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Quantitative analyses of molluscan communities and taphocoenoses of Bahia la Choya (Gulf of California, Sonora, Mexico)

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With 4 figures in the text

ABSTRACT

Q-mode cluster analysis of samples of the living fauna and of shelly remains reveal groups of samples that correspond to the major habitats of Bahia la Choya. Analysis of samples of the live fauna defines four groups: inner flats and marsh, outer and middle sand flats, rocky flats and channel, and subtidal. Analysis of samples of the shelly remains defines five groups: inner flats, marsh and channel, sandy subtidal, outer and middle sand flats, rocky subtidal, and rocky flats. Post-mortem transportation causes the association of channel samples with marsh and inner flat samples of shelly remains. Extensive time-averaging and the accumulation of diagnostic species in the more diverse samples of shelly remains permits the discrimination of rocky and sandy subtidal samples of shelly remains.

R-mode cluster analysis of species of the living fauna and species present in the shelly remains reveals species associations typical of the major habitats in Bahia la Choya. Analysis of species present in the live fauna defines five species associations: *Cerithium* – *Cardita* (rocky outer flats), *Tagelus* – *Theodoxus* (channel and inner flats), *Lucina* – *Oliva* (mid to outer sand flats), *Tellina* – *Agaronia* (shallow subtidal sand flats), and *Cerithidea* – *Mytella* (salt marsh). Analysis of species in the shelly remains defines 12 clusters, three of which are an artifact of the clustering technique. The remaining nine species clusters conform to the area's major habitats, with more than one species association common within each habitat: *Cardita* – *Caryocorbula* and *Petricola* – *Crucibulum* (both mixed rock and sand flats), *Agaronia* – *Glycymeris*, *Chione californiensis* – *Felaniella*, and *Oliva* – *Parvilucina* (all three occur in sandy, outer flat habitats), *Chione cortezi* – *Modiolus* and *Cerithium* – *Theodoxus* (both occur in the channel), *Nassarius* – *Cerithidea* and *Tagelus* – *Diodora* (both occur in the high intertidal firmgrounds of the marsh and inner flats). Transportation affects the composition of the *Tagelus* – *Diodora* cluster. Time-averaging results in high diversity and increases the resolution of the cluster analysis of the shelly remains.

KURZFASSUNG

Die Q-mode Cluster Analyse von Proben der Lebendfauna und der Taphozönosen ergibt Gruppierungen, die den wichtigsten Habitaten von Bahia la Choya entsprechen. Die Analyse von Proben der Lebendfauna definiert vier Gruppierungen: (1) Innenwatt und Salzmarsch, (2) äußeres und mittleres Sandwatt, (3) Felswatt und Gezeitenrinne und (4) Subtidal. Die Analyse von Proben der Taphozönosen definiert fünf Gruppierungen: (1) Innenwatt, Salzmarsch und Gezeitenrinne, (2) sandiges Subtidal, (3) äußeres und mittleres Sandwatt, (4) felsiges Subtidal und (5) Felswatt. Postmortaler Transport ist die Ursache für die Gruppierung von Taphozönosen der Gezeitenrinne mit denen der Salzmarsch und des Innenwatts. Eine langfristige zeitliche Mitteilung (time-averaging) und die Anhäufung diagnostischer Arten in den artenreicheren Proben der Taphozönosen erlauben die Unterscheidung von Proben des felsigen und sandigen Subtidals.

Die R-mode Cluster Analyse von Arten der Lebendfauna und der Taphozönosen ergibt Assoziationen, die die wichtigsten Habitate von Bahia la Choya charakterisieren. Die Analyse der lebenden Arten führt zu fünf Assoziationen: *Cerithium* – *Cardita* (felsiges Außenwatt), *Tagelus* – *Theodoxus* (Gezeitenrinne und Innenwatt), *Lucina* – *Oliva* (mittleres – äußeres Sandwatt), *Tellina* – *Agaronia* (flaches sandiges Subtidal) und *Cerithidea* – *Mytella* (Salzmarsch). Die Analyse der Arten der Taphozönosen führt zu 12 Gruppierungen, von

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denen drei ein Kunstprodukt der Cluster-Analyse sind. Die übrigen neun Artengruppierungen entsprechen den wichtigsten Habitaten von Bahia la Choya, wobei jedes Habitat durch mehr als eine Assoziation vertreten ist: *Cardita – Caryocorbula* und *Petricola – Crucibulum* (in Bereichen, in denen Fels- und Sandwatt sich kleinräumig ablösen); *Agaronia – Glycymeris, Chione californiensis – Felaniella* und *Oliva – Parvilucina* (alle drei treten im sandigen Außenwatt auf); *Chione cortezi – Modiolus* und *Cerithium – Theodoxus* (finden sich in der Gezeitenrinne); *Nassarius – Cerithidea* und *Tagelus – Diodora* (kommen in Festgründen des Innenwatts und der randlichen Salzmarsch vor). Schalentransport beeinflußt die Zusammensetzung der *Tagelus – Diodora* Gruppierung. Zeitliche Mittelung der Taphozönosen führt zu einer hohen Diversität und erhöht die Auflösungsschärfe der Cluster-Analyse.

INTRODUCTION

In this paper we use cluster analysis to define groups of samples and species in Bahia la Choya. Cluster analysis is a family of techniques used to objectively place entities into a hierarchical classification. In paleoecology, cluster analysis is often employed in an effort to reveal "natural" groupings of samples or species. When samples are grouped, the geographic distribution of the groups may reveal the geographic distribution of communities. Species groupings help reveal the composition of the communities. DAVIS (1986) and ANDERBERG (1973) provide a good introduction to the mathematics of cluster analysis and similar techniques. Cluster analysis programs are frequently available within many popular statistical software packages written for microcomputers and mainframes.

Cluster analysis has been widely employed in taphonomic studies. Particularly good examples can be found in SCOTT & WEST (1976). The technique is often used in order to compare the distribution and composition of the live communities to the distribution and composition of communities defined on the basis of only shelly remains. We continue that tradition in this paper. In addition, we illustrate how the taphonomic process of time-averaging may actually enhance the resolution of dendrograms produced by cluster analysis of shelly remains.

METHODS

Our analyses are based on samples of the live fauna and samples containing shelly remains. A full description of field sampling, sample processing, and sample locations is given by FURSICH et al. (this volume). We considered only those species that made up one percent or more of the total number of individuals in the sample. The data are given in Appendices 1–8.

Forty species were found alive in one or more of 92 samples. 119 species occurred as shelly remains in one or more of 101 samples.

We used the SPSS-X package of programs available on the University of Arizona mainframe computer (see NORUSIS 1985).

We used the cosine Θ measure of similarity to calculate similarity between each pair of samples or species. The cosine Θ measure of similarity recalculates abundances as percentages of the total number of individuals in the sample.

The principle of the cosine Θ similarity measure is illustrated in Fig. 1. Consider a simple case, where two samples, each containing two species are to be compared. The relative abundance of the two species in a sample defines a vector in the two-dimensional space illustrated. The degree of similarity between these two samples can be measured by the cosine of the angle Θ that ist between them. In practice, the number of dimensions is equal to the number of species in both samples, and cosine Θ is an angle measured in n-dimensional space.

The similarity measure takes into account both differences in species composition and differences in the relative abundance of species in common.

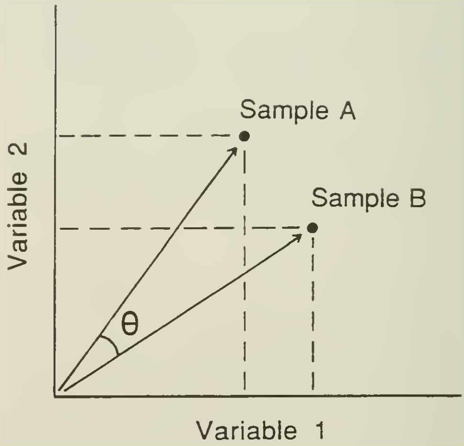


Fig. 1. Example of the cosine Θ similarity index. If Variable 1 is the relative abundance of species 1 and Variable 2 is the relative abundance of species 2, Samples A and B can be considered vectors whose position reflects the relative abundance of the species in the two samples. The angle Θ is a measure of the similitarity of the samples. When the angle between samples equals 0° (when the samples are identical in species composition and relative abundance) then the cosine of Θ equals 1. When the angle between samples equals 90° (when the samples have no species in common) then the cosine of Θ equals 0. Figure from MELDAHL (1990).

We used the conventional unweighted pair-group method to form the hierarchical clusters. This methods links samples (or species, or groups of samples or species) according to the greatest average similarity between samples (or species or groups of samples or species). The SPSS-X program rescales the similarity measure to a distance measure that varies from 0 to 25 (labelled "rescaled distance" in Figs. 2 and 3). A small distance value indicates high similarity. A high distance value indicates low similarity.

We use cluster analysis as an exploratory technique. No widely accepted method exists to assign statistical significance to the resulting clusters. The validity of the resulting clusters must be assessed in light of both the appropriateness of the methods and the reasonableness of the ecological and paleoecological interpretations.

ANALYSIS OF SIMILARITY AMONG SAMPLES

The cluster analysis of samples groups sample localities based on their compositional (e. g. faunal) similarity. This is frequently termed a Q-mode analysis. In this mode of analysis, samples of near-identical faunal composition and relative abundance will belong to the same group or cluster. Samples with no species in common will belong to different clusters.

We performed two Q-mode cluster analyses: one grouped samples based on the similarity of the live fauna; the other grouped samples based on the similarity of the shelly remains.

Q-mode analysis of samples containing live fauna

The dendrogram of samples containing live fauna is shown in Fig. 2a. 92 samples contained living species and the clusters distinguish four groups of samples.

1. Inner flats and marsh. These samples come from the firmgrounds of the inner flats and the elevated, firm, vegetated substrates of the marsh.

2. A large group of samples clusters at a high level of similarity and groups samples taken in the outer and middle flats. These samples are from the sandy portions of the mid and low intertidal zone.

3. The rocky flats and channel cluster groups samples taken from areas of hard substrates: either from the rocky flats in the northern part of Bahia la Choya or from the shell pavements in the main tidal channel in the south.

4. The subtidal cluster includes samples taken from the shallow subtidal.

Q-mode analysis of samples containing shelly remains.

The dendrogram of samples containing live fauna is shown in Fig. 2b. 101 samples contained shelly remains and the clusters distinguish five groups of samples.

1. Samples from the inner flats, marsh, and channel form a distinct cluster. These samples are from areas of firm (inner flats and marsh) or hard substrates and are often dominated numerically by individuals of either *Cerithium stercusmuscarum* or *Cerithidea mazatlanica*.

2. Sandy subtidal samples group together. These samples come from the shallow subtidal in the sandy, southern of Bahia la Choya.

3. Samples from the outer and middle flats form a large cluster. These samples range from the mid to low intertidal and are typically from sandy substrates.

4. A group of samples from the rocky subtidal forms a distinct cluster. These samples are from the rocky, northern part of Bahia la Choya.

5. Samples from the rocky flats comprise the fifth cluster. These samples typically contain encrusting, nestling or boring species. Samples come from the hard substrates of the northern part of Bahia la Choya and from a few isolated outcrops in the southern portion of the area.

Discussion

Both Q-mode cluster analyses display a common pattern: adjacent samples tend to cluster together. This pattern is a consequence of the fact that adjacent samples tend to have a similar faunal composition. In the cluster analysis of samples containing live fauna, this results from similar habitat preferences. In the analysis of the shelly remains, both original habitat preferences and common response to taphonomic processes cause the close association of nearby samples.

Both analyses reveal habitat-based clusters. Clusters are composed of samples from similar substrates and similar durations of tidal exposures.

The cluster analyses differ somewhat in the specific habitat groupings that are formed. Both distinguish a large group of samples from the outer and middle flats, an area of rippled sand extending from the mid-intertidal to the low intertidal. Both analyses serve to distinguish samples from the subtidal zone. These samples form a single cluster when based on the living fauna. Analysis of the shelly remains serves to distinguish samples from the rocky subtidal from those of the sandy subtidal.

Samples from the tidal channel are included with the rocky flats samples in the analysis of the live fauna. Analysis of the shelly remains, however, places tidal channel samples together with samples from the inner flats and marsh. The inclusion of channel samples with inner flat and marsh samples in the dendrograph of shelly remains may be a consequence of the "contamination" of tidal channel samples with many individuals of *Cerithidea mazatlanica* that are transported from within the marsh. Among samples containing living speci-

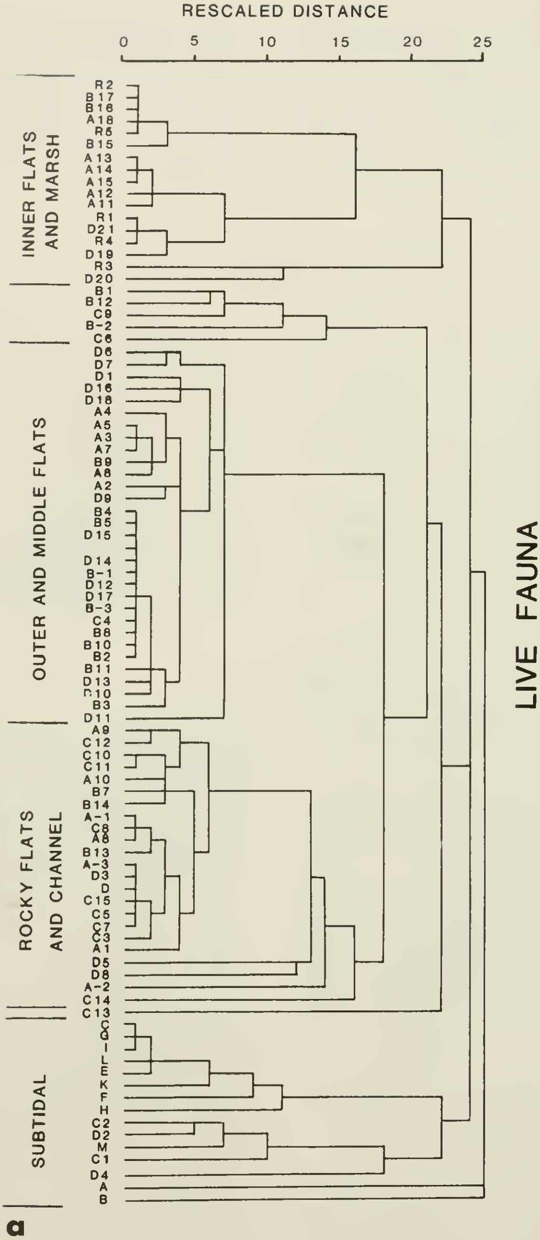
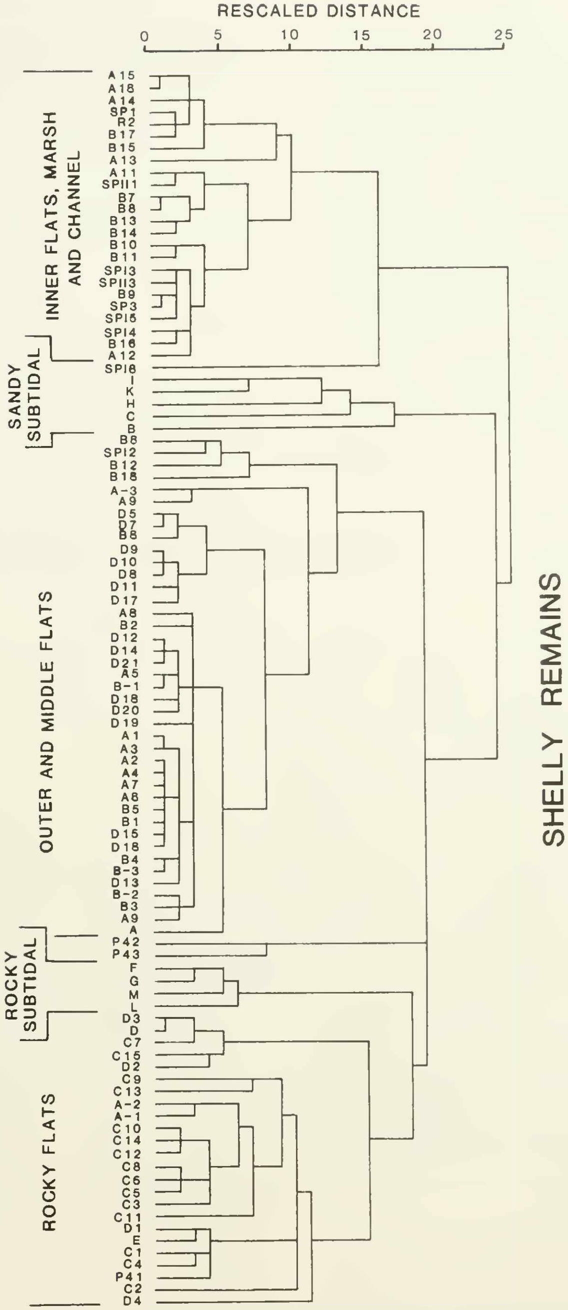


Fig. 2. a. Dendrogram of Q-mode cluster analysis of samples containing live fauna. b. Dendrogram of Q-mode cluster analysis of samples containing shelly remains. See text for explanation and discussion. Figure from FÜRSICH & FLESSA (1987).


RESCALED DISTANCE
0
5
10
15
20
25
INNER FLATS, MARSH AND CHANNEL
SANDY SUBTIDAL
OUTER AND MIDDLE FLATS
ROCKY SUBTIDAL
ROCKY FLATS
SHELLY REMAINS
A15
A18
A14
SP1
R2
B17
B15
A13
A11
SPII1
B7
B8
B13
B14
B10
B11
SPI3
SPII3
B9
SP3
SPI5
SPI4
B16
A12
SPI8
I
K
H
C
B
B6
SPI2
B12
B18
A-3
A9
D5
D7
B8
D9
D10
D8
D11
D17
A8
B2
D12
D14
D21
A5
B-1
D18
D20
D19
A1
A3
A2
A4
A7
A6
B5
B1
D15
D16
B4
B-3
D13
B-2
B3
A9
A
P42
P43
F
G
M
L
D3
D
C7
C15
D2
C9
C13
A-2
A-1
C10
C14
C12
C8
C6
C5
C3
C11
D1
E
C1
C4
P41
C2
D4

b

mens, the rocky flats and channel are characterized by relatively large populations of both *Cerithium stercusmuscarum* and *Theodoxus luteofasciatus* – grazing gastropods that feed on the algae growing on the rocky substrates of the northern flats or on the shell pavement that lines the tidal channel.

Dendrograms from Q-mode cluster analyses of shelly remains are often evaluated according to how well they match the dendrographs of analyses based on the living fauna. By this qualitative standard, they match reasonably well, differing principally in the inclusion of channel samples with rocky flat samples in one analysis (of the live fauna), and with inner flat and marsh samples in the other analysis (of the shelly remains). This particular mis-match is evidence of taphonomic processes. We interpret the clustering pattern in the analysis of shelly remains to reflect the transportation of *Cerithidea mazatlanica* shells from the marsh to the channel and inner flats.

In general, the good match is evidence that post-mortem processes do not completely redistribute shelly remains in a homogeneous fashion.

The cluster analysis of shelly remains may also be evaluated according to its power of resolution. By this standard, the cluster analysis does quite well because it serves to distinguish two groups of subtidal samples, rather than the one revealed in the analysis of the live remains. The greater resolution of habitats possible with shelly remains is a consequence of the much higher diversity of shelly remains. The greater number of species present among the shelly remains results from extensive time-averaging. Rare or transient species that may be diagnostic of particular habitats are more likely to be found in time-averaged accumulations of shells.

Our interpretation and comparison of the two dendrograms reveals that one taphonomic process (transportation) may serve to obscure important habitat distinctions – in the case of the channel samples. However, another taphonomic process (time-averaging) serves to enhance the resolution of habitats – in the case of the discrimination of the subtidal samples. This latter phenomenon is a good example of how taphonomic effects may add important information to a paleoenvironmental analysis.

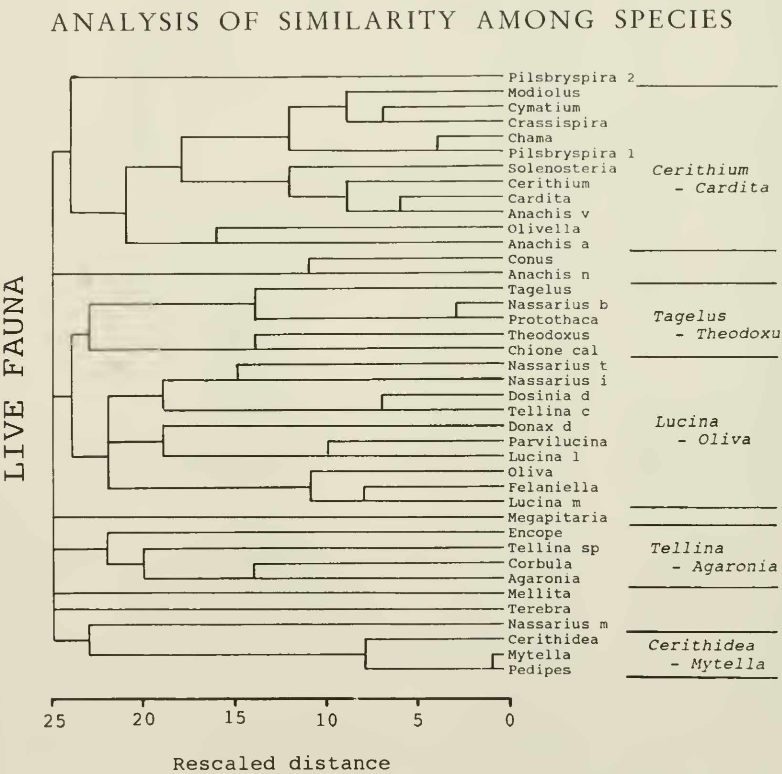


Fig. 3. Dendrogram of R-mode cluster analysis of species found alive in one or more samples. Italicized names indicate names given to species associations. See text for explanation and discussion.

The cluster analysis of species occurrences groups species together based on the degree to which they co-occur in samples. This is frequently termed an R-mode analysis. In this mode of analysis, species that invariably occur in the same samples will belong to the same group or cluster. Species which never occur in the same sample will be found in different clusters.

We performed two R-mode cluster analyses: one grouped living species based on their co-occurrences among the samples; the other grouped species of shell remains based on their co-occurrences among our samples.

R-mode analysis of species found alive in samples

The dendrogram of the 40 species found alive in one or more of our samples in shown in Fig. 3. The clusters form at relatively low levels of similarity, forming five species associations.

1. The *Cerithium* – *Cardita* association is characterized by epifaunal gastropods and nestling or encrusting bivalves. Members of this association are most common in the mixed rock and sand flats of the low intertidal in the northern part of the bay.

2. The *Tagelus* – *Theodoxus* association also includes two common shallow-infaunal venerid bivalves, *Chione californiensis* and *Protothaca grata* and the epifaunal gastropod *Nassarius brunneostoma*. These species typically occur in the vicinity of the main tidal channel and in the firmgrounds of the middle to inner flats.

3. The *Lucina* – *Oliva* association is dominated by the small infaunal bivalves *Felaniella, Lucina lampra, Lucina mazatlanica*, and *Parvilucina*. The gastropods *Oliva spicata* and *Nassarius iodes* are also typical. This assemblage is typical of the mid to outer sandflats of the low intertidal.

4. The *Tellina* – *Agaronia testacea* association is characterized by the shallow-burrowing echinoid *Encope micropora* and the shallow-burrowing gastropod *Agaronia testacea*. Members of this association typically occur in the shallow subtidal and lowest intertidal of the outer flats.

5. The *Cerithidea* – *Mytella* association consists of three species typical of the marsh/estero.

R-mode analysis of species found as shelly remains in samples

The dendrogram of the 119 species present in one or more sample of the shelly remains is shown in Fig. 4. The clusters form at relatively high levels of similarity, forming twelve species associations.

1. The *Tellina* – *Pteria* association is dominated by shallow burrowing and epifaunal bivalves. Many of the species are characteristic of the shallow subtidal of the mixed sandy and rocky flats of the northern part of Bahia la Choya.

2. The *Cardita* – *Caryocorbula* association is composed of dominantly hard substrate bivalves (either nestlers or cementers) and epifaunal gastropods. This association is often found in the low intertidal and shallow subtidal mixed rock and sand flats of the northern part of Bahia la Choya.

3. The *Petricola* – *Crucibulum* association is also composed of bivalves and gastropods typical of hard substrates (e. g. the two name-giving genera), plus a few species of small, shallow-burrowing bivalves. This association occurs in the mixed rock and sand flats in the shallow subtidal of the northern part of Bahia la Choya.

4. The *Chione cortezi* – *Modiolus* association is most frequently found in along the main tidal channel.

5. The *Chione californiensis* – *Felaniella* association is dominated by shallow-burrowing bivalves that typically occur in the mid to outer sand flats of the southern portion of Bahia la Choya.

6. The *Oliva* – *Parvilucina* association is dominated by species typical of the middle to outer sand flats. The inclusion of the hard substrate species *Vermetus* and *Crassostrea*, however, is a puzzle.

6a. *Nassarius brunneostoma* and *Cerithidea mazatlanica* form a distinct subgroup with the *Oliva* – *Parvilucina* cluster. *N. brunneostoma* and *C. mazatlanica* typically occur in inner flat areas.

7. The *Cerithium* – *Theodoxus* association. These two gastropods, together with *Nassarius iodes*, are commonly found in the main tidal channel and on the firmgrounds of the inner flat.

8. The *Agaronia* – *Glycymeris* association consists of species typical of the outer sand flats.

9. The *Anomia* – *Crepidula* association is dominated by encrusting species. This assemblage is suspect because it is defined principally by co-occurrence within a single subtidal sample.

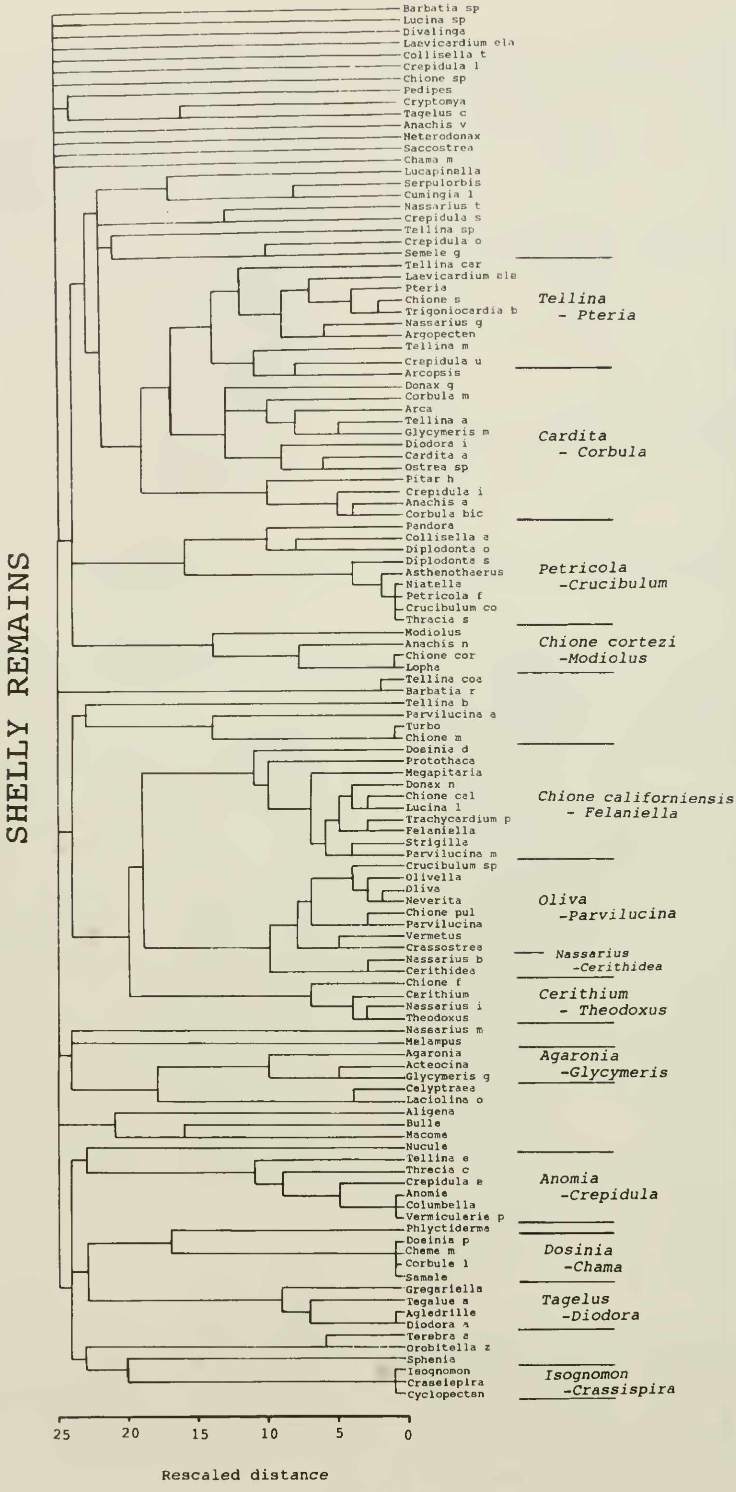
10. Species in the *Dosinia* – *Chama* association are typically found in the lowest intertidal and shallow subtidal of the sandy and rocky outer flats. However, this association is defined largely by the influence of a single, subtidal sample.

11. The *Tagelus* – *Diodora* association is a mixture of species inhabiting the inner flats near vegetated areas (*Tagelus* and *Gregariella*) and those washed out of the spit deposits at the strand line (*Diodora* and *Agladrillia*).

12. The *Isognomon* – *Crassispira* association is an outer flat, shallow subtidal assemblage found on the mixed rock and sand substrates of the northern part of Bahia la Choya. This assemblage is suspect because it is defined by the co-occurrence of three species in a single sample.

Discussion

The most dramatic difference between the two dendrographs is their size. Only 40 species were found alive in sufficient abundance in one or more sample. Almost three times as many (119) occurred in sufficient relative abundance (more than 1 %) in samples of shelly remains. The difference in diversity is a consequence of time-averaging. The very low sedimentation rates in Bahia la Choya permit the accumulation of the shells of rare and infrequent species.


SHELLY REMAINS
Barbatia sp
Lucina sp
Divalinga
Laevicardium ela
Collisella t
Crepidula l
Chione sp
Pedipes
Cryptomya
Tagelus c
Anachis v
Heterodonax
Saccostrea
Chama m
Lucapinella
Serpulorbis
Cumingia l
Nassarius t
Crepidula s
Tellina sp
Crepidula o
Semele g
Tellina car
Laevicardium ela
Pteria
Chione s
Trigoniocardia b
Nassarius g
Argopecten
Tellina m
Crepidula u
Arcopsis
Donax g
Corbula m
Arca
Tellina a
Glycymeris m
Diodora i
Cardita a
Ostrea sp
Pitar h
Crepidula i
Anachis a
Corbula bic
Pandora
Collisella a
Diplodonta o
Diplodonta s
Asthenothaerus
Niatella
Petricola f
Crucibulum co
Thracia s
Modiolus
Anachis n
Chione cor
Lopha
Tellina coa
Barbatia r
Tellina b
Parvilucina a
Turbo
Chione m
Dosinia d
Protothaca
Megapitaria
Donax n
Chione cal
Lucina l
Trachycardium p
Felaniella
Strigilla
Parvilucina m
Crucibulum sp
Olivella
Oliva
Neverita
Chione pul
Parvilucina
Vermetus
Crassostrea
Nassarius b
Cerithidea
Chione f
Cerithium
Nassarius i
Theodoxus
Nassarius m
Melampus
Agaronia
Acteocina
Glycymeris g
Calyptraea
Laciolina o
Aligena
Bulla
Macoma
Nucula
Tellina e
Thracia c
Crepidula e
Anomia
Columbella
Vermicularia p
Phlyctiderma
Dosinia p
Chama m
Corbula l
Semele
Gregariella
Tagalus a
Agladrilla
Diodora a
Terebra a
Orobitella z
Sphenia
Isognomon
Crassispira
Cyclopecten
Tellina - Pteria
Cardita - Corbula
Petricola -Crucibulum
Chione cortezi -Modiolus
Chione californiensis - Felaniella
Oliva -Parvilucina
Nassarius -Cerithidea
Cerithium - Theodoxus
Agaronia -Glycymeris
Anomia -Crepidula
Dosinia -Chama
Tagelus -Diodora
Isognomon -Crassispira
25
20
15
10
5
0
Rescaled distance

The greater number of species among the shelly remains also includes several species found only in one sample. These species are those that do not form subgroups and join the dendrograph only at very low levels of similarity. These are the species listed at the top of the dendrogram.

When two or more species co-occur in a single sample but occur in no other samples, the resulting high similarity among the species may result in a distinct cluster. These single-sample clusters (e. g. the *Dosinia – Chama* and *Isognomon – Crassispira* associations described above) should be considered suspect. Such clusters are based on rare species that occur in only one sample and should not be accorded much significance. In a sense, they represent accidents of species distributions and sampling.

The greater number of associations distinguished by the analyses of the shelly remains is a simple consequence of the greater diversity of species found among the shelly remains. More species (119 vs. 40) in more samples (92 vs. 101) will tend to produce more clusters.

Species in the living fauna form five clusters which roughly correspond to major habitats within Bahia la Choya. The *Cerithium – Cardita* association is typical of the hard substrates of the outer flats and the shell pavements of the tidal channel. The *Tagelus – Theodoxus* association is common along the tidal channel and inner flats. The middle and outer sand flats fauna typically includes members of the *Lucina – Oliva spicata* association. The *Tellina – Agaronia* association occurs in the shallow subtidal. The *Cerithidea – Mytella* association characterizes marsh habitats.

Associations formed by species found among the shelly remains also conform to Bahia la Choya's principal habitats. In many cases, however, more than one association occurs within a single habitat. Sandy, outer flat habitats contain three associations (*Agaronia – Glycymeris, Chione californiensis – Felaniella* and *Oliva – Parvilucina*), and the mixed rock and sand habitat of the low intertidal and subtidal includes three associations (*Tellina – Pteria, Cardita – Caryocorbula* and *Petricola – Crucibulum*). Two associations are commonly found in the channel (*Chione cortezi – Modiolus* and *Cerithium – Theodoxus*). The high intertidal firmgrounds of the inner flats include two associations (*Nassarius – Cerithidea* and *Tagelus – Diodora*). We dismiss the environmental significance of the remaining associations because they are often based on a single sample.

We interpret the greater resolution of the dendrogram of shelly remains as a result of the time-averaged nature of the shelly deposits. The long time during which shells have accumulated has allowed the accumulation of species diagnostic of the area's habitats and sub-habitats. Many of these species were probably not contemporaneous, but were nevertheless characteristic of a relatively limited set of environmental conditions. Samples of species that happen to be alive during a particular sampling interval are not likely to include all of the species that might inhabit the habitat over an extensive time interval. We are tempted to argue, therefore, that – as long as no environmental changes are involved – time-averaged samples provide a better means by which to discriminate habitats than samples that represent an "instant" in time. This would be the case in general only if between-habitat transportation was negligible.

The effects of transportation are evident in some of the associations formed from species in the shelly remains. For example, the *Tagelus – Diodora* association contains species that are winnowed out at the strandline of the spit. Thus, species from the spit deposits are recycled back into active sedimentary environments. The *Oliva – Parvilucina* association includes some species more characteristic of rocky substrates. Those species may have been transported in form the adjacent rocky flats.

CONCLUSION

We conclude that cluster analysis of shelly remains is an effective exploratory tool in paleoenvironmental analysis. A good correspondence exists between clusters based on the distribution of live fauna and the clusters based on the distribution of shelly remains.

The composition and distribution of the Bahia la Choya taphocoenoses is a function of both original species distributions, the original species composition of habitats and the taphonomic processes of time-averaging and transportation. Of the two taphonomic processes, time-averaging appears to exert the greatest effect. One beneficial side effect of time-averaging is the greater resolution achieved with cluster analysis of shelly remains. Time-averaged samples of shelly remains are more likely to contain environmentally diagnostic species.

Because both species composition and taphonomic processes vary significantly from habitat to habitat, the geographic distribution of the taphocoenoses, as shown in the dendrogram, is an excellent indicator of important habitat differences within Bahia la Choya. With the exception of species associations resulting from co-occurrence in single samples, species associations defined by cluster analysis permit the recognition of environmentally sensitive taphocoenoses.

◄ Fig. 4. Dendrogram of R-mode cluster analysis of species found as shelly remains in one or more samples. Italicized names indicate names given to species associations. See text for explanation and discussion.

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