Pergamon

Phys. Chem. Earth (B), Vol. 25, No. 1, pp. 1–8, 2000

1464-1909/00/$ - see front matter

PII: S1464-1909(99)00112-4

Hydrothermal Studies in the Aegean Sea

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Received 24 April 1998; accepted 9 July 1999

Abstract. The aims of the Aegean Hydrothermal Fluxes and Biological Production project were to estimate the fluxes of fluids, chemicals, heat and bacteria from hydrothermal vents, establish the controls on venting dynamics, measure the productivity in the region of the vents and establish the effect of the vents on biodiversity of both prokaryotes and eukaryotes. This paper presents an initial synthesis of the project results. Research was done both by land-based SCUBA diving and from several vessels at a number of active sites in the near-shore coastal regions of Milos and Kos, with some additional studies at Methana, Lesbos and Santorini. Vent water composition showed very large variations. This was due to the mixing, of hydrothermal reservoir fluids, vapour condensate and seawater altered by interactions of fluid-sediment-bacteria in different proportions, in the gasohydrothermal vents. The composition ranged from nearly sea water with only slightly reduced pH, to higher or lower salinity fluids with a pH as low as 3 and with large enrichments in heavy and trace metals. Phase separation was a common feature at these shallow vents. The dry gas phase was mainly CO_2, but with significant amounts of H_2S, CH_4 and H_2. These fluids commonly passed through soft sediments before venting from the seafloor and induced a convection cell of pore-water entrainment from deeper sediment layers into the water column with a consequent 're-charge' down-flow of seawater into the sediment around the vent outlets. Such complex conditions may well explain the high biodiversity of Bacteria, Archaea and epifaunal species surrounding the vents. As many as 44 % of the archaeal lineages detected were found to represent novel phyla. Epifaunal diversity was particularly high with over 200 species recorded at the shallower Milos vents. These vents may form a 'stepping-stone' for warmer water species to colonise the surrounding areas when water temperatures permit.

1. Introduction.

The subduction of the African plate below Europe has resulted in the formation of the Mediterranean Ridge and deep subduction basins as well as volcanism in the Hellenic Volcanic Arc and back-arc extension in the Aegean Sea (Dewey et al., 1989; Robertson and Grasso, 1995). Major hydrothermal systems are found along the Volcanic Arc at Methana, Sousaki, Milos, Santorini, Kos, Yali and Nisiros (Dando et al., 1999; Georgalas, 1962). Geothermal areas are also found in many coastal regions and islands around the edge of the Aegean, including the regions around the Antemus, Volvi-Langada, Strymon, Nestos-Xanthi and Alexandroupoli basins in the north, Lesbos in the east and the Gulf of Maliachos and Sperkios basins in the west (Dominico and Papastamatoki, 1975; Minissale, 1989; Vrouzi, 1985).

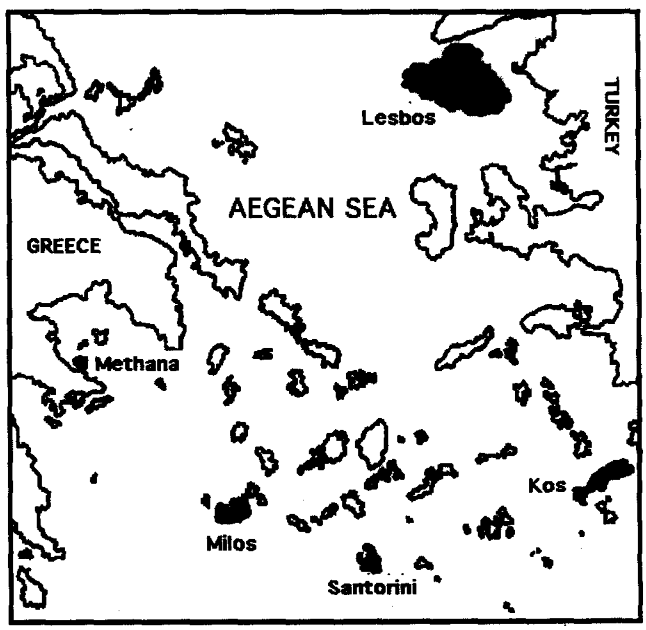

Fig. 1, The southern Aegean Sea showing those hydrothermal areas investigated (shaded) during the project

The areas studied in the current project are shown in Fig. 1. Previous studies in this area have recently been reviewed (Dando et al., 1999a). Most of the hydrothermal areas are

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concentrated on the Volcanic Arc where the submarine hydrothermal areas investigated so far are at relatively shallow depths (1 - 300 m water depth) with the issuing fluids mainly below 150 °C. One of the characteristics of volcanic arc hydrothermal systems is the large volume of gas released, both because of the degassing of the subducted slab as well as the mantle and also the thermal and chemical breakdown of marine sediments. Since most of the known venting is from shallow vents the resultant outlets are frequently of the gasohydrothermal type with high gas flow rates (Dando et al., 1995a). The major component of the gas is carbon dioxide, although significant amounts of other components, including hydrogen, methane, hydrogen sulphide, sulphur dioxide and nitrogen, can also be present. Stable isotope studies have confirmed that at some locations there is a magmatic contribution to the released gases (Botz et al., 1996; Nagao et al., 1991).

Milos, an island in the middle of the Volcanic Arc with some 35 km^2 of geothermally active seabed (Dando et al., 1995a), is one of the best studied hydrothermal areas in the Aegean, both because of an EC-funded comparison of geophysical methods to detect hydrothermal reservoirs (Fytikas, 1989 ; Fytikas et al., 1989) and because of studies on the biology and geochemistry of the area carried out as part of MAST-1 and MAST-2 projects (Botz, et al., 1996; Cronan and Varnavas, 1993; Dando, et al., 1995a; Dando et al., 1995b ; Dando et al., 1995c; Fitzsimons et al., 1997; Gamenick et al., 1998; Southward et al., 1997 ; Stüben, and Glasby, in press; Thiermann et al., 1997; Thiermann, Windoffer & Giere, 1994). During the latter project several expeditions were made to Palaeochori Bay on the south east coast of Milos, an easily accessible location with a great variety of hydrothermal vents. This Bay was chosen for many of the process and fine-scale studies during the present project. Additionally, several sites in Voudia Bay (NE Milos), Adamas Bay (Central Milos), other sites along the south coast of Milos as well as Paradise Beach and Brostherma in Kos and Methana were investigated by land-based SCUBA divers. Deeper coastal regions south off Milos and Kos as well as around Santorini were investigated using various vessels.

2. Results and Discussion.

2.1 Vent distribution, plumes and currents

Gasohydrothermal vent positions were located by a 33 kHz single-beam echo-sounder and accurately positioned using DGPS, allowing detailed vent maps to be produced for the Milos hydrothermal fields. SCUBA diving observations combined with those from echosounders showed that only a proportion of the outgassing vents, as few as 1 in 7, were detected by echosounder. Diffuse water vents were not detected by this method, but could be observed by divers (Robinson et al., 1997). To the S, SE and E of Milos, the strongly degassing vents were heterogenously scattered and were most probably concentrated at intensively fractured regions. For example, high venting activity was recorded along a graben-like structure E of Milos. Similarly, in Palaeochori Bay, the vent shapes delineated by white fluffy deposits were clearly related to fault lines. For Kos and Santorini, no vent maps were produced, but hydrothermal plumes were found which could be correlated to zones of faulting shown on the geological maps (Perissoratis, 1995; Triantafyllis, 1994).

Venting activity caused measurable changes in the chemical composition of the water column. The extent and magnitude of these changes were dependent on the chemical parameter used, since different vents or groups of vents differed in composition. Thus one should speak of e.g. a methane plume or silicate plume. Parameters used to detect plumes at Milos, Santorini and Kos were: pH, oxygen, dissolved Si, Rb, Ba, methane, hydrogen and, in some cases, metals such as Fe, Mn, Cu and Zn. In most cases, not all of these attributes occurred together. South of Palaeochori Bay two different types of plumes were found. There was a superficial plume extending some 4 - 6 km to the SW, characterised by slightly reduced pH and salinity, and increasing values of dissolved Si and Ba. The second type was a bottom plume of water, enriched in e.g. methane, 10 - 30 m above the seabed. Plume locations were not constant, probably due to differential venting activity and to the water currents which change seasonally.

During Meteor cruise 40/2 in December 1997, water samples were taken along a grid to the south and east of Milos from approximately 36° 54'N to 36° 39'N and from 24° 25'E to 24° 49'E. A plot of plume positions, which were superimposed onto a provisional bathymetric charts based on Hydrosweep data, indicated that most of the vents lay along an approximately E-W ridge and parallel valley system (Fig. 2). Vent areas were shown to be located along fault lines that have been well described for the island (Wetzenstein, 1972) and continue under the sea. Venting activity was most intense where these faults intercept. The main hydrothermal plume, plotted from methane anomalies, lay at approximately 100 m depth and did not extend into the main channel between Polyaigos and Pholegandros. South of Milos an E-W line of stations showed that the methane was exported in a plume at 70-90 m depth, westwards from the hydrothermal field. Within the plume regions, the enrichments in Li, Rb, Sr, Ba, Si were very

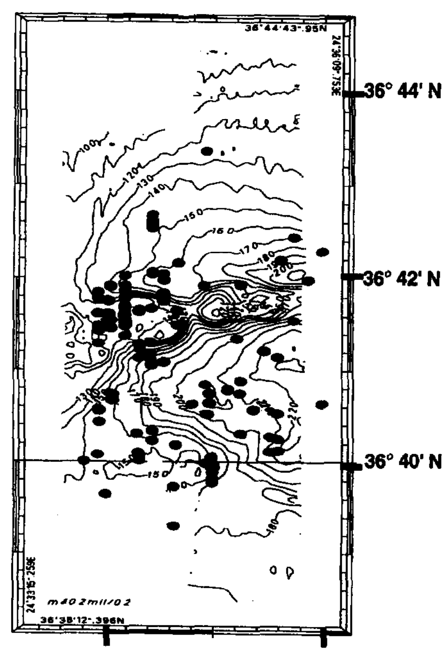

Fig.2., Area east of Milos showing vent positions, located by echosounding, (●) superimposed onto a provisional bathymetry chart based on Hydrosweep data.

weak, possibly due to a high sea water : hydrothermal fluid ratio in the fluids discharged from the vents.

Two current meter moorings were deployed 2 km offshore, in a water depth of 90 m to the SE of Milos (Fig. 3). One was located off Palaeochori Bay (mooring C), where vents are known to occur, and another off Provatas Bay (mooring A) 3.5 miles to the west, in an area presumed to be free from major vent influence. Data was collected for one year starting from June 1996. The currents were very variable during the year with the surface currents being directed predominantly southwards. Close to the bottom at mooring C, current velocities were low and variable, with the average transport in the summer being towards the SW.

At mooring A the variability was even greater, with a clockwise vortex in the lower water column. A general SW transport was evident in the layers down to 60 m depth, while deeper, a clockwise change in direction was recorded. The mean transport was towards the W at 70m, NW at 74m and N at 78m depth. Bottom water current measurements within Palaeochori Bay in September 1996 and June 1997 revealed a flow to the south (0 - 7 cm s^{-1}) over the main part of the Bay. At Spathi Point, the eastern boundary of the Bay, the flow was south easterly (mean velocity 2 cm s^{-1}).

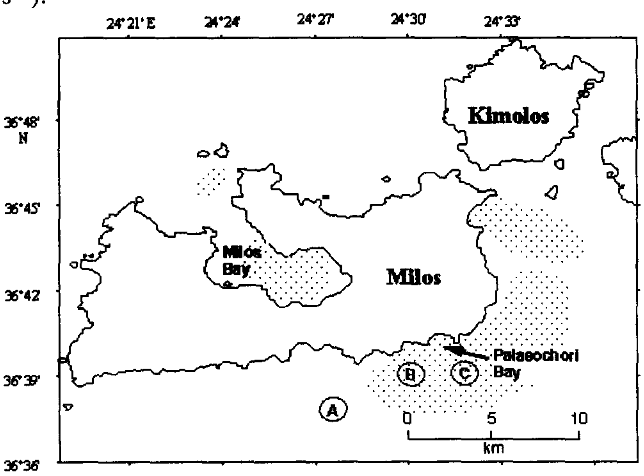

Fig. 3. Milos, showing the main submarine hydrothermal areas (dotted) and positions of current meter moorings and sediment trap positions.

South of Kos, water column profiles for dissolved methane were taken from 7 stations along a single north-south transect from 36°44.5'N to 36°34.5'N to locate possible venting. Methane maxima were found at depths ranging from 100 to 450 m. These methane anomalies are indicative of a previously unknown deep hydrothermal field to the south of the island and could not be explained by venting activity within the known coastal locations (Bardintzeff, 1989; Bianchi and Morri, 1983; Varnavas and Cronan, 1991).

Similar hydrothermal plume tracing within the caldera of Santorini showed very low methane concentrations (< 5 nM), both to the north and south of the channel between the Kameni Islands where known hydrothermal venting occurs. This agreed with the low methane content in the Kameni vents, from where a single gas sample from a vent was found to contain little methane (17 ppm). In contrast, at the northern entrance to the Caldera, 8 nM methane was found dissolved in water close to the bottom, suggesting active venting in this area. However, even higher dissolved methane concentrations (up to 20 nM) were found outside the Caldera at 100 - 150 m water depth, along the lines of known fracture zones. Such concentrations could not be explained by methane export from the Caldera and it is believed that this methane came from venting activity on the Santorini Slope.

2.2 Composition of venting fluids and fluid flows

A schematic geological section through Palaeochori Bay, from the shore southwards, is shown in Figure 4. The underlying rock is metamorphic, showing block movements along faults. It is overlain by marine and volcanoclastic sediments of varying thickness, consisting predominantly of sand with variable mud and gravel components. The permeability is locally highly variable. It ranges from the nearly impermeable, due to the formation of hydrothermal precipitates, to the highly permeable. The sediment grains are mostly chemically resistant minerals such as quartz, feldspar and mica, that are abundant in the underlying metamorphic rock.

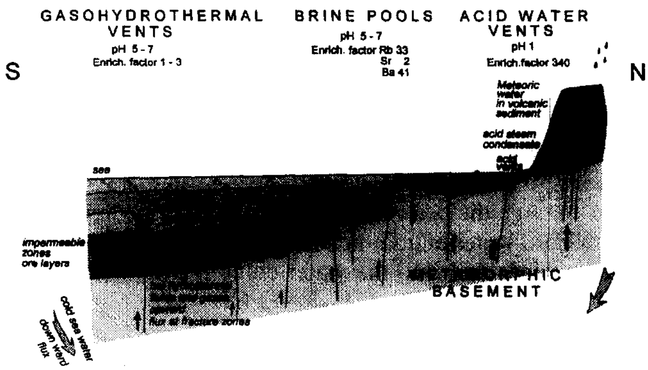

Fig. 4. Schematic diagram of the geothermal system in Palaeochori Bay, Milos

The fault zones serve as conduits for the hot, acidic and reducing fluids and gases from the geothermal system. These fluids percolated through the sediment and were discharged both diffusely, without visible vents, as well as from well-defined vent sites. The vents were often delineated by white and yellow fluffy mats and/or gas bubbles. Chemically, the vent fluids could be distinguished by higher or lower salinities than the ambient sea water. A clear trend of increasing concentrations of soluble elements and pH with decreasing vent depth could be shown within the inner part of Palaeochori Bay. Vents close to the shore showed up to 340-fold enrichments in Li, Rb, Sr, Ba, Si compared to ambient sea water. At deeper vents, enrichments only up to the three-fold sea water values were found. It is possible that as the thickness of sandy sediments increases, with increasing distance from the shore, the sub-surface mixing with seawater increases, thus decreasing the concentrations of these solutes in the fluid venting from the seabed. However, there may additionally be a primary decrease in solute content due to subsurface processes with increasing distance from the centre of the reservoir (Bischoff and Rosenbauer, 1989).

Three fluid sources could be distinguished by their acidity, chlorinity and enrichment of solute contents compared to ambient sea water. These were: 1. a magmatic source indicated by the presence of a mantle-derived He component (Botz et al., 1996; Nagao et al., 1991), 2. fluids showing seawater-rock interactions in the deeper crust and 3. fluids exhibiting fluid-sediment-bacterial interactions in the upper few dm of the sediment. The second source could be separated into three end members (Stüben and Glasby, in press): a highly saline brine, a low saline vapour phase and altered sea water. The exact origin of the latter is still somewhat unclear, it may well originate between sources 2 and 3. In the uppermost source 3, within the sediment, the hydrothermal fluids are mixed with entrained sea water in different ratios which leads to the large differences in the composition of fluids exiting the sediment. It is likely that the acidic fluids (pH 3) close to the shore contain some steam condensate which has seeped out of the sub-aerial sediment, where H_2S was oxidised to sulphuric acid. Complex redox reactions take place within the sediment due to mixing with cold, oxygenated sea water as well as to biological processes. The main mineral phases precipitated were Fe/Mn sulphides, arsenic sulphides, elemental sulphur, baryte and gypsum. These locally reduced the permeability of the sediment by cementation. Such changes in permeability may cause major local shifts in the position of vent outlets and in the shape of vent fields.

In-situ measurements of temperature, pH, redox-potential, H_2S and O_2 confirmed that the shallow vent sites were extreme environments with low pH, high sulphide and high temperature. Repeated measurements during three field trips to the same sites have demonstrated the stability of some of the vents over a two year period. The outflow of gas or hot water through the permeable sediment induces a convection cell of pore-water entrainment from deeper sediment layers to the surface and into the water column (Robinson et al., 1997). Nutrients, metals, H_2S and CO_2 were transported upward from the sediment by advective processes in the permeable vent surroundings. This outflow was compensated by an inflow of oxygen- rich water in a `recharge area´ at a certain distance from the centre of the vent (Fig. 5). These geochemical conditions were reflected in the type and structure of the precipitate or mat forming at the sediment surface and also in the geochemical zonation patterns, the distribution of micro-organisms and the metabolic activity in the sediment.

The mean water and gas flows from individual vent outlets were, respectively, 26.1 (range 0.7 to 124.3) and 8.1 (range 0.1 to 56.6) l h^{-1}, at Milos and 39.9 (range 4.8 to 96.0) and 16.4 (range 1.7 to 65.2) l h^{-1} at Kos, gas volumes being measured at STP. There was a large variation in flow rates both between and within sites as well as from the same vent at different times. It has not been possible to show a clear tidal periodicity in vent fluid fluxes by direct measurement, possibly because of the difficulty of measuring flows without disturbing the vent channels through the soft sediment. A major part of the water flux is due to water which has been entrained within the sediment by the escaping gas bubbles (O'Hara et al., 1995). Only a minor part of the vented water at gasohydrothermal outlets is hydrothermal fluid which has risen from the underlying reservoir.

The measurement of fluid flows and chemical fluxes is extremely complicated in shallow water gasohydrothermal vent fields. The sub-surface water entrainment (Fig. 5) is enhanced by the rising gas bubbles and any funnel system placed on top of a vent outlet to collect venting fluids may enclose part of the re-charge zone. In normal conditions vented water would be carried away by the current. In addition the low temperature of seawater boiling in shallow systems means that sub-surface boiling is common, indeed water even boils on the seafloor in areas of high heat flow. This results in phase separation and leaves a residual hydrothermal brine which diffuses through the sediment, discharging on the seafloor. Venting outlets have different temperatures and salinities and the exciting fluids therefore have very different densities so that simple buoyant plumes, as seen at mid-ocean ridge vents, are uncommon. For all these reasons flux estimates are difficult to achieve.

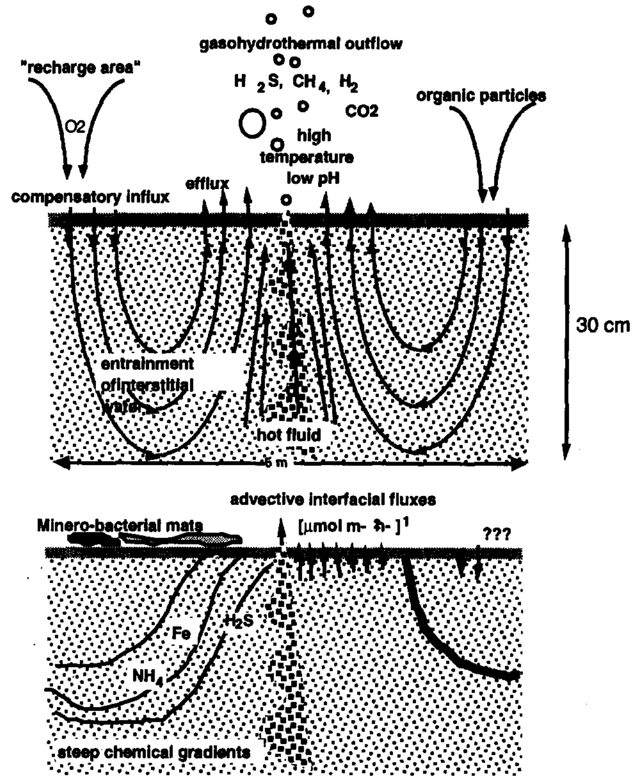

Fig. 5. Diagram of water entrainment and geochemical changes around vent outlets

Gas composition, as well as flow rate, was variable, both between sites and between vents. Fluids were collected by placing a funnel over a vent outlet and collecting the fluids in a polythene bag fitted with a tap inlet. The collected gases contained up to 95% CO_2, 9% H_2, 3% H_2S and 1.8% CH_4. Calculations of the number of vents in an area, average flow rate of fluids and their free and dissolved gas composition will enable us to estimate the global importance of the Aegean vents in geochemical budgets. Provisional estimates suggest that the total flux of CO_2 and CH_4 as free gas from the Milos submarine hydrothermal system may be 0.2-0.8 x 10^{11} moles yr^{-1} and 0.2-0.8 x 10^9 moles yr^{-1} respectively. This is, for Milos alone, approximately 10 % of the estimated global fluxes from the mid-Ocean ridges, 0.63-1.26 x 10^{12} moles yr^{-1} for CO_2 (Gerlach, 1989) and 4.9 x 10^9 for CH_4 (Welhan and Craig, 1983), suggesting that venting at volcanic arcs is important in the global geochemical cycle.

2.3 Time series studies.

The temperature of fluids from a given vent can be considered as a quasi-conservative tracer of the degree of mixing between the hydrothermal fluids and seawater and is highly correlated with chemical parameters such as sulphide and salinity (Johnson, Childress and Beehler, 1988). Temperature logger records were obtained from vent sites off Methana (Dando, et al., 1999a), Milos (Aliani et al., 1998a), Kos and Lesbos. The longest continuous records cover an approximately 8.5 month period between September 1996 and June 1997. By correlating these with synoptic measurements of bottom pressure (Aliani et al., 1998a), it was possible to demonstrate that the four main tidal components were the major determinants of temperature variation. The exact way in which changes in water level cause fluctuations in vent temperature is still uncertain but may be due to changes in the free gas volume of the system which would directly affect water flow. Episodic events were also noted and these ranged from those affecting the entire hydrothermal system, for example the 1992 earthquake south of Milos (Dando et al., 1995c), to those affecting a single vent outlet (Aliani, et al., 1998a). Records from a hydrothermal spring on Lesbos additionally revealed a clear lunar monthly periodicity as well as diurnal and semi-diurnal fluctuations.

A seismic network of three-component digital stations was installed in the area of Milos during the summers of 1996 and 1997 and in Kos during September 1997. During 1996 the seismic stations were on triggering mode and recorded 400 local micro-earthquakes, 300 regional earthquakes and 500 hydrothermal signals (with spectral peaks of 1-5 Hz, depending on the station). The seismicity pattern of the area, as inferred from the earthquake catalogue for Greece (Makropoulos and Burton, 1981), revealed low seismicity, mainly with intermediate depth earthquakes. The same picture was observed during 1996, seismicity was mainly characterised by micro-earthquakes, which are most probably associated with the existing hydrothermal field of the area. Spectral analysis on selected hydrothermal signals revealed high values of energy density around 2-3 Hz, which is characteristic of variable fluid flow rates. The peak of frequency was characteristic for each station, showing that it was a local phenomenon. Qualitative analysis of the occurrence of micro-earthquakes and hydrothermal signals showed that the absence of micro-earthquakes was generally related to absence of hydrothermal signals. A peak value of bottom water pressure coincided with a high concentration of micro-earthquakes and hydrothermal signals.

2.4 Photosynthesis and respiration.

Higher photosynthetic rates than normal have been reported in the vicinity of shallow water hydrothermal vents, due to the release of nutrients such as phosphate and ammonia, although rates directly over the vents may be depressed due to the high concentrations of hydrogen sulphide and metals (Gerlach, 1989; Tarasov et al., 1999; Tarasov et al., 1990). However, in studies off Milos, the oligotrophic nature of the Aegean Sea was corroborated (Robinson et al., 1997) with measured plankton photosynthetic rates of <1 mmol O_2 m^{-3} d^{-1} and chlorophyll concentrations less than 0.14 mg m^{-3}. An exception to this were high photosynthetic rates (up to 26 mmol O_2 m^{-3} d^{-1}) measured on bottom water samples at two vent sites. These are believed to be due to resuspension of an active benthic algal mat, dense diatom deposits have been reported from the vicinity of the brine seeps in Palaeochori Bay (Dando, et al., 1995c; Fitzsimons et al., 1997). Photosynthesis rates up to 31 mmol O_2 m^{-2} d^{-1} were found in the sediment around the vents.

Respiration rates around Milos ranged from 1 to 4 mmol O_2 m^{-3} d^{-1} (Robinson et al., 1997). The range in photosynthetic and respiration rates was not directly linked with the presence or absence of visible venting of fluids or the concentration of dissolved inorganic carbon, which ranged from 2300 mmol m^{-3} at a non-venting site to 2500 mmol m^{-3} at a venting site. The temperature of the Palaeochori Bay water samples had only a small effect on plankton photosynthesis, with the optimum temperature for photosynthesis occurring very close to the *in situ* temperature. This may be an artefact of the very low rates of photosynthesis, or be due to the photosynthetic rates being more strongly limited by light at the higher temperatures. In contrast, small changes in temperature (≤ 2°C) had a profound effect on the respiration rate (oxygen consumption rate) of the microplankton, with calculated temperature coefficients, i.e. the relative rate increase with a 10°C rise in temperature, Q_{10}, being higher than the conventional value of 2, for plankton respiration.

2.5 Particulates and sediment trap studies.

Analyses of bottom water samples, taken with a small bottom water sampler equipped with a particle camera, showed higher values of particulate material as well as phytoplankton and zooplankton in June 1997 than in September 1996. Bottom water samples were enriched, in terms of particulate organic carbon and nitrogen, total particulates and chlorophyll, down-current (southwards) from the active vent areas. These components must be exported from the Bay in the observed bottom water current.

The suspended particulate matter (SPM) from venting waters, collected by SCUBA divers, was analysed for Fe, Mn, Cu, Pb, Al, Ba, Sr, Ca, Si and Li. In Palaeochori Bay, Milos, particulate Si and Cd increased in waters of low conductivity, while Ba increased in vents with high fluid flows. Gas/water flow ratios were elevated in the vents of low pH while there was a rise in the suspended particulate matter (SPM) and particulate Si with increasing pH. Both SPM, Fe, Al, Cu, Pb, Cd and Ba decreased with increasing water temperature. In contrast, Si tended to increase with increasing vent temperature. In Voudia Bay, Ba values were high, when compared to all other submarine hydrothermal vents off Milos, while average particulate Si was lower, compared to the vents of Palaeochori Bay. Time series analysis of SPM filtered from vent water samples, collected at intervals over a 4-day period by SCUBA divers from representative vent outlets in Palaeochori Bay, using inverted funnels, during June 1997, showed that the diurnal variation in the element SPM concentrations varied from one vent to another.

Sediment traps were attached to the current meter moorings *A* and *C* to measure particulate fluxes at 60 m over a bottom of 90 m depth. The vertical particulate fluxes were integrated over periods of 12 days. Currents at the trap depth rarely reached 5-10 cm s^{-1}. Vertical mass fluxes were extremely variable at both sites, ranging from 7 to 5900 mg m^2 d^{-1}, with mean mass fluxes over one order of magnitude higher at the vent site, increasing to as much as 200 times higher during periods of maximum mass flux

(Miquel et al., 1998). Carbon and nitrogen fluxes in the collected material showed similar patterns, whereas the accumulation of chlorophyll showed a completely different variability over time. Large pulsed fluxes of particulate organic matter were observed in the summer at the vent site (C) and these were due to large numbers of faecal pellets settling into the traps.

Total bacterial counts of the sediment trap samples showed large fluctuations in the flux of bacteria, correlating quite well with total particulates. Fluxes of bacteria were, in general, one order of magnitude higher at sediment trap station C. Nevertheless the amount of carbon transported in form of bacterial biomass was a minor part of the total flux.

The white mats around the vents in Palaeochori Bay were analysed for their chemical composition. The major components of fresh mats were sulphur (up to 50 - 80 % of the total dry weight) and silica, the composition varying with time and with site. In addition the mats concentrated heavy metals, including Hg (up to 1.1 mg g^{-1} dry weight). In the course of a few days, sulphur declined relative to silica and a substantial amount of inorganic detritus collected. It is probable that the tight web of the mats acts as a filter, retaining hydrothermal components and causing them to precipitate along the sharp redox gradient within the 1-2 cm thick mat. The mats are easily swept away by strong bottom currents, so that much of the hydrothermal export from shallow sites is discontinuous as has been found in sediment trap studies south of Milos (Miquel et al., 1988). The formation and alteration of these precipitates, as well as the quantity and the distribution of exported material from the vent sites, is the subject of ongoing investigations..

2.6 Biodiversity.

Studies of the diversity of Bacteria and Archaea at vent and control sites are being undertaken by both culture and culture-independent techniques (nucleic acid extraction from sediments with PCR-amplification and cloning or fingerprinting of the bacterial communities by denaturing gradient gel electrophoresis (DGGE), Muyzer et al., 1993). The results obtained by DGGE-analysis indicate that the different physicochemically characterized zones around a vent site were inhabited by distinct bacterial populations. DGGE-analysis also revealed that Bacteria from the subphylum *Cytophaga*, which are known to be degraders of polysaccharides such as cellulose or starch, constitute an important part of the microbial community. Possible sources of polysaccharides could be the fragments of seagrass which form meadows in the bay of Palaeochori. All of the 10 isolates of sulphur-oxidising bacteria obtained appear to be obligate chemolithoautotrophs. Phylogenetically two of them belonged to the sulphur-oxidising genus *Thiomicrospira*, one had a similarity of 93 % of the 16S rDNA sequence to *Thiobacillus hydrothermalis* (Durand et al., 1993), and the others may represent new species or genera. *Thiomicrospira* spp. were found to be important members of the bacterial community by cultivation-based techniques and culture-independent techniques, i.e. DGGE analysis. This is in accordance with studies carried out at deep-sea hydrothermal vents (Muyzer et al., 1995). A new thermophilic sulphate-reducing bacterium most closely related to *Desulfacinum infernum* (Rees et al., 1995) was isolated from sediments close to the vent centre. In addition, a new *Chlorobium* species with 95 % similarity of the 16S rDNA sequence to *Chlorobium vibrioforme* was isolated. However, their low numbers suggests that while these bacteria were present they did not play a significant role in this environment.

Besides the novel genus *Stetteria* that has been described previously (Jochimsen et al., 1997), 35 cultures of hyperthermophiles were isolated. Among these were a new genus belonging to the order Thermococcales and new species of *Pyrococcus*, *Thermococcus* and *Staphylothermus*. Of 20 isolates characterised by the sequencing of 16S rRNA and DNA-DNA-hybridization, 10 were similar to *Staphylothermus* and 3 to *Pyrococcus*. 30 additional hyperthermophilic isolates were obtained from samples taken during a field trip in September 1996.and are currently being characterised. No aerobic hyperthermophiles or thermophiles could be detected, although 80 mesophilic aerobic strains were isolated. 39 of these aerobes were spore-forming Bacteria, suggesting that spore formation may enable the bacteria to survive in unfavourable conditions in these rapidly-changing conditions. One of the spore forming isolates will be described as a new genus that is related to *Bacillus*.

DNA, extracted from hot sediments and from sediment trap material, was analysed by PCR and sequencing for the 16S rRNA genes of the archaeal microbial communities. Two clusters of related clones were obtained. The first group was related to the Crenarchaeota "*Thermodiscus maritimus*" and "*Aeropyrum pernix*". The second group clustered around the species *Staphylothermus marinus*, *Stetteria hydrogenophila* and *Desulfurococcus mobilis*, which are all members of the family of Desulfurococcaceae. One clone obtained represented a novel phylogenetic lineage related to Desulfurococcaceae. Our studies identified members of this family as the dominant archaeal group present in the hot sediment. All the clones showed less than 97% sequence similarity to cultivated species. At the sediment trap C, DNA was extracted from material collected over a 12 day period. The clones obtained by PCR again clustered within the *Staphylothermus/Stetteria*- group, again confirming that members of the family Desulfurococcaceae are the dominant archaeal species at the hot vents in this part of the Aegean Sea.

Most microorganisms inhabiting the white mineral precipitate surrounding many of the vent sites were shown, by applying fluorescent *in situ* hybridisation, to be Bacteria. Archaea could not be detected with the oligonucleotide probe used. Over 90 % of the total counts obtained with DAPI-staining were detected with an oligonucleotide probe specific for the bacterial domain, indicating that they were physiologically active. The dominant morphotype in the white mineral precipitate was shown, by the application of a genus-specific oligonucleotide probe, to belong to the genus *Arcobacter* . This organism may play a role in the deposition of sulphur in the white 'precipitate', as has been described previously by Taylor and Wirsen (1997).

Surface sediments around low temperature vents at the lander sites at 46-47 m depth off Palaeochori contained giant sulphur-oxidising bacteria, including *Achromatium volutans* and *Thioploca* sp., both of which were grown in microcosms in the laboratory and observed using time-lapse video photography. These bacteria moved within the sediment along sulphide-oxygen gradients (Dando et al., 1998).

The seagrasses *Cymodocea nodosa* (Ucria) Ascherson and *Posidonia oceanica* (L.) Delile formed extensive meadows in Palaeochori Bay, but only the former lived in close proximity to actively venting sites and brine seepage areas (Aliani et al., 1998b). Sessile epifauna was sampled at six sites off the SE coast of Milos at depths between 2 and 90 m by a variety of methods including SCUBA diving, box corers, collection of fouling organisms on moored instruments and from photographs. A total of 211 species (or varieties) belonging to seven higher taxa was found: poriferans (24), cnidarians (32), molluscs (8), serpuloidean polychaetes (33), bryozoans (89), brachiopods (4), and ascidians (21) (Bianchi et al., in press). These groups were differentialy represented, in terms of the relative number of species, in the six sampling sites with the highest number of species (122) coming from the deepest sites at areas of low temperature venting. Cumulative plots of the number of species against the number of samples from each site (11-20) indicated that each area was adequately sampled. The proximity of the sampled site to the vents appeared to correlate positively with high epifaunal biodiversity. Although there are no comparable inventories of marine sessile epifauna in the Aegean, the high number of species found with a relatively low sampling effort in a restricted area indicates that the marine biodiversity of the region is not as low as traditionally believed (Fredj et al., 1992).

The cover of epibenthic communities was severely reduced only in the close proximity of vents and the larger-scale effects of vents were not detected (Cocito et al., 1999). However, a general warm-water affinity was recognisable in both algal (Sartoni and De Biasi, in press) and animal dominated communities, which may be related to higher winter temperature in the vent area. Epifaunal communities under overhangs were composed of distinct groups of suspension feeders in vent and non-vent sites: this might indicate differences in trophic conditions. Mounds of the bioconstructional coralline alga *Mesophyllum lichenoides* were conspicuous only at vent sites, thus suggesting enhanced biodeposition of carbonates due to vent activity.

No obligate vent species were noted at Milos in the epifauna, in agreement with previous observations on the infauna (Dando et al., 1995c; Thiermann et al., 1997). The deep-burrowing decapod shrimp *Callianassa truncata* concentrated at the fringe of the vent systems with abundances 20-fold greater than in the surrounding area. The sediment temperature in this distinct zone was 40-60 °C. Although not a specialised vent organism this species seems to take advantage of the extreme conditions in this sedimentary environment.

3. Conclusions.

Although the aim of this project was not to systematically survey the Hellenic Volcanic Arc for sites of hydrothermal venting it is clear from preliminary studies of the unexpectedly and newly found active sites that hydrothermal venting is even more extensive than was previously believed. We now have a clearer understanding of the factors influencing the distribution of hydrothermal plumes from these shallow vents. The detailed mapping, together with flow measurements and chemical composition of the fluids and the results of water column analysis, allows us to make an initial assessment of the importance of these vents in chemical inputs into the Aegean Sea.

It is already clear that the circulation of seawater through the sediment, caused by the venting, is an important process in the sedimented areas, resulting in steep chemical gradients in both chemical and biological parameters and important interactions between bacteria and chemicals which greatly modify the output from the vents into the water column. Although estimates of overall fluxes are still being calculated it is clear that gas fluxes are at a level which is important on a global scale and metal fluxes are of regional importance. Photosynthetic rates in the water column do not appear to be enhanced by the venting and it may be that much of the photosynthetic productivity, at least in the shallow water sites south of Milos, is due to the seagrass meadows and carbon from this source may be a major input to the heterotrophic bacteria surrounding the vents. Particulate organic matter fluxes to the bottom were exceptionally high for short periods in the vent area compared to the control area, due to the fallout of faecal pellets. However the exact contribution which bacterial productivity at the vents makes to zooplankton production is currently unclear.

The diversity of microbial species, at the vent sites studied in detail, was large, with a high percentage of new taxa being found. Some of these new taxa are expected to be of biotechnological potential. Epifaunal diversity was also surprisingly high although, in agreement with preliminary studies, no vent-specific species were found. The discovery of several exotic thermophilic species around the vents suggests that the biota at vent sites in the Mediterranean can be used to predict changes in the ecosystem which may occur as a result of rising sea temperatures.

Acknowledgements. We acknowledge part-funding for this study from the EC under contract number MAS3-CT95-0021, support for *Meteor* cruise 40/2 from the German Ministry of Science, Research and Technology and the German Science Foundation, support for the studies on thermophilic bacteria from Fonds der Chemischen Industrie and equipment grants from the Royal Society. Thanks are due to the Greek Ministry of Culture for diving permission to undertake these studies, the National Meteorological Organization of Greece for providing meteorological data and to the University of Patras group for the logistical organisation. We wish to express especial thanks to all the scientists, divers, dive co-ordinators and ships crews who have participated in this project and made the collection of these results possible. Our thanks are due to Dr. B. Murton, Prof. A. H. F. Robertson and Prof. A. J. Southward for their helpful suggestions on improving the manuscript. The IAEA Marine Environment Laboratory operates under an agreement between the International Atomic Energy Agency and the Government of the Principality of Monaco.

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