoria	8	*Columbella mercatoria*	9
Chione cancellata	7	*Modulus modulus*	8
Codakia orbicularis	6	*Turbo castanea*	7
Pyramidella crenulata	5	*Crepidula sp. C*	7
Parvilucina sp.	4	*Jaspidella jaspidea*	6
Divalinga quadrisulcata	3	*Conus jaspideus*	6
Tellina similis	3	*Codakia orbicularis*	5
Prunum sp.	2	*Tellina mera*	5
Lucina pensylvanica	2	*Astralium brevispina*	3
Zafrona pulchella	1	*Divalinga quadrisulcata*	1
Lithopoma tectum	1	*Tellina listeri*	1
Cerithium litteratum	1	*Calliostoma sp.*	1
Crepidula convexa	1	*Eulithidium affine*	1
Melanella sp.	1	*Olivella dealbata*	1
Tegula fasciata	1	*Pilsbryspira nodata*	1
Turbo castanea	1		
Arcopsis adamsi	1		
Americardia guppyi	1		
Tellina radiata	1		

While there are many potential causes for the observed temporal transition, it is likely that the signal reflects an environmental change throughout Smuggler's Cove. The precise nature of this change, be it alteration of sea surface temperature, nutrient levels, salinity, change in available food resources, or some other variable remains to be determined. At the same time, it is clear that the transition was not induced artificially by variations in sampling or analytical protocols, for several reasons: (1) care was taken in the study to ensure that only taxa with a lateral dimension of at least 4 mm were included in tallies; (2) specimens from 2002 were compared directly with specimens from the 1980 study ensuring that identifications of key taxa were equivalent in both cases; (3) rare taxa were removed from our data matrices to minimize disparities between the datasets; (4) although the precise locations of individual sampling stations were likely not precisely identical in the two investigations, the broad nature of the transition demonstrates that it transcends any small differences in sample localities.

There are a variety of potential causes for the decline in abundance of *C. litteratum* in Smuggler's Cove, some of which can be investigated retrospectively and some that cannot. The eastern end of St. Croix has experienced notable residential development over the past two decades that may have affected the frequency and content of runoff in the study area. By themselves, however, historical rainfall trends do not indicate changes over the last 22 years. In contrast, sea surface temperature (SST) data indicate a marked increase in mean annual temperature over the same period, opening the possibility of a temperature-induced response (Fig. 6; Physical Oceanography DAAC, 1985–2005; Boulon, unpublished data). Alternatively, random population cycles may be common components of the life history of many shallow, benthic marine species and could produce varying abundance signals unrelated to environmental factors (Connell, 1985; Gaines and Bertness, 1992). Finally, mass species mortality because of disease has been recorded in the Caribbean in recent decades and many also play a role in explaining shifts in faunal composition through time (Lessios et al., 1984; Aronson et al., 2004). As noted earlier, there was a general increase in seagrass coverage throughout the study area; in nearly all cases, seagrass coefficients for 2002 were greater than those for 1980. The vegetation shift appears driven by an increase in *Thalassia* density and may have been a contributing factor to the compositional shift noted here in the molluscan assemblage.

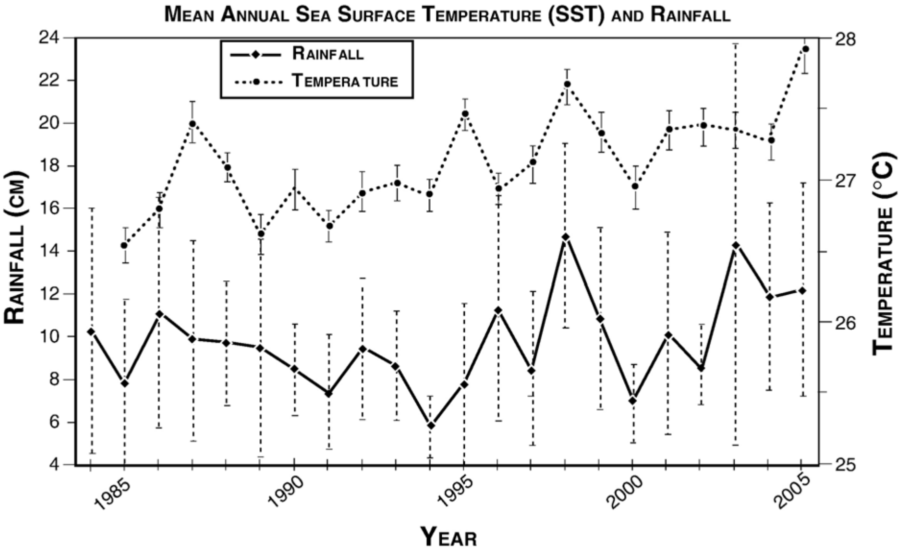

Fig. 6. Comparison of Mean Annual Sea Surface Temperature (SST) and Rainfall Totals for the US Virgin Islands. Annual rainfall means were compiled from monthly totals provided from Trunk Bay, St. John, US Virgin Islands (Boulon, unpublished data). Sea Surface Temperature data collected by the National Oceanic and Atmospheric Administration's Advanced Very-High-Resolution Radiometer (AVHRR), aboard the Pathfinder v.5 satellite, recording daily nighttime temperature measurements at a 4-km spatial resolution. Data were accessed in time-series format using the PO.DAAC Ocean ESIP Tool (POET) interface (Physical Oceanography DAAC, 1985–2005) and binned for the region of the US Virgin Islands (a zone of compiled SST readings from the region encapsulated as 17°–19° N and 63.5°–65.5° W). Error bars represent 95% confidence intervals. These data show that there has been no appreciable change in rainfall on St. John and, by proxy, the region, during the last two decades. However, Sea Surface Temperature has increased from a mean of ~26.5 °C in 1985 to nearly 28 °C by 2005, and this regional increase generally corresponds with a global temperature increase over the last four decades (Smith and Reynolds, 2005).

The results of this study demonstrate the dynamic nature of actively accumulating subfossil assemblages on decadal time scales and at the same time that broad ecological relationships recorded in a death assemblage gradient may nevertheless remain robust over prolonged intervals. These outcomes also raise a fundamental question about the incorporation of skeletal elements into death assemblages. Is the *Cerithium-Eulithidium* transition over 22 years the product of preservational biases, environmentally-induced range changes, or the vagaries of larval settlement? The possible role of preservational biases may lie in differential preservation potential associated with epifaunal and infaunal life habits. Because long-term preservation of skeletal material is largely dependent upon burial (Kidwell and Bosence, 1991; Meldahl et al., 1997; but also see Callender et al., 2002 for a discussion the complexities of burial effects), epifaunal molluscs may be significantly more prone to taphonomic degradation (Best and Kidwell, 2000; Lazo, 2004) than those living within the sediment, which have a head start along the road to preservation. Our data suggest that, in Smuggler's Cove, epifaunal gastropods are far more prolific components of life assemblages than are infaunal bivalves (Table 1), but this is not carried over into the death assemblage (Table 2), implying an under representation of the epifauna as components of molluscan death assemblages.

Table 2
Rank percent abundance of species common in the death assemblage

%	2002	1980	%
22.40	*Chione cancellata*	*Chione cancellata*	17.60
17.09	*Eulithidium affine*	*Cerithium litteratum*	12.89
10.89	*Nassarius albus*	*Transennella stimpsoni*	12.42
9.33	*Americardia guppyi*	*Nassarius albus*	11.82
7.08	*Transennella stimpsoni*	*Americardia guppyi*	11.19
6.02	*Atys caribaea*	*Bulla striata*	9.91
4.21	*Bulla striata*	*Cerithium eburneum*	5.02
3.41	*Olivella dealbata*	*Modulus modulus*	3.06
2.83	*Parvilucina costata*	*Diplodonta* sp.	2.13
2.57	*Smaragdia viridis*	*Parvilucina costata*	1.96
2.42	*Cerithium litteratum*	*Atys caribaea*	1.38
2.06	*Modulus modulus*	*Callucina keenae*	1.20
1.95	*Cerithium eburneum*	*Olivella dealbata*	1.17
1.53	*Codakia orbicularis*	*Tegula fasciata*	1.11
1.45	*Diplodonta* sp.	*Smaragdia viridis*	0.93
0.84	*Callucina keenae*	*Columbella mercatoria*	0.85
0.69	*Laevicardium* sp.	*Eulithidium affine*	0.79
0.50	*Tegula fasciata*	*Turbo castanea*	0.77
0.47	*Columbella mercatoria*	*Laevicardium* sp.	0.66
0.43	*Divalinga quadrisulcata*	*Codakia orbicularis*	0.64
0.43	*Tellina mera*	*Conus jaspideus*	0.55
0.41	*Turbo castanea*	*Tellina mera*	0.51
0.37	*Jaspidella jaspidea*	*Lucina pensylvanica*	0.46
0.24	*Lucina pensylvanica*	*Astralium phoebium*	0.46
0.22	*Conus jaspideus*	*Divalinga quadrisulcata*	0.37
0.16	*Astralium phoebium*	*Jaspidella jaspidea*	0.14

Variability over time in the composition of molluscan communities can directly impact the makeup of skeletal death assemblages accumulating on the seafloor. The apparent decoupling of life (Table 1) and death assemblages (Table 2) suggest that the loss of *C. litteratum* from the death assemblage is a consequence of this species' decline in live communities. As populations of *C. litteratum* declined, fewer shells would be available to populate death assemblages and those already present, particularly near the sediment–water interface in *Thalassia*-dominated seagrass beds where, sedimentation rates are low and bioturbation limited, would be far more vulnerable to taphonomic destruction than specimens buried more deeply in the sedimentary column (Meldahl et al., 1997; Olszewski, 1999). It is, therefore, reasonable to conclude that, barring a large depositional event such as storm induced runoff from the adjacent mainland of St. Croix sufficiently burying skeletal material near the sediment surface, the numerical dominance of *E. affine*, or virtually any other gastropod of similar life habit, in molluscan death assemblages is ephemeral and subject to rapid change in the event that its corresponding live populations were to decline.

5. Conclusions

It is clear that evidence of decadal-scale compositional change is preserved in the molluscan death assemblages of Smuggler's Cove, despite ongoing processes of time-averaging. At the same time, the faunal gradient first described by Miller (1988) in Smuggler's Cove remains largely intact, and continues to reflect the associated environmental gradient, more than two decades after the original investigation. Abundances of some of the most numerically abundant taxa changed dramatically on this time scale, and evidence of this potential population shift was incorporated into the time-averaged subfossil assemblage in the upper sedimentary veneer. Strikingly, however, *C. litteratum* declined dramatically in death assemblages during the intervening 22 years across environmental zones, suggesting the existence of a strong taphonomic bias against epifaunal molluscs in the accumulating death assemblages of Smuggler's Cove.

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