

Research Article

Photosynthetic Pigments Contained in Surface Sediments from the Hydrothermal System of Guaymas Basin, Gulf of California

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In the exploration of the hydrothermal system of the Guaymas Basin (GB) between 27° 00' 35" and 27° 00' 50" N and 111° 24' 15" and 111° 24' 40" W in the Gulf of California, carried out on the R/V Atlantis and of the DSRV/Alvin in October 2008, four cores of surface sediments were obtained to analyse photosynthetic pigments at two locations with contrasting extreme conditions: Oil Town and Great Pagoda. We identified nine pigments: Chlorophyll-*a*, Phaeophytin-*a*, Phaeophorbide-*a*, Pyropheophytin-*a* (degradation Chlorophyll-*a* products), β -Carotene, Alloxanthin, Zeaxanthin, Diadinoxanthin, and Prasinolaxanthin (carotenoids). The maximum pigment concentration was registered in the Great Pagoda (10,309 ng/g) and the minimum in Oil Town (918 ng/g). It is demonstrated that photosynthetic pigment profiles in surface sediments depend on the heterogeneity of the extreme conditions of each site caused mainly by temperature and bacterial substrates. Therefore, there were significant differences ($p < 0.05$) in the pigmentary profile of the four sedimentary cores analyzed. However, no statistical differences ($p > 0.05$) in the concentration of pigments have been detected. We conclude that the photosynthetic pigments contained in the surface sediments of the hydrothermal vents in the Guaymas Basin are primarily of chemoautotrophic bacterial origin.

1. Introduction

An unusually high heat flow zone characterizes the Gulf of California due to convection currents in the magmatic chamber rising below this region through the Eastern Pacific Rift (EPR) [1]. These propagation mechanisms of the crust in the central Gulf of California, associated with intense tectonic dynamics of the place, give rise to a deep hydrothermal system in the southern part of the Guaymas Basin (GB). The sediments in Guaymas Basin are a mixture of immature, first-cycle erosional detritus, and biogenic material [1]. This system is covered with a sedimentary layer rich in organic matter, with a thickness of approximately 400 m [2]. It is composed of siliceous material of biogenic origin (mainly of diatoms > 50%) and terrigenous sediments rich in plagioclase [3],

in addition to the precipitates originated from hydrothermal fluids rich in particulate manganese and dissolved silica [4, 5].

Photosynthetic pigments contained in marine sediments are useful indicators of oxidized terrigenous organic matter and eutrophication conditions [6, 7] and have also been used in the evaluation of phototrophic communities [8]. Kowalewska [7] mentions that in a sedimentary sequence (0-10 cm), the content of pigments in the deep layers is similar and generally lower than in the surface layers and that these differences are caused by (1) sedimentation rates, (2) bacterial degradation, photooxidation, and temperature change in the water column, and (3) primary production.

The general biogeochemical conditions prevailing in GB are reasonably known [1, 9-13]. Our current knowledge on the diagenesis of chlorophyll derivatives in the Gulf

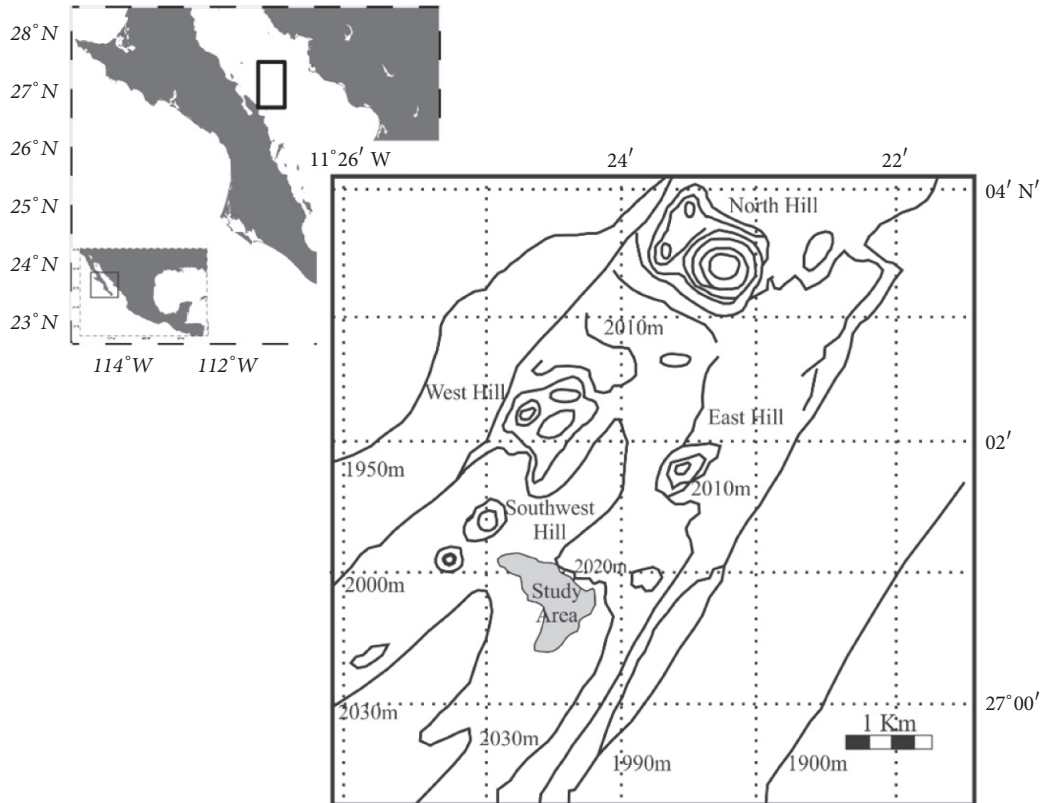


FIGURE 1: Guaymas Basin (GB) and study area location in the Central Gulf of California. Modified from Soto [13].

of California is restricted to the geochemical analysis of sediments obtained by the Deep Sea Drilling Project Leg 64 [14]. Our study intends to elucidate if the composition and concentration of study's focus is on the class of photosynthetic pigments (tetrapyrrole and tetraterpenoid) contained in and their concentration in surface sediments from two active hydrothermal sites in GB suffered alteration due to the exhibiting contrasting extreme conditions prevailing at each site. We postulate that such conditions may alter the diagenesis of chlorophyll derivatives as potential organic sources for heterotrophs in the studied vent system.

2. Materials and Methods

2.1. Study Area. The Guaymas Basin is located in the central part of the Gulf of California between $27^{\circ} 00' 35''$ and $27^{\circ} 00' 50''$ N and $111^{\circ} 24' 15''$ and $111^{\circ} 24' 40''$ W. It is a semienclosed Basin formed by two (northern and southern) axial troughs bounded by extensive systems of axial-parallel fault lines separated by a fault 20 km long and 3 to 5 km wide at a depth of 2,030 m with temperatures of 2.8°C in the bottom [15–18] (Figure 1). The site is distinguished by having a high sedimentation rate greater than $1\text{--}1.2\text{ m } 1,000\text{ years}^{-1}$ [14] forming a combination of terrigenous detritus and biogenic matter [1]. This high sedimentation rate favours the concentration of considerable organic matter at the bottom of the Basin that is subject to hydrothermal stress [9, 10, 14].

The most distinctive feature of the Basin is the active hydrothermalism in the Southern Trough formed a complex

hydrothermal landscape on the seafloor [19], in which mineral deposits are formed in the form of mounds, spires, pagoda-like structures, and tall pillars distributed over a terrain covered by fine sediment [9, 13] which contains a complex mixture of aliphatic and aromatic hydrocarbons that are formed by the hydrothermal alteration of sedimentary organic matter [11, 18, 20].

One of the sampling sites is the area called “Grand Pagoda.” It is a large hydrothermal formation. The area is covered by orange and white *Beggiatoa* spp. bacterial mats and *Riftia* colonies, indicating diffuse venting. In the upper part of the formation, it is covered by lobed extensions spreading that extend approximately one meter on each side towards the water column. Small chimneys appeared in the center of some flanges. Part of the hydrothermal fluid flow seeps and rises through the center of small chimneys [16]. The other site, “Old Town,” includes sulphide edifices with diffuse flow, bearing clusters of *R. pachyptila*, but notorious for the presence of liquid hydrocarbons in the adjacent sediments.

The presence of organic carbon allows for high biological productivity at the site, despite being a zone of extreme conditions. The conjugation between sulphides and hydrocarbons from hydrothermal discharges provides the necessary energy for the development of a complex hydrothermal biological community whose existence depends on chemosynthetic processes [13, 21].

2.2. Sampling. Four sediment push-cores (33 cm length x 16 cm diameter) were obtained during the AT 15-38 expedition

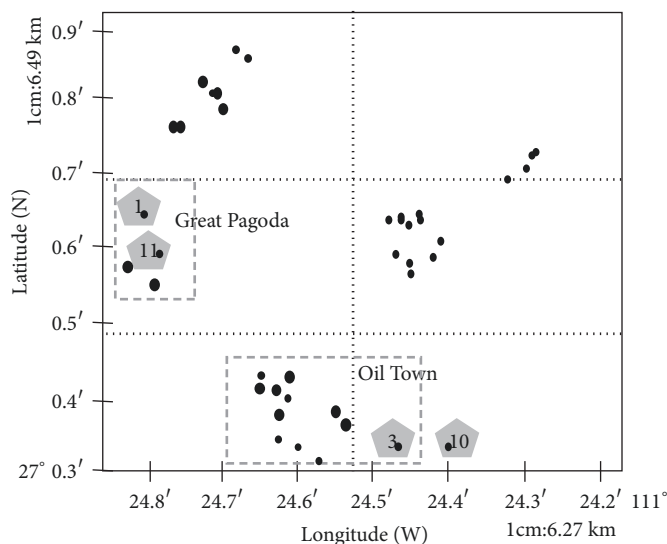


FIGURE 2: Spatial location of sediment cores recovered (3, 10, 1, and 11) by the DSRV-*Alvin* during the AT 15-38 campaign. • Active sites.

on board of the R/V *Atlantis* in October 2010 at GB, Gulf of California (Figure 2). The push-cores were recovered by the DSRV-2 *Alvin* (Woods Hole Oceanographic Institution) during three dives at Oil Town and Great Pagoda located in the Southern Trough. Each site showed different physical characteristics (Table 1). The sediment surface temperature (0-30 cm) was recorded with the R/V *Alvin* High-T and Low-T probes.

Once on board, the sediments of ~1 cm from the seafloor were subsampled and stored under dark conditions at -70°C until processed. Pigment analysis was performed according to the method described by Vidussi et al. [22] employing high-performance liquid chromatography (HPLC).

2.3. Pigment Extraction. Five grams of surface sediment from each core was processed. The extractions were made with 4 cm³ of 100% HPLC grade acetone. The samples were kept in the dark for 24 h at -20°C. They were then centrifuged at 4,000 rpm for 15 min at 5°C. The extract was filtered through in 47 mm fiberglass membrane and 0.45 μm pore size. The volume was recovered in 2 cm³ Eppendorf vials and stored at -20°C, 20 μL; afterward, the volume was injected into the High-Performance Liquid Chromatograph (Model 1100, Hewlett Packard).

2.4. HPLC Pigment Analysis. A mobile phase was used by mixing two solutions: Solution A: methanol HPLC grade combined with 1 N aqueous ammonium acetate to form a 70:30 v/v mixture and Solution B: methanol HPLC grade. The separation was carried out in a Hypersil MOS C8 column 100 x 4.6 mm, 5 μm particle size [22]. To identify the pigments, we compared the retention time of the sample peaks with those of the pure standards and the absorption spectra of the problem sample with those of the generated library of the standards (precision < 1%). The pigments quantification was done by constructing a calibration curve (R^2 =from 0.9107 to 1) that include the concentrations for each standard (20, 30, 40, 50, 60, and 100 ng).

2.5. Statistical Analysis. A Chi-square test (X^2) was performed to determine whether the pigment type depended on the sedimentary core from which the sample was extracted. Similarly, an analysis of variance in a randomized block design (ANDEVA) was applied to assess the existence of significant statistical differences ($p \leq 0.05$) in the concentration (ng/gr) and in the variety of pigments between the cores. Through Tukey's multiple means comparison test ($p \leq 0.05$), the statistical differences between mean pigment concentrations were determined [23].

3. Results

3.1. Pigment Identification and Quantification. Nine pigments were identified whose concentrations are listed in Table 2. Six of these photosynthetic pigments corresponded to Chlorophyll-*a*, β-Carotene, Zeaxanthin, Alloxanthin, Diadinoxanthin, and Prasincoxanthin. The other three pigments, resulting from the Chl-*a* degradation, were Pyropheophytin-*a*, Phaeophytin-*a*, and Phaeophorbide-*a* (Figure 3). Not all the nine pigments identified were present in a single core.

In four cores, the most abundant Chl-*a* derivatives were Pyropheophytin-*a* (3,684 ng/g), which represented 24.6% of the total concentration of pigments analyzed (14,962 ng/g), Phaeophorbide-*a* with 23.2% (3,478 ng/g), Phaeophytin-*a* with 7.2% (1,074 ng/g), and Chlorophyll-*a* with 2.6% (386 ng/g) the least abundant. On the other hand, the predominant carotenoid pigments were Prasincoxanthin (21.5%, 3,209 ng/g), β-Carotene (14.1%, 2,114 ng/g), and Zeaxanthin (5.6%, 841 ng/g). Diadinoxanthin and Alloxanthin had the lowest pigment concentration (168 and 8 ng/g, respectively) (Table 2).

The highest pigment concentration was recorded in core 11 (10,309 ng/g) and the lowest in core 3 (918 ng/g). Cores 1 and 10 had similar concentrations (1,876 and 1,859 ng/g, respectively).

The presence of Phaeophorbide-*a*, Prasincoxanthin, Zeaxanthin, and β-Carotene was recorded in all the cores

TABLE 1: Physical characteristics of the sediment samples obtained by the DSRV *Alvin* in the Guaymas Basin, Gulf of California (Cruise AT 15-38).

DSRV- <i>Alvin</i> Immersion No.	Core	Location	Position	
4457	3	Oil Town	27° 00.7039' N	111° 24.3179' W
<i>Substrate</i> : the temperature recorded in the first 0-20 cm of depth was 30°C (ambient temperature). White and orange bacterial mats were found on surface.				
4459	10	Oil Town	27° 00.7039' N	111° 24.3179' W
<i>Substrate</i> : the temperature recorded in the first 0-20 cm of depth was > 200°C. High concentrations of oil and gas were observed. The external matrix with bacterial growth, consisting of <i>Beggiatoa</i> spp. patches.				
4460	1	Great Pagoda	27° 00.67636' N	11° 24.416833' W
<i>Substrate</i> : the temperature has a gradient of 19.2 to 71.0°C in the first 6 cm depth. Orange bacterial mat was found on surface.				
4460	11	Great Pagoda	27° 00.67636' N	11° 24.41683' W
<i>Substrate</i> : the temperature has a gradient of 5 to 16°C in the first 6 cm depth. Olive green-black sediment. Yellow <i>Beggiatoa</i> spp. bacterial mat was found.				

TABLE 2: Retention time (min) and pigment concentration (ng/g) recorded in the sediment cores obtained at the Great Pagoda and Oil Town sites in the Guaymas Basin hydrothermal system. DL = detection limit (ng). A: absent.

Pigment Profile	Retention Time	DL	Each Pigment Concentration			
			Great Pagoda		Oil Town	
			I	II	3	10
<i>Tetraterpenoid</i>						
β -Carotene	14.7	0.14	440	914	341	419
Zeaxanthin	7.98	0.44	197	324	99	221
Alloxanthin	7.05	0.13	A	A	8	A
Diadinoxanthin	6.87	0.34	141	A	27	A
Prasincoxanthin	6.03	0.22	820	1866	213	312
<i>Tetrapyrrole</i>						
Chlorophyll- <i>a</i>	12.39	0.23	A	298	A	87
Pyropheophytin- <i>a</i>	14.22	1.84	A	3514	169	A
Phaeophytin- <i>a</i>	13.31	2.22	A	618	A	455
Phaeophorbide- <i>a</i>	5.02	1.36	277	2775	62	364
<i>Pigments Concentration per Core</i>			1876	10309	918	1859
<i>Pigments Concentration Total</i>						14,962

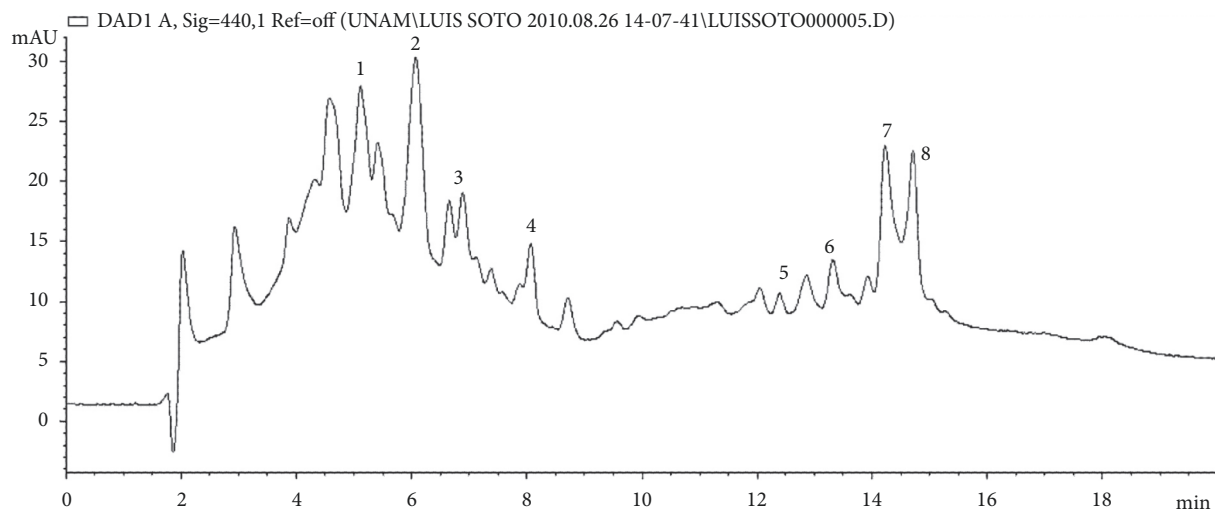


FIGURE 3: Chromatogram obtained from the sediment core 11. (1) Phaeophorbide-*a*, (2) Prasincoxanthin, (3) Diadinoxanthin, (4) Zeaxanthin, (5) Chlorophyll-*a*, (6) Phaeophytin-*a*, (7) Pyropheophytin-*a*, and (8) β -Carotene.

examined and only traces of Alloxanthin (8 ng/g) in core 11 (Table 2). Diadinoxanthin was present in cores 1 and 3, whereas Chl-*a* and Phaeophytin-*a* were only found in cores 10 and 11. The core 11 exhibited the maximum pigment concentration (10,309 ng/g) in comparison with the other cores (Table 2), although in the core 3 there were also seven pigments identified in low concentrations.

With the Chi-square test (1% significance level), it is concluded that the characteristics of the substrate and temperature of each recovered core with respect to the pigments concentration and presence registered in the study area are independent (Chi-square test $p < 0.0001$). In contrast, the estimated concentration for each identified pigment was significantly different between the cores analyzed (ANDEVA, $F = 5.31$, $p > 0.006$). However, no differences in the number of pigments recorded in each core were statistically significant (ANDEVA, $F = 1.36$, $p = 0.26$).

Tukey's multiple comparison tests ($p \leq 0.05$) showed that cores from Great Pagoda core 1 and Oil Town cores 3 and 10 did not have significant statistical differences since they have a similar average pigment concentration. However, they differed from core 11 from Great Pagoda which had the highest average pigments concentration.

4. Discussions

The study of pigments in marine sediments is relatively recent [6, 7]. Nevertheless, their analysis can provide vital information to determine the environmental conditions in a particular area. Chl-*a* represents the most common photosynthetic pigment in nature. It has been the focus of numerous studies because it is the best chemical indicator of phytoplankton biomass and sources of organic carbon [24]. It is also known that Chl-*a* depends on light energy to maintain its activity and therefore, some inferences can be made concerning the light and temperature conditions prevailing at the sites in which this photosynthetic pigment is detected [25]. Other pigments are considered secondary or accessory since they represent photoprotective cell membrane adaptations [26, 27].

Presumably, at depth in excess of 2,000 m, as is the case of the GB, the light conditions are of total darkness. However, Reynolds and Lutz [28] have demonstrated that in the deep-ocean there are several sources of light, namely, bioluminescence, cosmic rays, and radioactivity. These authors conclude that the spectral composition of this light is not visible for the human vision but can be detected by deep abyssal dwellers and perhaps contributes in maintaining the activity of photosynthetic pigments. This fact may explain the presence of Chl-*a* recorded in low concentrations in cores 10 and 11 (298 and 87 ng/g, respectively, Table 2), occupying the third less abundant pigment (2.6%). Although these cores were spatially separated by approximately 20 km, they were collected at substrate covered by extensive bacterial mats and olive green sediments, indicative of the possible presence of Chl-*a* or some of its derivatives (Phaeophytin-*a*, Phaeophorbide-*a*, or Pyropheophytin-*a*). It is worth mentioning that these findings add support to early assumptions that deep-sea hydrothermal ecosystems are capable of producing photosynthesis without relying on

solar energy [29, 30]. The facultative photosynthetic bacteria (producers of bacteriochlorophyll or other pigments) through a photochemical adaptation potential exploited at low levels of light take advantage of the photon flow emitted by hydrothermal fluids at extreme temperatures [30].

Chl-*a* is characterized by being less thermostable compared to Chl-*b* or *c*, depending on the environmental conditions. The Chl-*a* molecule is highly susceptible, and therefore, its degradation is quite rapid [31, 32]. Approximately 90% of the Chl-*a* is broken down into colorless products [24]. The degradation process is due to a combination of biotic factors (microorganisms or heterotrophic organisms) and abiotic factors (temperature, light intensity, and oxygen concentration) that foster this process, whose final products are known as chloropigments, phaeopigments, or degradation products [24, 26, 33–36]. In the vent system of GB, the Chl-*a* degradation process due to the prevailing extreme conditions resulted in the formation of Phaeophytin-*a*, Phaeophorbide-*a*, and Pyropheophytin-*a*.

The Phaeophytin-*a* is the product of the loss of magnesium in the Chl-*a* molecule [26, 34]. Afterward, its characteristic green color becomes an olive-brown tone. This pigment, like the Chl-*a*, was restricted to the cores 10 and 11, but with a higher relative concentrations (386 and 1074 ng/g, respectively). According to Yentsch [33], Chl-*a* fractions are rapidly decomposed with the increase in water depth, the loss of light intensity, and the change in ambient temperature.

When Chl-*a* loses a phytol group, Chlorophyllide is formed, which in turn eliminates a magnesium molecule giving rise to Phaeophorbide-*a* [31, 35] showing that the Chl-*a* degradation to form Phaeophorbide-*a* is initiated by extreme factors such as stress, light conditions, temperature changes, or their combined action. The presence of Chlorophyllide in all the cores obtained in the study area is probably due to extreme physicochemical conditions promoted by the hydrothermal fluids liberated at venting sites of GB [1]; such conditions seem to favor the formation of Phaeophorbide-*a*, which had the second highest concentration (3478 ng/g) among the nine pigments identified here.

The Pyropheophytin-*a* is the Chl-*a* degradation final product which is formed by the decomposition of Phaeophytin-*a*, due to the loss of a carboxyl group, thus acquiring more stability and better preservation. Its presence indicates old and anoxic sediments with high organic carbon content [7, 24, 26, 33].

The high sedimentation rate of GB generates a thick layer of fine-grained sediments (> 400 m) that favors the concentration of organic matter, reaching high organic carbon concentrations (3.4 to 12.4%) [2, 3, 10, 12]. Edgcomb et al. [37] mentioned that the Basin is a hydrothermally active environment that includes vent plugs, filtrations, and anoxic sediments. These characteristics could explain the presence of Pyropheophytin-*a* (3,514 ng/g), Chl-*a* (298 ng/g), and Phaeophytin-*a* (618 ng/g) in the Great Pagoda core 11 and that of Pyropheophytin-*a* (169 ng/g) in the Oil Town core 3.

In the present study, of the nine pigments identified, five belong to the group of carotenoids: β -Carotene, Prasiinoxanthin, Zeaxanthin, Alloxanthin, and Diadinoxanthin. In the Gulf of California, carotenoid downward flux is

attributed to the predominance of Bacillariophyceae [14]. On the other hand, Van Dover [30] pointed out that diverse organisms that inhabit hydrothermal sites have the need to include carotenoid pigments in their diet, but they are unable to synthesize them. According to Nègre-Sadargues et al. [38], carotenoid pigments are obtained from bacteria, fungi, or plants. DeBevoise et al. [39] suggested that the carotenoids found in the crab eggs of *Bythograea thermydron* are produced in situ by chemoautotrophic bacteria present and are not derived from phytodetritus as one may expect.

β -Carotene is found in almost all algae except Cryptophytes and Rhodophyta and is produced by a large number of bacteria [36]. Its color is yellow, orange, or red and is the most abundant carotenoid in nature [27]. Nègre-Sadargues et al. [38] and DeBevoise et al. [39] identified this pigment as one of the factors responsible for the coloration of some crustaceans, such as *Bythograea thermydron* and *Rimicaris exoculata*, both abundant in hydrothermal vent sites of the Mid-Atlantic Ridge. β -Carotene was present in all the sediment cores recovered at Great Pagoda and Oil Town sites, where extensive bacterial mats of yellow, orange, and red colors were detected. Diadinoxanthin has a yellow coloration which is probably formed by the conversion of the final allylic group of neoxanthin, and Prasinolaxanthin is a dark pink pigment [36]. The main source of these pigments is the exoskeleton or the tissues of some species of macrocrustaceans or molluscs [22]. The sampled sites in GB probably involve a complex of chemoautotrophic bacterial consortiums capable of producing photosynthetic pigments [39–43].

Alloxanthin and Zeaxanthin are orange or yellow pigments that belong to the group of xanthophylls and are usually found in bacteria, algae, and higher plants or animals [36, 44]. The presence of Alloxanthin in our study can again be ascribed to the existence of complex bacterial consortiums and to the occurrence of some copepods (e.g., *Temora longicornis* and *Centropages hamatus*) that concentrate this pigment in their digestive system [44]. On the other hand, Zeaxanthin can be an indicator of picocyanobacteria and cyanobacteria abundantly embedded in old sediments [45]. Zeaxanthin does not have photoadaptive properties, so its concentration in a cell can be constant despite changes in light conditions. Besides, it is so stable that it is considered a useful biomarker, even when the site conditions are oligotrophic including ancient sediments [45].

Another possible mechanism for the production of pigments or degradation products occurs during the digestive process of some gastropods such as *Littorina littorea* [46] which is distributed in the intertidal zone of the North Atlantic coasts. Thus, it cannot be ruled out that the pigments identified in the study area have a similar origin in bacterivorous molluscs associated with hydrothermal vents such as *Provanna laevis* [13].

The processes of vertical distribution of phaeopigments in the ocean are not dismissed. Kalle [47] showed that seawater contains soluble pigments produced by phytoplankton metabolism. However, studies conducted by other authors [26, 33, 48–51] did not reveal whether these pigments can be accumulated at deep hydrothermal vents without altering

their structure. In GB, the $\delta^{13}\text{C}$ signature of TOC surficial sediments reveals depleted values (-32.0 ‰) for sulfur-rich sediments, while values are significantly enriched (-18.0 ‰) away from the vent, reflecting input of photosynthetic based carbon [13].

5. Conclusions

Free-living organisms are essential in hydrothermal systems for the production of pigments. They function as sinks of inorganic sulphides and reducing components and promote the production of organic carbon particles from inorganic carbon, by complex bacterial consortiums, zooplankters, and benthic organisms. The microorganisms inhabiting extreme thermal and chemical environments have a high diversity of metabolites and are essentially chemosynthetic. Although cores 11 and 10 were obtained from different zones, Great Pagoda and Oil Town, respectively, they both shared similar *Beggiatoa* spp. substrate mats. The same occurred in cores 1 and 3 from Great Pagoda and Oil Town, respectively, which presented large orange bacterial mats. Chl-*a* and its derivatives (Phaeophytin-*a*, Phaeophorbide-*a*, and Pyropheophytin-*a*) attained their highest concentration in core Great Pagoda 11, branded by its olive green color containing black large bacterial mats. The presence and concentration of the extracted pigments varied among sites. There were significant statistical differences in the concentrations of pigments between cores. The nine photosynthetic pigments analyzed in this study seem to be a common feature in the surface sediments of the GB hydrothermal vent system whose presence and concentration under extreme thermal and chemical conditions essentially relies on the metabolism of a diversity of the chemoautotrophic bacterial consortium.

Guaymas Basin hydrothermal vents are rich in organic matter, sulphur, carbonates, and silicate materials. The photosynthetic pigments accumulated in the surface sediments at venting sites of the GB hydrothermal system are essentially of chemoautotrophic bacterial origin.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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