

Zonation of molluscan life habit groups across the tidal flats of Bahia la Choya (Gulf of California, Sonora, Mexico): Paleoenvironmental significance

By

FRANZ T. FÜRSICH and SUSANNE SCHÖDLBAUER*)

With 5 figures in the text

ABSTRACT

Life habit groups of time-averaged molluscan taphocoenoses of Bahia la Choya, a shallow protected bay in the northern Gulf of California, exhibit a zonation from shallow subtidal to high intertidal environments. The distribution of epifauna and hard substrate fauna is largely governed by the availability of hard substrate. The distribution of trophic groups is

mainly a function of the energy level, time of subaerial exposure, and food source. The taphocoenoses of Bahia la Choya apparently underwent little lateral transport and consequently their life habit groups serve as useful environmental indicators.

KURZFASSUNG

Ernährungstypen und Typen von Lebensweisen zeitlich gemittelter Mollusken-Taphozönosen von Bahia la Choya, einer flachen geschützten Bucht im nördlichen Golf von Kalifornien, zeigen eine Zonierung vom flachen Subtidal bis zum höheren Intertidal. Das Auftreten von Epifauna und Hartsubstratfauna steht in einem engen Zusammenhang mit der Verteilung von hartem Substrat entweder in Form pleistozäner Felsgründe oder schillführender Kies- und Feingeröll-La-

gen. Die Verteilung der Ernährungstypen ist vorwiegend eine Funktion des Energieniveaus, der im Auftauchbereich verbrachten Zeit und des Nahrungsangebots. Die Taphozönosen von Bahia la Choya wurden offensichtlich nur geringfügig transportiert; das Verteilungsmuster ihrer Ernährungstypen und Typen von Lebensweisen ist deshalb ein brauchbarer Milieuindikator.

INTRODUCTION

In paleoenvironmental analysis life habit groups of benthic macrofauna have commonly been used to infer parameters such as bathymetry, energy level, substrate stability, oxygen level, and food supply (e. g. RHOADS et al. 1972, SCOTT 1974, FÜRSICH & WENDT 1977, OSCHMANN 1988). Recent benthic faunas are known to exhibit a good correlation between such environmental parameters and their life habit groups (e. g. SANDERS 1958, SAVILOV 1957, DRISCOLL & BRANDON 1973). A similar relationship could also be demonstrated for ancient ben-

thic faunas (e. g. FÜRSICH 1976). However, also studies suggest that such relationships are spurious and that the life habit group composition of fossil communities is considerably distorted when compared to that of living communities (e. g. STANTON & DODD 1976, BOSENCE 1979).

In investigating the molluscan fauna of a tidal flat we hope to contribute to this issue by examining the distribution of life habit groups of taphocoenoses across the tidal flat. Is there any meaningful zonation? We are not so much concerned whether the life habit groups of the taphocoenoses are identical with those of the living communities, but whether the groupings preserved in the taphocoenoses are correlated with the environment.

* F. T. FÜRSICH, Institut für Paläontologie der Universität, Pleicherwall 1, W-8700 Würzburg, Germany; S. SCHÖDLBAUER, Franz-Wolter-Straße 6, W-8000 München 81, Germany.

Bahia la Choya is a protected bay in the northern Gulf of California (Fig. 1). Due to a high tidal range, a sandy tidal flat covering more than 10 km² is exposed at spring low tide. The sediment varies from gravel (major tidal channel), fine and medium sand (outer to mid flat) to fine-sandy silt (inner flat) the latter forming a firmground. An extensive salt marsh exists adjacent to the inner flat, and is partly separated from it by a shelly spit. The marsh is inundated only during spring high tide. Salt marsh and tidal flat are drained by one major tidal channel. There is no freshwater input into the area at any time except for rare monsoonal rainstorms – Bahia la Choya borders the Sonoran desert.

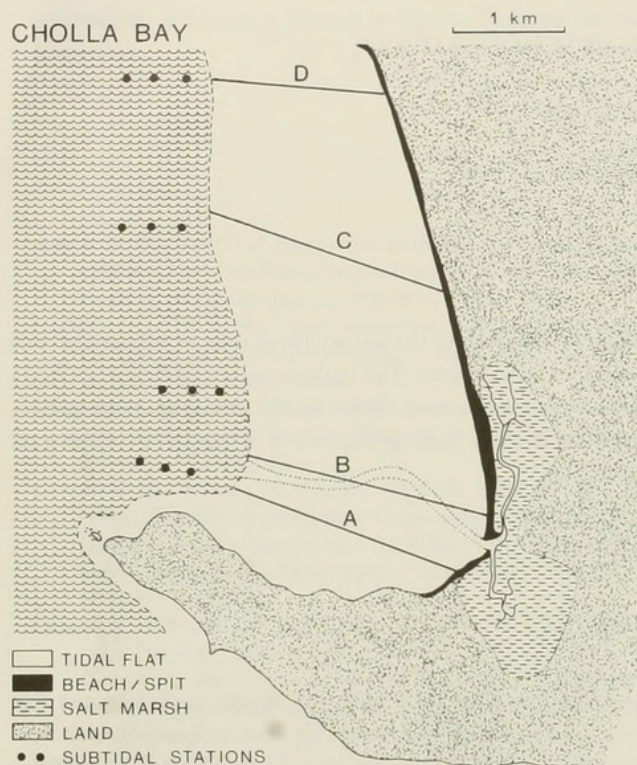


Fig. 1: Map of Bahia la Choya showing tidal flat, location of the four transects (A–D), and position of the subtidal stations.

Net rates of sedimentation are very low: Pleistocene rocks are exposed or covered by only a few centimetres of sediment over large parts of the tidal flat and within the shallow subtidal. This is particularly true of the northern part of the bay. Due to the low sedimentation rate shells and shell debris are a conspicuous part of the sediment, constituting up to 80 % of the sediment and forming highly time-averaged deposits. Bioturbation is fairly abundant destroying most internal sedimentary structures. A particularly striking feature are large feeding structures of rays. Rays, together with callianassid shrimps significantly contribute to sediment reworking. Physical sedimentary structures are therefore restricted largely to the sediment surface and the uppermost few centimetres. They include sandwaves (outer flat), megaripples (shallow subtidal and inner channel), current ripples (outer to inner flat), linguoid ripples (small tidal creeks), and current lamination (mid channel). A detailed description of the various subenvironments and ecological parameters are found in FÜRSICH et al. (this volume).

During December 1985 to May 1986 samples were taken along four transects. Sampling started in shallow (6 m deep) subtidal environments with a sampling distance of 200 m. It continued up to the shoreline. Samples were taken at 100 m intervals within the intertidal zone. Samples were washed and sieved in the laboratory (screen diameter: 3 mm). Specimens were counted and identified to species level. In the case of disarticulated bivalves, the larger valve number was used to determine number of specimens. (For detailed description of sampling and laboratory techniques see FÜRSICH et al. this volume.)

The mode of life and trophic group of each molluscan species was determined either by personal observations in Bahia la Choya, by literature survey, or, more rarely, by a functional analysis of the morphology. Species lists of the molluscan fauna from Bahia la Choya including also information on mode of life and feeding habits are found in FÜRSICH et al. (this volume, tables 1 and 2).

DISTRIBUTION PATTERN OF LIFE HABIT GROUPS

Fig. 2 shows the distribution of epifauna and infauna among the molluscan fauna of the taphocoenoses along the four transects. Epifaunal species include most gastropods such as *Cerithidea mazatlanica*, *Cerithium stercusmuscarum*, *Anachis*, and limpets. Characteristic epifaunal bivalves are *Cardita affinis*, *Modiolus capax*, *Ostrea*, *Pteria sterna* and arcids (*Arca*, *Arcopsis*). Semi-infaunal forms, counted here with the infauna, are *Mytella guaymasensis* and *Atrina* sp.. The infauna is dominated by bivalves (e. g. *Lucina lampra*, *Parvilucina mazatlanica*, *Felaniella sericata*, *Strigilla interrupta*, *Chione californiensis*, *Protothaca grata*, *Corbula marmorata*, species of *Tellina*, *Trachycardium panamense*, *Donax navicula*). All these species are shallow burrowers. Deep infaunal forms include *Tagelus* and *Cumingia*. Rocky infaunal (boring) species are *Lithophaga attenuata*, *L. abboti*, and *Gastrochaena ovata*. Infaunal taxa occur also among the gas-

tropoda. Abundant taxa are *Turritella*, *Agaronia*, *Oliva*, *Olivella*, *Terebra*, and naticids.

In Transects A and B (Fig. 2) which cross a largely sandy habitat infaunal molluscs dominate from the shallow subtidal zone to the mid flat. Epifaunal elements prevail in mid flat and inner flat environments as well as in the tidal channel.

The distribution of the epifauna is explained by the algal cover on shells and gravel in the channel and the diatom film developed on the firmground of the inner flat. These floras are exploited by algal grazers (e. g. *Cerithium stercusmuscarum*) and detritus feeders (e. g. *Cerithidea mazatlanica*). In addition, the firm substrate of the inner flat makes burrowing very difficult, except for a few species such as *Tagelus* and *Cryptomya*.

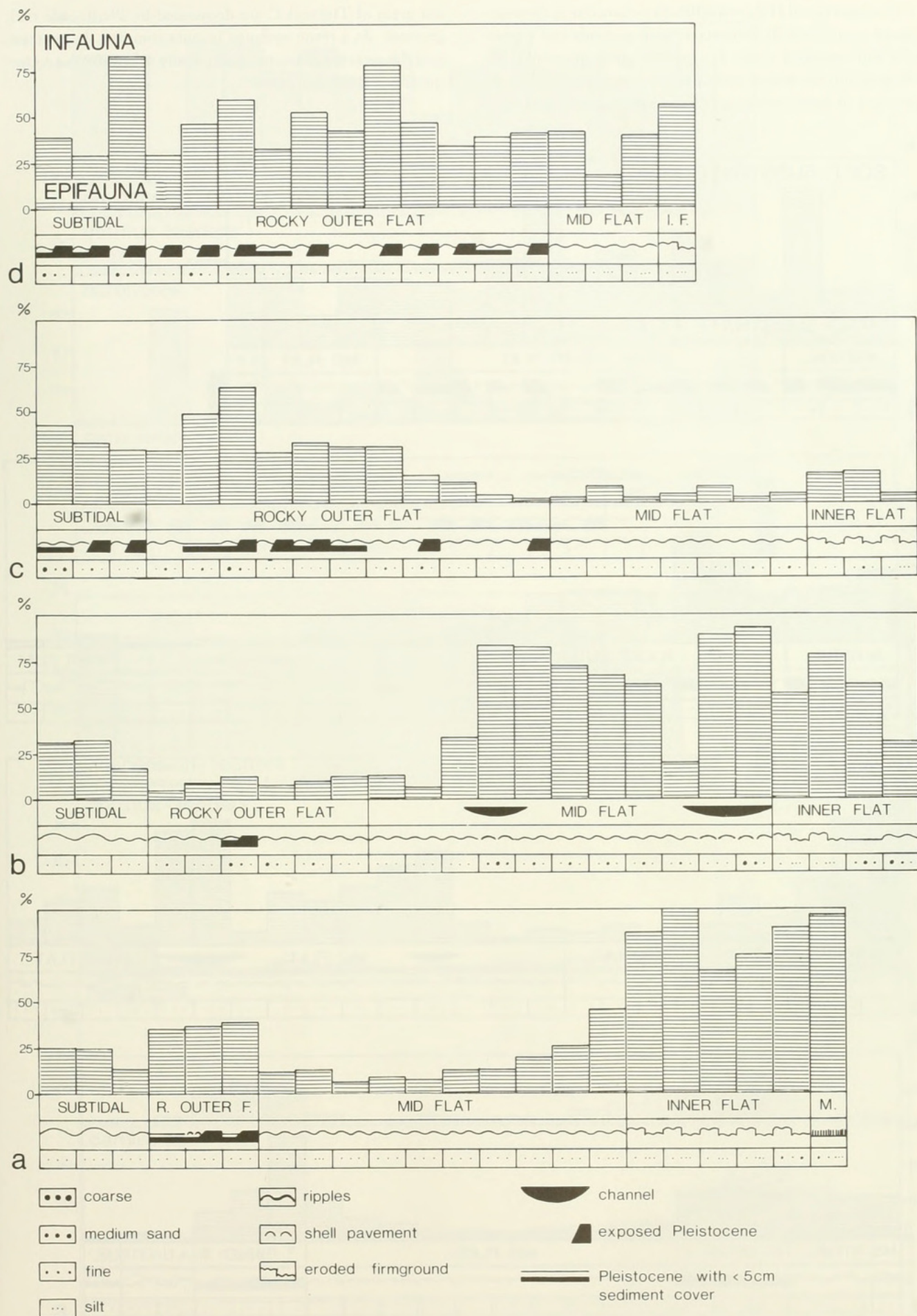


Fig. 2: Percentage distribution of epifauna/infauna across the tidal flat. a–d: Transects A–D.

Transects C and D show a different picture due to the widespread occurrence of Pleistocene rock grounds and a generally thin sediment cover. No onshore-offshore trend is developed, but the distribution pattern is solely related to the presence of hard substrate. For example, subtidal and outer

flat areas of Transect C are dominated by Pleistocene rock grounds. As a result epifauna is quite common. In contrast, mid flat areas are characterised by sandy substrate: as a consequence, infauna dominates.

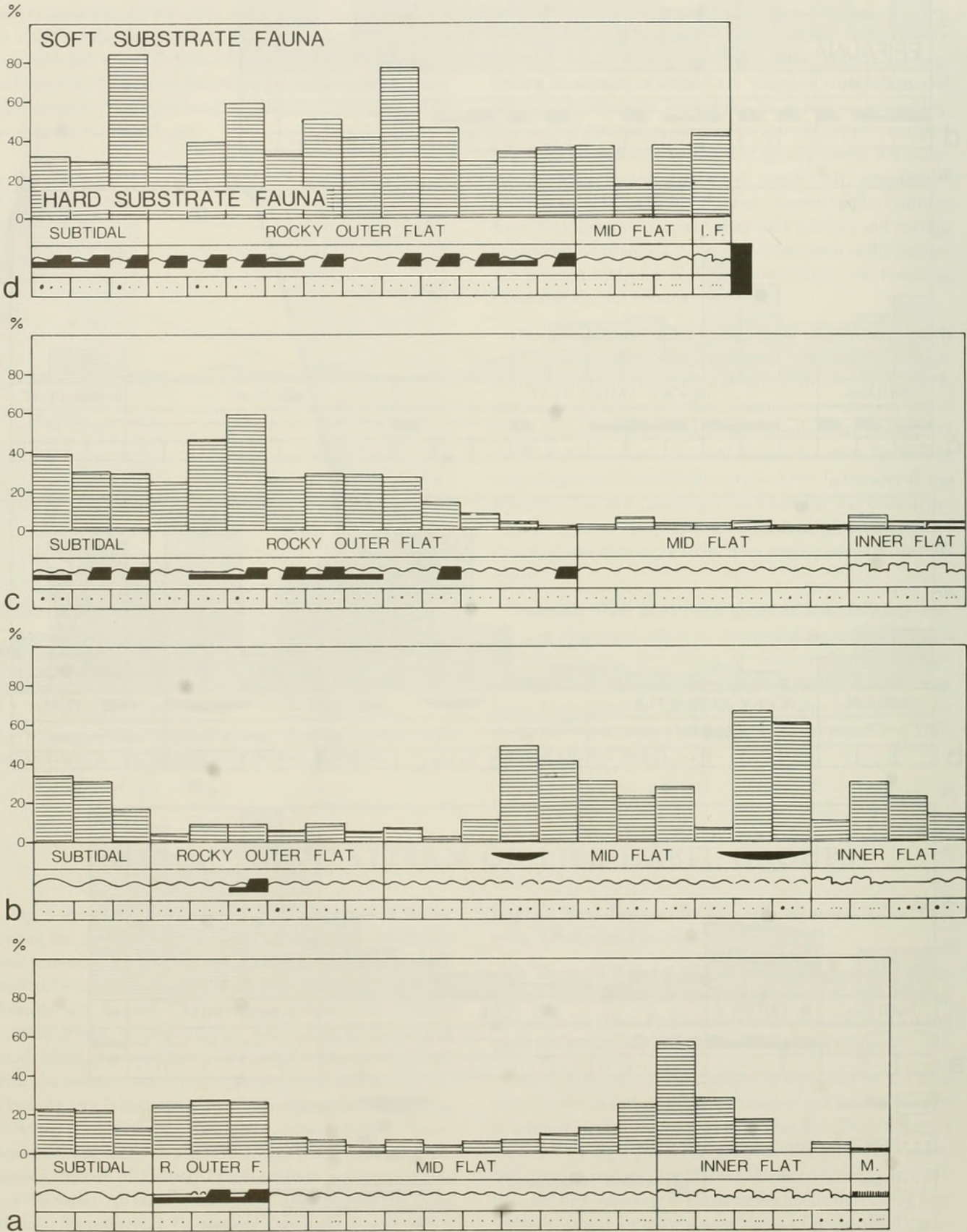


Fig. 3: Percentage distribution of hard and soft substrate molluscan fauna across the tidal flat. a-d: Transects A-D. Key as in Fig. 2.

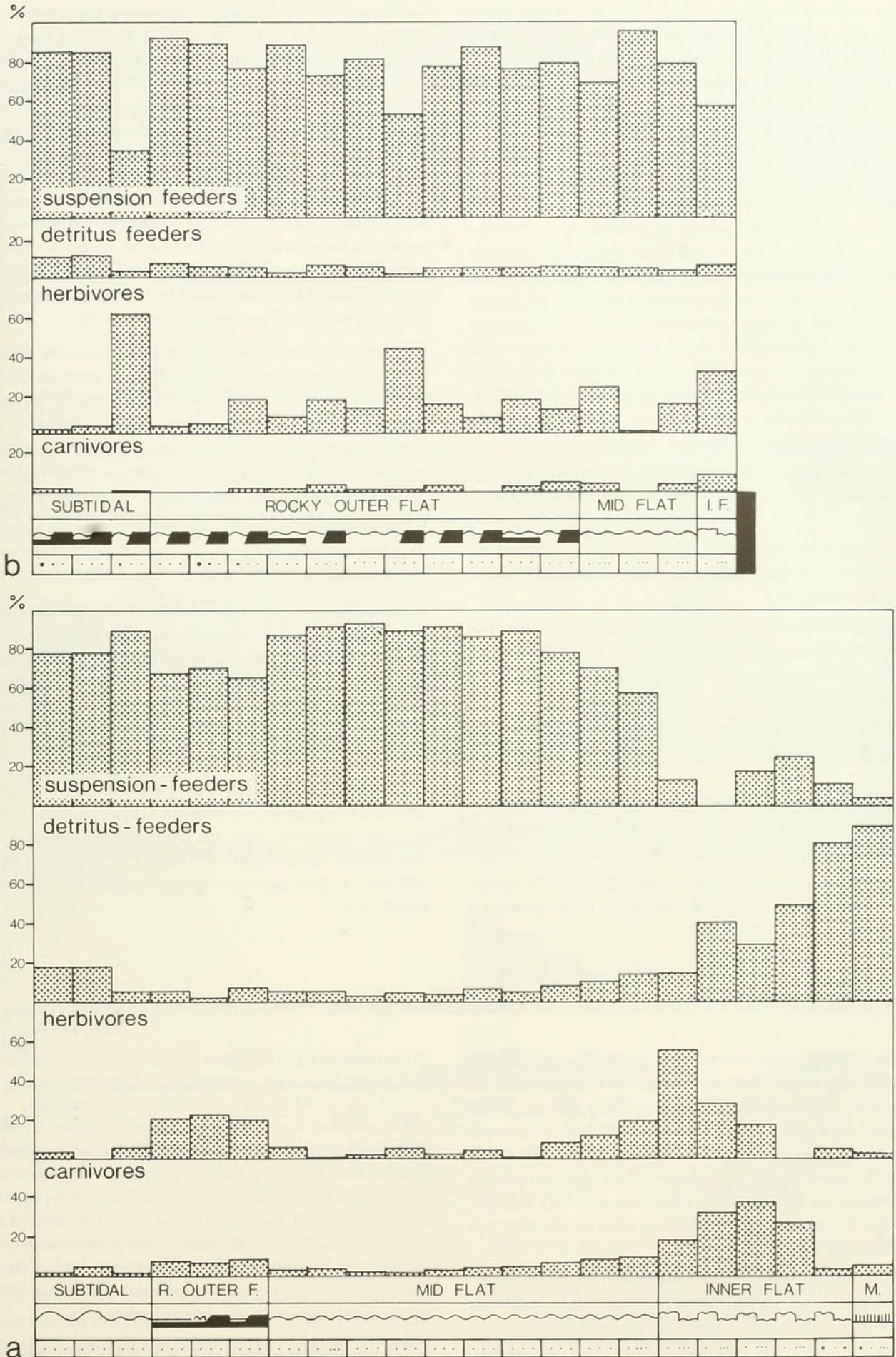


Fig. 4: Distribution of trophic groups across the tidal flat. a: Transect A; b: Transect D. Key as in Fig. 2.

Fig. 3 shows the distribution of hard substrate forms along the four transects. Among bivalves, they include boring taxa (e. g. *Lithophaga*, *Gastrochaena*), nestling species (e. g. *Gregariella coarctata*), epibyssate forms (e. g. *Cardita*, *Modiolus*, *Pteria*) and cemented taxa (*Chama*, *Ostrea*). Epifaunal free living gastropods (e. g. *Cerithium*, *Solenosteira*), largely sessile gastropods (e. g. *Crucibulum*, *Crepidula*) and, more rarely, cemented forms (vermetids) complement the list.

Hard substrate taxa predominate in gravelly sediments of the major tidal channel (Transect B) or else are limited to hard substrate in Transects A, C, and D. In Transect D the rocky Pleistocene terrace that forms the shoreline causes an increase of hard substrate taxa in the innermost tidal flat. Altogether there is a good correspondance between hard substrate species and hard substrate: this suggests very little transport. The only exception is the peak of hard substrate taxa in inner flat sediments of Transect A, caused largely by abundant *Cerithium stercusmuscarum*. This anomaly appears to have been caused by the transport of shells by hermit crabs.

Figs 4 and 5 record the distribution of trophic groups across Bahia la Choya. The following groups were distinguished:

(1) suspension-feeders which include nearly all bivalves and, amongst the gastropods, *Turritella*, *Crucibulum*, *Crepidula*, and vermetids;

(2) detritus/deposit-feeders, which include the numerically insignificant scaphopods *Dentalium* and *Fustiaria*, the bivalves *Tellina* and *Nucula*, and several gastropods (e. g. *Cerithidea*, *Anachis*);

(3) herbivores, exclusively gastropods (e. g. *Theodoxus*, *Diodora*, *Lucapinella*, *Cerithium*, *Epitonium*, *Melampus*); and

(4) carnivores, which include both predatory and scavenging gastropods (e. g. naticids, turrids, olivids, *Nassarius*, *Conus*, *Terebra*).

The assignment to a particular trophic groups is not always easy, as several species are omnivorous (e. g. the gastropod

Calliostoma). The distinction between detritus-eaters and scavengers is also somewhat artificial depending largely on the size of the food particles. For example, the various species of *Nassarius* are here classified as scavengers (and thus grouped with the carnivores), but could probably be as easily grouped with the detritus-eaters. Conversely, species of the gastropods *Anachis*, *Columbella* and *Mitrella* are both detritus-eaters and microcarnivores (e. g. MORRIS et al. 1980), but have been grouped here with the former. The very abundant *Cerithidea mazatlanica*, here classified as a detritus-eater, could also be regarded as a herbivore as the diatom film on inner flat sediments apparently serves as the main food source. These difficulties should be kept in mind when the following patterns (Figs. 4 and 5) are discussed.

Overall, suspension-feeders are the dominant trophic group throughout Transects C and D. Suspension-feeders also dominate from subtidal throughout mid flat environments of Transects A and B (except in the tidal channel). Their distribution records the higher energy level prevailing in the northern part of Bahia la Choya compared to the southern, more protected part.

Detritus-eaters are rare in Transects C and D, but very abundant in the inner flat of Transects A and B. They reach moderate numbers in the channel (Transect B).

Herbivores are generally related to the presence of hard substrate: either exposed Pleistocene rocks (Transects A, C, D) or shelly gravel (channel) where their food source, algae, grows. An anomaly is the abundance of herbivores in inner flat sediments of Transect A which is caused by the occurrence of *Cerithium* shells. As mentioned above, their presence is mainly due to transport by hermit crabs.

Carnivores, including predators and scavengers are generally of low abundance, especially in Transects C and D. They are more common in inner flat sediments of Transect A and mid to inner flat sediments of Transect B. This is due to the presence of abundant scavenging *Nassarius brunneostoma* and *N. iodes*.

DISCUSSION

The distribution pattern of both trophic groups and life habit groups within Bahia la Choya taphocoenoses can be related to environmental parameters. Most obvious is the correlation of epifauna and hard substrate fauna to exposed Pleistocene rocks of shallow subtidal and intertidal areas and to shelly gravel of the tidal channel. This close correlation documents that little transport takes place across the tidal flat and that even time-averaging does not substantially alter this relationship.

Substrate thus appears to have been the overriding environmental parameter governing the distribution of epifauna. Other parameters such as length of subaerial exposure and energy level exert only a minor influence. This is particularly well seen in Transects A and C where in one case (Transect C) infauna dominates in mid to inner flat settings due to presence

of sandy substrate, while infauna is rare in inner flat sediments of Transect A which form a firmground (Fig. 2).

The correlation of trophic groups to particular environmental parameters is more complex. There is a clear relationship between relative abundance of suspension-feeders and energy level: This group by far dominates in the less protected northern part of Bahia la Choya and in shallow subtidal and outer flat areas (Figs. 4–5) where a large proportion of organic matter is kept in suspension. Suspension-feeders are, on the whole, less common towards the shoreline due to longer subaerial exposure time and shorter feeding time.

The distribution of herbivores is strongly correlated with their food source, benthic algae. Because algae require a hard substrate for their growth, herbivores also show a very good

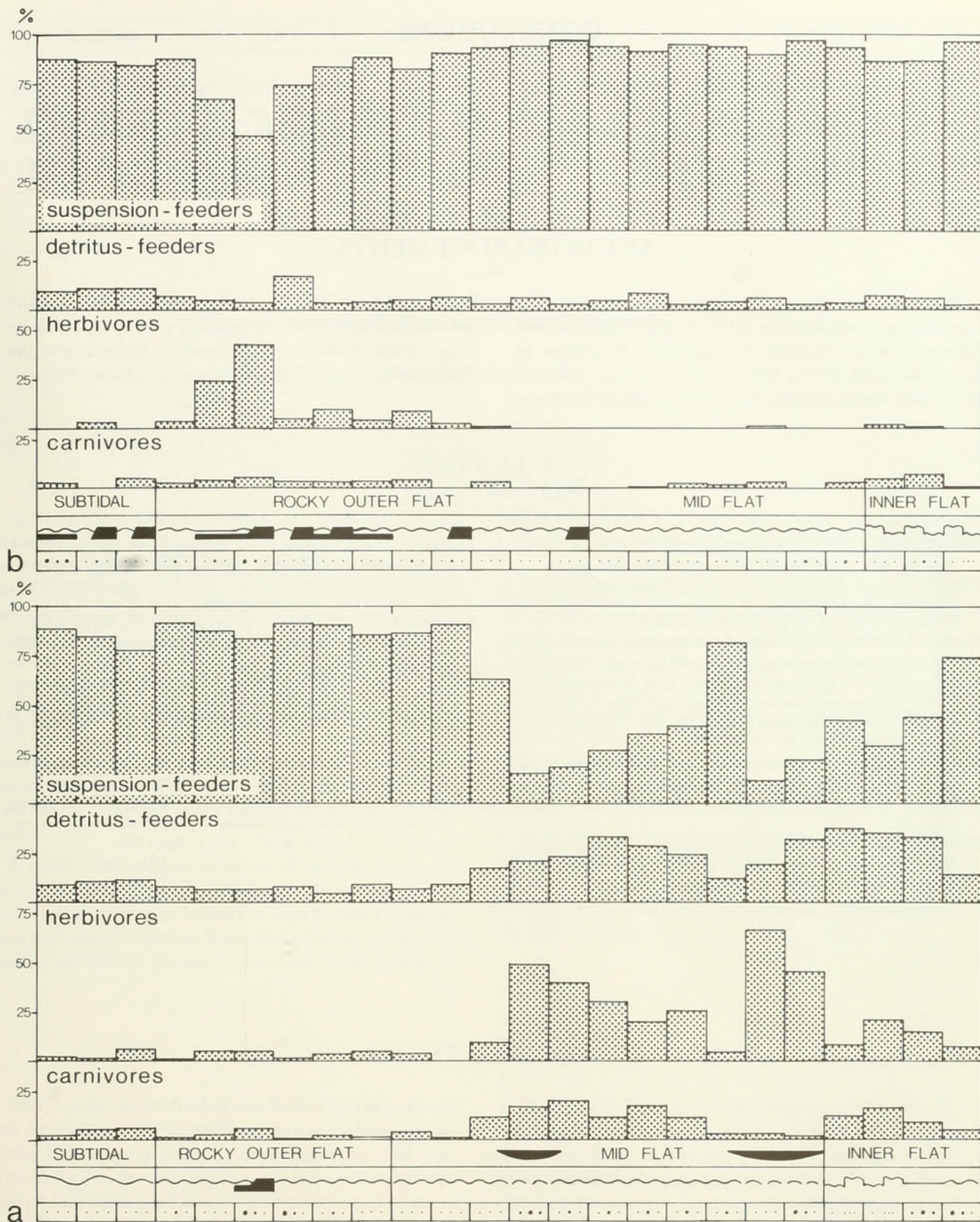


Fig. 5: Distribution of trophic groups across the tidal flat. a: Transect B; b: Transect C. Key as in Fig. 2.

correlation with exposed Pleistocene rock grounds and shelly gravel.

The dominance of detritus/deposit-feeders on inner flat firmgrounds is most likely related to the presence of a diatom film which covers the sediment surface, and to the lower energy level of this subenvironment which causes particulate organic matter to accumulate on the sediment surface.

Carnivores are, on the whole, not very abundant. This is particularly true of predators which – as one would expect – represent only a small fraction of the benthic fauna. Scavengers, many of which could be as easily classified as detritus-eaters (see above), have their peak distribution on inner flat substrates.

CONCLUSIONS

The distribution of life habit groups and trophic groups of Bahia la Choya mollusc taphocoenoses correlates well with several environmental parameters. Most important are substrate, food distribution (in combination with time of subae-

rial exposure), and energy level. Original trophic proportions and life habit groupings are well preserved despite pronounced time-averaging and strong tidal currents. Trophic and life habit groups can be useful environmental indicators.

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