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# Plankton gross production and respiration in the shallow water hydrothermal systems of Milos, Aegean Sea

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**Abstract.** Plankton gross production, net community production and dark community respiration were measured at coastal sites around the island of Milos, Aegean Sea, during June and September 1996 and June 1997. Sampling sites were chosen to include those with and without visible signs of hydrothermal activity. Plankton gross production ranged from undetectable (<0.3 mmol $O_2$ $m^{-3}$ $day^{-1}$) to 3 mmol $O_2$ $m^{-3}$ $day^{-1}$; respiration rates ranged from 1 to 6 mmol $O_2$ $m^{-3}$ $day^{-1}$. No significant difference was found between gross production or respiration rates measured at hydrothermally active areas and gross production or respiration rates measured at non-venting areas. The dissolved inorganic carbon concentration varied by ~200 mmol C $m^{-3}$ between venting and non-venting sites. Temperature had a pronounced stimulatory effect on the rate of plankton dark community respiration. The $T_{opt}$ for plankton dark community respiration always lay above the highest incubation temperature of 30°C (i.e. >6°C above *in situ* temperature). Temperature had less of a stimulatory effect on the rate of gross production.

## Introduction

The distribution of plankton biomass and production has been sparsely studied in the oligotrophic eastern Mediterranean Sea. Early estimates of primary production [cited in (Dugdale and Wilkerson, 1988)] average 25.2 g C $m^{-2}$ $year^{-1}$ (~6 mmol C $m^{-2}$ $day^{-1}$) for the estimated $1.8 \times 10^{11}$ $m^2$ of Aegean Sea. Antoine *et al*. derived annual means of sea surface chlorophyll (Chl) and production from coastal zone color scanner (CZCS) data of 0.28 mg Chl $m^{-3}$ and 0.385 g C $m^{-2}$ $day^{-1}$ (32 mmol C $m^{-2}$ $day^{-1}$), respectively, for the Aegean Sea (Antoine *et al*., 1995). Results currently emerging from the Mediterranean Targeted Project (CEC/MAST-MTP) support the view that the Aegean Sea is one of the most oligotrophic regions of the world (Ignatiades, 1998), that increased oligotrophy is linked to an increased ratio of heterotrophic to autotrophic production (Estrada and Lykousis, 1998) and that the region is very sensitive to anthropogenic disturbance (Balopoulos *et al.*, 1998). Tourism is a significant source of revenue in the Aegean, and hence seasonal and inter-annual measurements of microbial processes, which may relate to water quality and fish production, are of socio-economic as well as scientific value.

The Hellenic volcanic arc in the Aegean Sea is a site of active hydrothermalism (Holm, 1988; Bardintzeff *et al*., 1989; Dando *et al*., 1995). Submarine vents release gases and liquids rich in carbon dioxide, hydrogen, methane, hydrogen sulphide, sulphur dioxide, metals such as iron, manganese, copper and zinc, and dissolved lithium, barium, silicate and rubinium (Dando *et al*., 1999). The island of Milos is one of the most studied hydrothermal areas in the region. Coastal submarine gasohydrothermal vent sites with high gas evasion rates (up to

20 $dm^3$ $h^{-1}$ of 92% carbon dioxide) can be easily located by echo-sounders (Dando *et al*., 1995), while vents with diffuse liquid flow can be observed by divers (Robinson *et al*., 1997). Shallow water vent activity is clearly related to fault lines and can be delineated from the water surface by white and yellow benthic silicate- and sulphur-rich mats and/or gas bubbles. While the benthic biology, microbiology and geochemistry of shallow hydrothermal vents have received much scientific attention [e.g. (Botz *et al*., 1996; Fitzsimons *et al*., 1997; Southward *et al*., 1997; Thiermann *et al*., 1997; Dando *et al.*, 1998; Gamenick *et al*., 1998; Morri *et al*., 1999)], there are relatively few studies on the ecology of plankton communities in hydrothermal environments (Tarasov *et al.*, 1990; Acosta Pomar and Giuffrè, 1996; Sorokin *et al*., 1998; Tarasov *et al*., 1999).

The waters of shallow gasohydrothermal regions may be enriched with nutrients (e.g. phosphate) and trace metals (Sedwick and Stuben, 1996; Dando *et al.*, 1999), which may stimulate microbial processes; they may be acidic, have low salinity or be enriched with heavy metals (Sedwick and Stuben, 1996), which may inhibit some microbial processes, and they may be enriched with reduced sulphur compounds, methane and hydrogen gases (Dando *et al*., 1995), which may shift the microbial population to one dominated by chemosynthetic organisms (Sorokin *et al*., 1998). Tarasov *et al.* described high rates of planktonic and benthic production in the stable hydrothermally influenced waters of the crater of the Ushishir Volcano in the Pacific Ocean (Tarasov *et al.*, 1990). Sorokin *et al*. report significant stimulatory and inhibitory effects on microplankton photosynthesis and bacterial chemosynthesis in shallow hydrothermal areas compared with adjacent waters away from hydrothermal influence (Sorokin *et al*., 1998). However, since different vents or groups of vents can vary dramatically in their chemical signature due to the geology, hydrography and geochemistry of the specific area, such measurable effects may not be universal. Recently, Tarasov *et al*. suggested that pronounced changes in plankton activity due to hydrothermalism may only occur in areas which are largely isolated from the open sea (Tarasov *et al*., 1999).

Temperature is an important regulator of plankton metabolic activity, and any differential sensitivity of gross production and respiration to temperature will be critical in determining community structure and carbon flow [(Robinson and Williams, 1993) and references therein]. Sediment temperatures around the Milos vents range from ambient (~23°C) to 110°C (Dando *et al*., 1995), hence the opportunity exists to investigate the response of plankton gross production and respiration in these hydrothermal areas to changes in temperature.

This paper describes research undertaken during three 2-week visits to Milos, Aegean Sea, to determine the effect of hydrothermal venting and temperature changes on plankton gross production and respiration. The present study forms part of the MAST-3 project 'Hydrothermal Fluxes and Biological Production in the Aegean Sea'. Concomitant studies determined the chemical composition of venting fluids and gases, sediment biogeochemistry (Ziebis *et al*., submitted), sediment bacterial diversity and distribution (Dando *et al*., 1998; Sievert *et al*., 1999), and the effects of hydrothermalism on benthic algal and bacterial production (Wenzhofer *et al*., 2000).

## Method

### *Sampling stations*

Sample areas were chosen to represent regions of visible venting of both gas bubbles and hydrothermal fluids (Palaeochori Bay and Voudia Bay), and areas with no visible evidence of venting (Provatas Bay, Flakopis Bay and Ag Ioannou Bay) (Figure 1).

Within a particular venting area, water samples were collected in the vicinity of visible venting loci to assess the vertical and horizontal extent of hydrothermal impact.

### *Sampling*

Bulk water samples were collected either by opening a polypropylene aspirator at the sea surface or by a hand-operated diaphragm pump operated within a small boat whilst the inlet hose was positioned at specific depths by divers.

### *Temperature, salinity, particulate organic carbon, particulate organic nitrogen, chlorophyll* a*, pH*

*In situ* water temperature was measured by a thermistor incorporated in a dive timer. Water temperature immediately after sampling was determined with a hand-held thermometer (Digitron Model T208) and sediment temperatures were

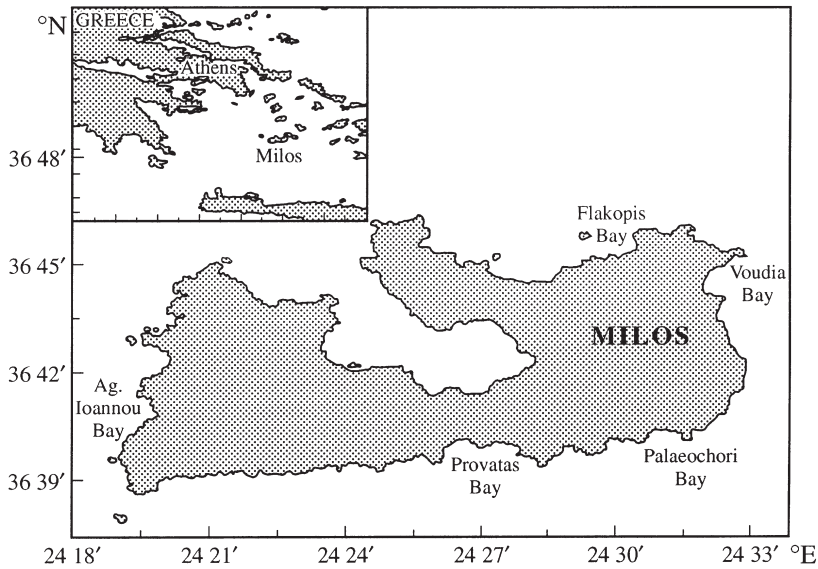


**Fig. 1.** Map of the sampling areas around the coast of Milos. The inset shows the position of Milos in the Aegean Sea.

measured with submersible hand-held temperature probes. Salinity was measured with an 'Autosal' salinometer. Samples for analysis of particulate organic carbon (POC) and nitrogen (PON) (3–8 $dm^3$) were filtered through 25 mm pre-combusted (500°C for 3 h) GF/F filters, dried overnight at 40°C and stored over silica gel for later analysis. The mean SD of duplicate samples was 1.1 mmol C $m^{-3}$ and 0.11 mmol N $m^{-3}$. Chlorophyll *a* samples (3–8 $dm^3$) were filtered through 47 mm GF/F filters and frozen. On return to the UK, phytopigments were extracted in neutralized 90% acetone and measured fluorometrically. The mean SD of duplicate samples was 0.01 mg Chl *a* $m^{-3}$. pH was measured potentiometrically using an Orion Ross combination pH electrode and automatic temperature compensation probe fitted to an Orion EA940 ion analyser calibrated with proprietary NBS buffers (pH 4.00, 7.00 and 10.00) (Sigma). The $pH_{NBS}$ determinations made in the field were converted to the $pH_{Total}$ scale using concomitant spectrophotometric measurements of $[H^+]_{Total}$ and potentiometric measurements of $\{H^+\}$ undertaken in the laboratory to calculate the conversion factor $f_{H+}$.

*Dissolved oxygen and dissolved inorganic carbon*

Water samples for analysis of dissolved oxygen and dissolved inorganic carbon (DIC) were siphoned into acid-washed 125 $cm^3$ borosilicate glass bottles using silicon tubing. Measurements of dissolved oxygen were made with an automated Winkler titration system developed from that described in Williams and Jenkinson (Williams and Jenkinson, 1982); DIC was measured by coulometric titration (Robinson and Williams, 1991; Dickson and Goyet, 1994). Analysis of seawater DIC reference materials certified at 1995.19 ± 0.7 μmol C $kg^{-1}$ during the fieldwork (mean = 1995.48 ± 4.4 μmol C $kg^{-1}$; $n = 10$) provides an indication of the long-term precision and accuracy of the DIC measurements.

*Gross production, net community production and dark community respiration*

Water samples for the determination of plankton rate processes were collected and incubated *in situ*. A productivity 'rig' was constructed from a weight connected to a surface buoy. Acid-washed 125 $cm^3$ borosilicate glass bottles filled with deionized water were clipped to perspex racks, which were attached to the rig at each of four depths. This rig was deployed at the sampling site from an inflatable boat. The deionized water was siphoned out of the sample bottles at the requisite depth by divers using a 60 $cm^3$ syringe and silicon tubing. Preliminary experiments confirmed that the deionized water was completely replaced with sea water after 5–6 syringe volumes. Samples to be analysed for initial dissolved oxygen and DIC concentration were returned to the boat to be fixed. Samples to be incubated in the light were left on the rig at the sampling depth, while samples to be incubated in the dark were enclosed in an opaque bag within a mesh bag and suspended from another buoyed weight close to the productivity rig. After 24 h, the incubated samples were recovered and the samples fixed and stored underwater prior to analysis (within 24 h).

Weather, dive permission and logistical constraints precluded the deployment of a 24 h *in situ* rig at some sites. On these occasions, samples were incubated under simulated *in situ* conditions at 3 m water depth in transparent and opaque perspex incubators.

Net community production (NCP) was defined as the net change in oxygen and DIC in the 'light' bottles, dark community respiration (DCR) as the decrease in oxygen and increase in DIC in the 'dark' bottles, and gross production (GP) as the difference in oxygen and DIC concentration between the means of the 'light' and 'dark' bottles. All rates are presented as mmol $m^{-3}$ $day^{-1}$ ± SE. The mean of the SEs of NCP and DCR derived from dissolved oxygen flux was 0.8 mmol $O_2$ $m^{-3}$ $day^{-1}$.

*Temperature response of plankton metabolism*

A bulk water sample was collected using a hand-operated diaphragm pump. This was then siphoned into 54 × 150 $cm^3$ borosilicate glass bottles. Six sample bottles were fixed immediately for measurement of 'zero' time oxygen concentration, and the remainder were placed in temperature gradient incubators (one 12 h light:12 h dark, one 24 h dark) for 24 h. Each incubator consisted of an aluminium block into which had been bored 24 holes for the sample bottles in a matrix of 6 × 4. The blocks were cooled at one end and heated at the other to achieve a temperature gradient along the length, which covered a temperature range of >10°C with *in situ* temperature at approximately mid-range. The samples in the light incubator experienced a constant irradiance of 50 μmol $m^{-2}$ $s^{-1}$, provided by fluorescent tubes (Thorn, F18135) (Lefèvre *et al*., 1994). After 24 h, the samples were fixed and analysed for oxygen concentration. NCP and DCR could then be calculated at each of 24 temperatures.

Gross production is conventionally calculated by subtracting community respiration from net community production. However, as it was not possible to obtain identical temperature gradients in the two gradient blocks, this approach could not be used. An alternative procedure, as outlined in Lefèvre *et al.* (Lefèvre *et al*., 1994), was adopted. Second-order polynomial equations were derived to describe the DCR versus temperature and NCP versus temperature data. The constants for gross production were then calculated as the difference between the two polynomial equations.

A number of time series–temperature gradient experiments were also undertaken in order to check the linearity of respiration rate with time at different incubation temperatures. Production and respiration rates measured during the temperature gradient experiments are reported as μmol $kg^{-1}$ $day^{-1}$ in order to eliminate artefacts due to temperature:volume changes. The temperature coefficient ($Q_{10}$) of dark community respiration was estimated from the slope (activation energy $E_a$/gas constant $R$) of an Arrhenius plot of $\log_e$ respiration rate against the reciprocal of absolute temperature as described in Raven and Geider (Raven and Geider, 1988) and discussed in Robinson and Williams (Robinson and Williams, 1993).

## Results

*Site descriptions*

Station W2 (36°40.356′N, 24°31.093′E) in Palaeochori Bay (SE Milos; Figure 1) was chosen as the main 'vent' site. The sediment/sand lay below 9.4 m water depth and was covered in a T-shaped mat of white, yellow and orange coloration, surrounded by other white mats and sea grass beds. This sediment coloration, mat shape and position were remarkably consistent between sampling occasions (June 1996–September 1996–June 1997) and were visible from the sea surface (Figure 2).

Numerous vents ejected gas bubbles, which did not dissolve completely before reaching the water surface. In September 1996, the surface water temperature was 23°C, salinity lay between 38.7 and 38.8, and sediment temperatures were between 80 and 110°C. Chlorophyll *a* concentrations ranged from 0.06 to 0.14 mg $m^{-3}$, POC concentration from 5.5 to 13 mmol C $m^{-3}$, PON from 0.5 to 0.9 mmol N $m^{-3}$ and DIC from 2370 to 2400 mmol C $m^{-3}$. In June 1997, the surface water temperature was 24°C, Chl *a* ranged from 0.04 to 0.14 mg $m^{-3}$, POC concentration ranged from 6.9 to 11.6 mmol C $m^{-3}$, PON concentration ranged from 0.6 to 1 mmol N $m^{-3}$, and DIC concentration varied between 2350 mmol C $m^{-3}$ at the surface and 2490 mmol C $m^{-3}$ just above the sediment. Horizontal visibility was >10 m with a visible 'haze' above some vents where venting liquid mixed with ambient sea water. The $pH_{Total}$ of water samples collected within a few centimetres of the active vents ranged from only slightly acidic to slightly alkaline with

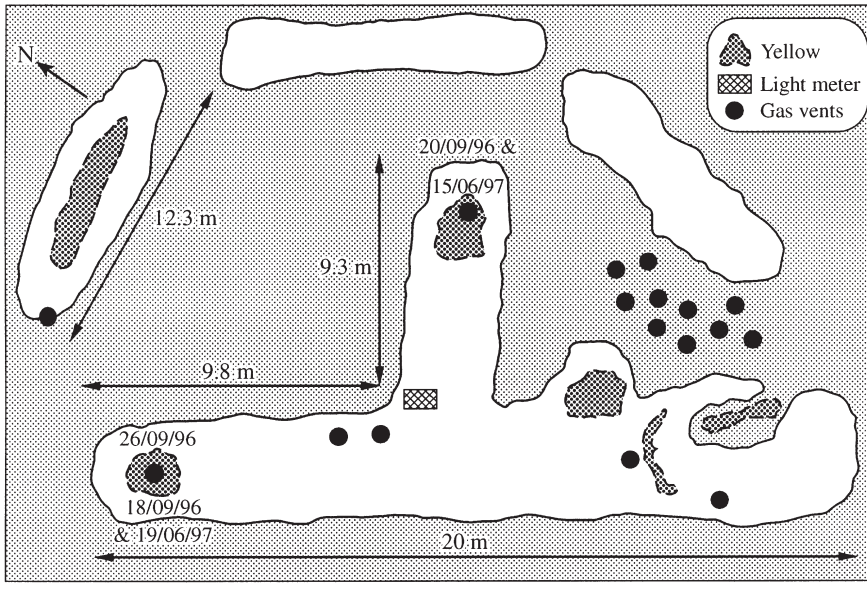


**Fig. 2.** Sketch of sampling site W2 in Palaeochori Bay showing the T-shaped mat of white and yellow coloration, and the date and position of the productivity rig sites.

respect to the bulk sea water. No thermal stratification was measured in the water column, except at ~5 cm above the sediment where the water temperature was 1°C above or below that of the rest of the water column. This variability was presumably due to the relative strengths of the venting and any bottom current.

The venting site at Voudia Bay (NE Milos; Figure 1), sampled in June 1997, lay to the southern end of the beach with a water depth of 3.5 m. The substratum consisted of rock and coarse grain sand, which was covered with a white fluffy precipitate. Gas bubbles vented amongst the rock and benthic algae. The surface water temperature was 25°C and horizontal visibility only 5 m due to suspension of the white flocculent material. The DIC concentration ranged between 2340 mmol C $m^{-3}$ at the surface at the northern end of the beach where no gas vents were visible and 2510 mmol C $m^{-3}$ at 3.5 m at the venting site. POC concentrations ranged between 7 and 8 mmol C $m^{-3}$, Chl *a* ranged from 0.05 to 0.14 mg $m^{-3}$ and PON remained stable at 0.6 mmol N $m^{-3}$.

Flakopis Bay (NE Milos; Figure 1) was sampled as a non-venting area in June 1997. Access to the site was by snorkelling from the beach. Surface water samples were collected from the 4 m water column above a sandy floor. The water temperature was 25°C and horizontal visibility was >10 m. No benthic mats or gas bubbles were visible, and the sand was not warm to the touch. DIC concentrations at this site were the lowest measured around the island (2308 and 2316 mmol C $m^{-3}$). POC ranged from 7 to 10 mmol C $m^{-3}$, PON from 0.8 to 1 mmol N $m^{-3}$ and Chl *a* was 0.16 mg $m^{-3}$.

Ormos Ag Ioannou (SW Milos; Figure 1) was also investigated as a non-venting area in June 1997. Access was again by snorkelling from the beach, water depth was 4.4 m and the substratum was sandy with no visible mats, gas streams or increased temperature. DIC concentration was 2325–2330 mmol C $m^{-3}$, POC concentration was 8 mmol C $m^{-3}$, PON was 0.7 mmol N $m^{-3}$ and Chl *a* was 0.06 mg $m^{-3}$. Unfortunately, the difficult access across the island to this site precluded its use as a 'non-venting' site for production measurements.

At Provatas Bay (S Milos; Figure 1), sampled in September 1996, water depth was 7.4 m and horizontal visibility reduced to 5 m on the particular sampling day due to benthic resuspension by wave action. The sandy bottom was not covered in 'mats' and the pore water temperature was the same as the bulk water temperature of 22.7°C. No gas streams or liquid 'haze' were visible. POC concentration was 9 mmol C $m^{-3}$, PON was 0.9 mmol N $m^{-3}$ and Chl *a* was 0.08 mg $m^{-3}$.

### *Gross production and dark community respiration measurements*

Table I summarizes the gross production, net community production and dark community respiration measurements made at Palaeochori, Voudia, Provatas and Flakopis bays in June 1996, September 1996 and June 1997, expressed in units of dissolved oxygen flux.

The data describe a predominantly heterotrophically dominated water column. Rates of gross production were often less than the analytical error, whereas plankton community respiration rates lay in the range 1–6 mmol $O_2$ $m^{-3}$ $day^{-1}$. On two occasions, very high rates of gross production were measured (8 and

**Table I.** Dissolved inorganic carbon (DIC), particulate organic carbon (POC), Chl *a*, gross production (GP), net community production (NCP) and dark community respiration (DCR) derived from *in vitro* changes in dissolved oxygen [$O_2$] and dissolved inorganic carbon [DIC] ([a]using a photosynthetic quotient of 1) at venting and non-venting sites around Milos

| | Date and time | Depth (m) | DIC (mmol C $m^{-3}$) | POC (mmol C $m^{-3}$) | Chl *a* (mg $m^{-3}$) | GP[$O_2$] ± SE (mmol $m^{-3}$ $day^{-1}$) | NCP[$O_2$] ± SE (mmol $m^{-3}$ $day^{-1}$) | DCR[$O_2$] ± SE (mmol $m^{-3}$ $day^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Venting site | | | | | | | | |
| Palaeochori | 24/06/96 16:00 | 7 | | | | 26.2 ± 1.2 | 13.8 ± 1.5 | 12.4 ± 1.7 |
| | | 7 | | | | 1.9 ± 2.0 | –1.2 ± 1.9 | 3.1 ± 1.7 |
| | | 7 | | | | 2.8 ± 1.7 | –1.2 ± 1.0 | 4.0 ± 1.4 |
| Palaeochori | 17/09/96 09:30 | 7 | 2400 | 5.5 | 0.08 | | | |
| Palaeochori | 18/09/96 08:50 | 9.4 | | | | 1.3 ± 0.2 | –0.5 ± 0.2 | 1.8 ± 0.2 |
| Palaeochori | 18/09/96 14:00 | 4 | | 7.7 | 0.07 | | | |
| Palaeochori | 19/09/96 18:00 | 2 | | 12.5 | 0.08 | | | |
| | | 5 | | 8.5 | 0.14 | | | |
| Palaeochori | 20/09/96 08:50 | 2.3 | | 7 | 0.08 | 1.9 ± 0.7 | –4.0 ± 1.2 | 5.8 ± 1.0 |
| | | 4.7 | | 7 | 0.09 | 0.5 ± 0.8 | –1.0 ± 0.3 | 1.6 ± 0.8 |
| | | 7.4 | | | | 0.5 ± 0.7 | –2.2 ± 0.7 | 2.7 ± 0.5 |
| | | 8.4 | | | | 0.5 ± 0.9 | –3.0 ± 1.2 | 3.5 ± 1.0 |
| Palaeochori | 21/09/96 13:00 | 2 | 2370 | | | | | |
| Palaeochori | 26/09/96 09:10 | 1.2 | 2394 | 6.5 | 0.1 | 0.3 ± 0.7 | –2.1 ± 0.4 | 2.3 ± 0.7 |
| | | 3.2 | | 8 | 0.08 | 0.0 ± 0.2 | –4.3 ± 0.2 | 4.3 ± 0.2 |
| | | 5.2 | 2390 | 7.7 | 0.06 | 1.2 ± 0.5 | –1.6 ± 0.3 | 2.8 ± 0.3 |
| | | 7.2 | | 13.2 | 0.07 | –0.2 ± 1.6 | –3.1 ± 1.2 | 2.9 ± 1.0 |
| Palaeochori | 15/06/97 | 5.7 | 2350 | 8.2 | 0.04 | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 10:00 | | | | | | | |
| | | 8.6 | 2450 | 11.6 (52.4) | | 8.1 ± 1.2 | 4.3 ± 1.1 | 3.8 ± 0.8 |
| Palaeochori | 16/06/97 08:30 | 1 | | 8.8 | 0.1 | | | |
| | | 3.2 | | 8.2 | 0.11 | | | |
| | | 7.2 | | 6.9 | 0.07 | | | |
| Voudia | 17/06/97 16:30 | 1 | 2340 | 8.2 | 0.14 | | | |
| Palaeochori | 19/06/97 08:30 | 7.6 | 2490 | 10.9 | 0.14 | 3.4 ± 1.3[a] | | |
| Palaeochori | 20/06/97 08:30 | 7 | | 9.4 | 0.1 | | | |
| Palaeochori | 22/06/97 19:30 | 1 | 2360 | 10.6 | 0.08 | | | |
| Voudia | 23/06/97 10:00 | 0.5 | 2470 | 7.4 | 0.05 | | | |
| | | 1.5 | 2490 | | | | | |
| | | 3 | 2510 | 8.5 | 0.09 | 1.0 ± 0.5 | –0.6 ± 0.4 | 1.6 ± 0.5 |
| Non-venting site | | | | | | | | |
| Provatas | 25/09/96 11:00 | 1.2 | 2347 | 9.2 | 0.08 | 0.8 ± 0.7 | –1.9 ± 0.6 | 2.7 ± 0.3 |
| Ormos Ag Ionnou | 14/06/97 11:00 | 1 | 2330 2325 | 8.1 | 0.06 | | | |
| Flakopis | 18/06/97 08:30 | 1 | 2316 | 10.6 | 0.16 | | | |
| Flakopis | 23/06/97 07:40 | 1 | 2308 | 7.1 | | 3.4 ± 1.0[a] | | |

26 mmol $O_2$ $m^{-3}$ $day^{-1}$). These samples were collected from very near to the sediment surface and hence resuspension of benthic algae is a possible cause of the high rates measured. Figure 3 shows depth profiles of gross production, net community production and dark community respiration measured at station W2 during September 1996. No consistent depth distribution of plankton rate processes is discernible.

*Influence of hydrothermal activity on plankton production and respiration*

The major component of venting gas in Palaeochori Bay is carbon dioxide (Dando *et al*., 1995), hence the DIC concentration of the coastal waters around Milos may be used as an indication of the presence of hydrothermal activity. This analogy was supported by the almost 200 mmol C $m^{-3}$ increase in DIC concentration between non-venting (Flakopis Bay) and venting sites (Palaeochori and Voudia bays), and the up to 140 mmol C $m^{-3}$ vertical increase in DIC between samples collected at the water surface and those collected near the venting substratum. The presence or absence of hydrothermalism (as indicated by seawater DIC concentration) had no measurable effect on the magnitude of plankton gross production or respiration (Figure 4).



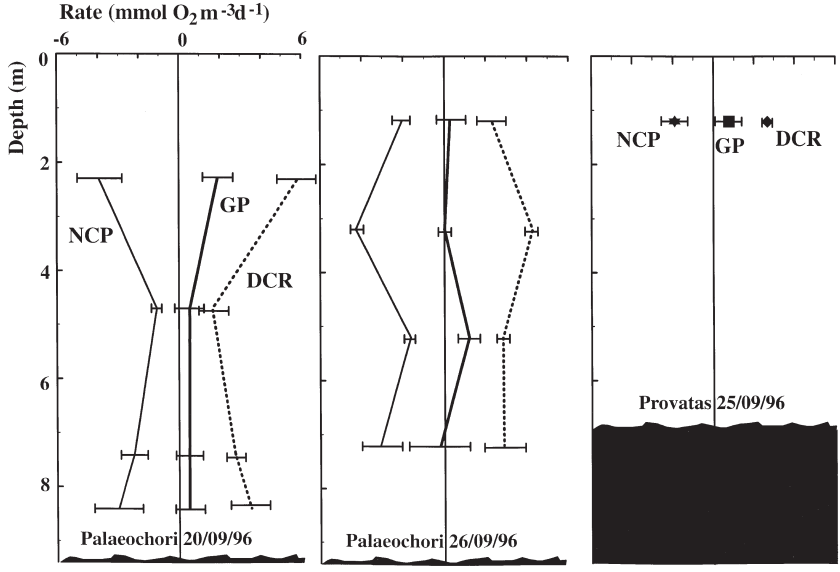


**Fig. 3.** The depth distribution of gross production (GP), net community production (NCP) and dark community respiration (DCR) (mmol $O_2$ $m^{-3}$ $day^{-1}$ ± SE) at Palaeochori and Provatas bays in September 1996.

*Influence of temperature on plankton production and respiration*

The large range of temperature between sediment surface and bulk sea water, and the visible mixing of vent fluids and bulk sea water, suggest that temperature may have an influence on plankton gross production and respiration rates.

Preliminary experiments to investigate the linearity of respiration with time at different incubation temperatures revealed that respiration was linear at temperatures up to 30°C (i.e. 6°C above *in situ* temperature). However, above this

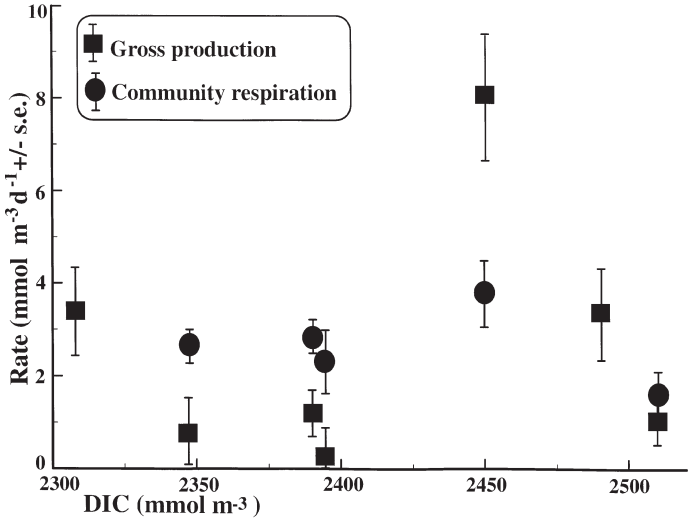


**Fig. 4.** Plankton gross production and dark community respiration (mmol $m^{-3}$ $day^{-1}$ ± SE) as a function of seawater dissolved inorganic carbon (DIC) concentration (mmol C $m^{-3}$).

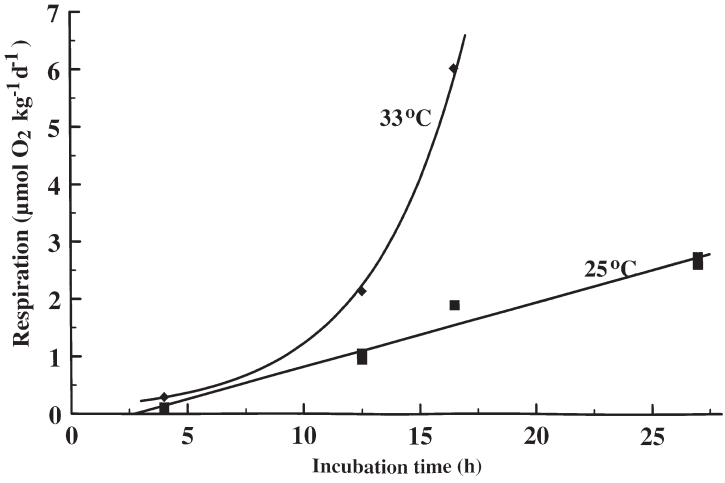


**Fig. 5.** The temporal response of plankton dark community respiration at different incubation temperatures.

temperature, dark community respiration showed an exponential increase with incubation time (Figure 5). Data analysis therefore includes only those data collected at incubation temperatures below 30°C.

Temperature gradient experiments showed that an increase in incubation

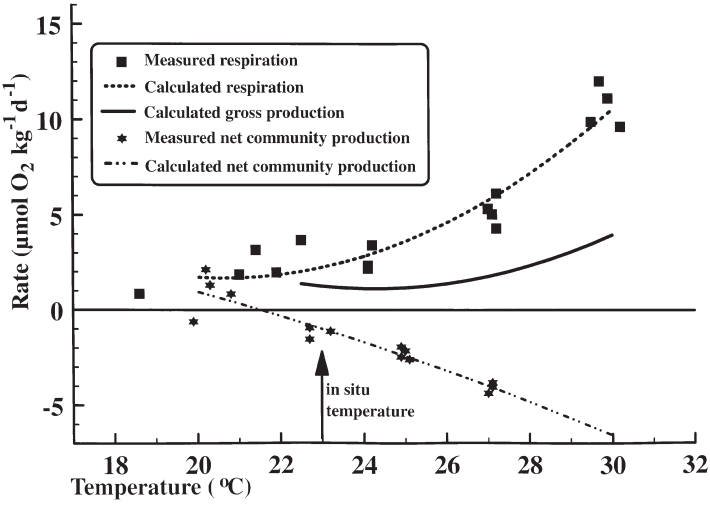


**Fig. 6.** The effect of incubation temperature on plankton net community production, dark community respiration and gross production derived from *in vitro* changes in dissolved oxygen (µmol $O_2$ $kg^{-1}$ $day^{-1}$) on 17 September 1996. Respiration = $0.1007t^2 - 4.1559t + 44.559$ ($r^2 = 0.91$) and net community production = $-0.0152t^2 + 0.0072t + 6.8916$ ($r^2 = 0.88$) where $t$ is temperature (°C).

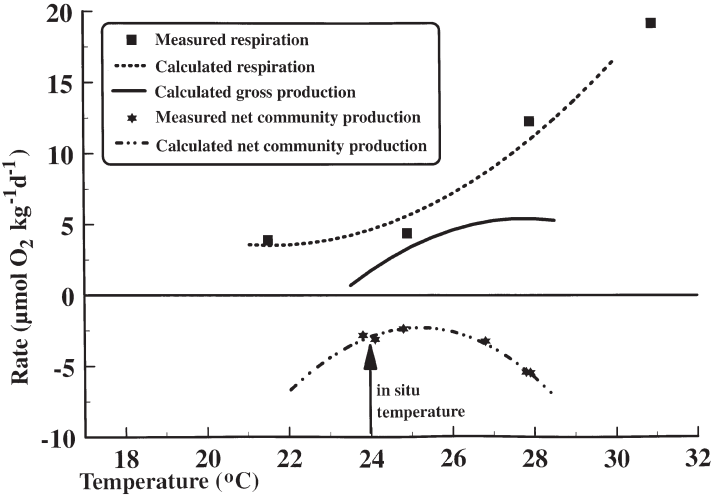


**Fig. 7.** The effect of incubation temperature on plankton net community production, dark community respiration and gross production derived from *in vitro* changes in dissolved oxygen (µmol $O_2$ $kg^{-1}$ $day^{-1}$) on 16 June 1997. Respiration = $0.1843t^2 - 7.9434t + 89.116$ ($r^2 = 0.98$) and net community production = $-0.4429t^2 + 22.31t - 283.23$ ($r^2 = 0.97$) where $t$ is temperature (°C).

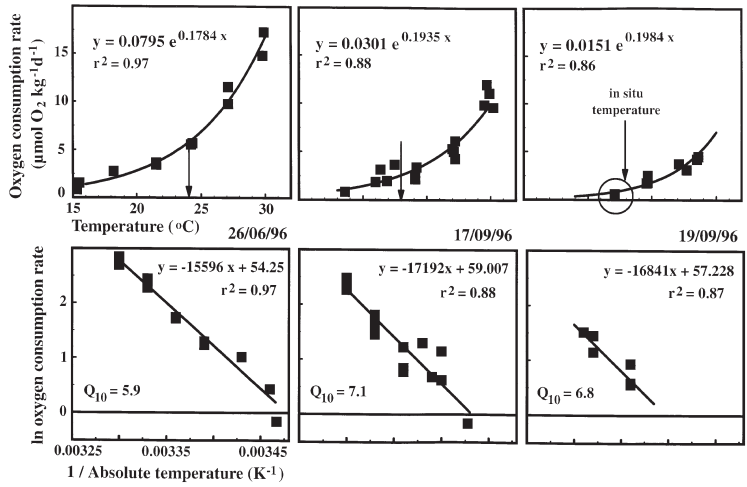


**Fig. 8.** The effect of incubation temperature on the oxygen consumption rate (µmol $O_2$ $kg^{-1}$ $day^{-1}$) of the plankton community sampled from the water column of a visible venting area (Palaeochori Bay). Circled data fall below the mean SE of the rate measurements and so have been excluded from the $Q_{10}$ calculation.

temperature had a greater stimulatory effect on dark community respiration rate than on gross production (Figures 6 and 7). An increase in temperature always had a marked positive effect on dark community respiration rate, with the temperature at which the maximum respiration rate occurred ($T_{opt}$) being higher than the highest experimental temperature of 30°C. An increase in temperature had a lesser stimulatory effect on gross production (Figure 6) and a sample collected in June 1997 exhibited a $T_{opt}$ for gross production of 27.8°C (i.e. ~4°C above *in situ*) (Figure 7).

The rate of dark community respiration exhibited a typical exponential increase with increasing temperature (Figure 8). Temperature coefficients ($Q_{10}$s) of dark community respiration calculated from the slope of an Arrhenius plot (6–7) were higher than commonly accepted values of bacterial growth and plankton community respiration (2–4) [see Table III in Robinson and Williams (Robinson and Williams, 1993)].

## Discussion

### *Site descriptions*

Sample sites were chosen to test the hypothesis that the shallow water hydrothermal vents around Milos, which exude hot fluids and gases enriched in heavy and trace metals, carbon dioxide, methane and hydrogen sulphide (Dando *et al.*, 1999), would have a measurable effect on the activity of the plankton. However, there was no significant difference in the magnitude of Chl *a*, POC or PON

between venting and non-venting areas. This may indicate either that there is no hydrothermal stimulatory or inhibitory influence on plankton biomass, or that any potential influence is rapidly eliminated by the hydrography of the region. This elimination was reported by Acosta Pomar and Giuffrè in the hydrothermal coastal region of the Eolian Archipelago, Tyrrhenian Sea (Acosta Pomar and Giuffrè, 1996).

Any potential hydrothermal influence was therefore investigated on a smaller space scale. At the metre space scale, there was no consistent vertical pattern to the distribution of Chl *a*, POC or PON in samples taken above sporadically venting areas at site W2 in Palaeochori Bay. Samples collected on 26 September 1996 and 15 June 1997 showed highest concentrations of POC occurring within 1 m of the sediment surface, whereas on 16 June 1997 samples collected within 1 m of the sediment surface had Chl *a* and POC concentrations less than those of samples taken at shallower depths above the same vent. This variability is not unexpected, bearing in mind the intermittent frequency of venting, the variability of the force and position of venting, and presumably also the changing ratio of gas:fluid of the vent exudates, as witnessed by the scientific divers.

*Plankton production and respiration rates*

The complex biogeochemical environment and the method of sampling 125 $cm^3$ replicates *in situ*, rather than collecting a bulk sample for distribution into replicate smaller samples, presumably contributed to the lower than usual precision of the gross production and respiration rate measurements. The mean of the SEs of net community production and respiration derived from *in vitro* changes in DIC (data not shown) was 2.6 mmol C $m^{-3}$ $day^{-1}$, and that of NCP and DCR derived from dissolved oxygen flux was 0.8 mmol $O_2$ $m^{-3}$ $day^{-1}$ as opposed to 1 mmol C $m^{-3}$ $day^{-1}$, 1.5 mmol C $m^{-3}$ $day^{-1}$, 0.6 mmol $O_2$ $m^{-3}$ $day^{-1}$, 0.5 mmol $O_2$ $m^{-3}$ $day^{-1}$ and 0.3 mmol $O_2$ $m^{-3}$ $day^{-1}$ found previously (Robinson and Williams, 1993, 1999; Boyd *et al*., 1995; Robinson *et al*., 1999).

The mean oligotrophic nature of the Aegean Sea was corroborated at Palaeochori Bay, Milos, with plankton gross production rates lying between undetectable and 3 mmol $O_2$ $m^{-3}$ $day^{-1}$ and Chl *a* concentrations <0.15 mg $m^{-3}$. No discernible seasonal pattern in either Chl *a* or gross production was seen during the present study, with the range in Chl *a* (0.04–0.14 mg $m^{-3}$) during June 1997 overlapping the range (0.07–0.14 mg $m^{-3}$) measured during September 1996. The low seasonal signal and range of Chl *a* measured agree well with previous studies in the Aegean Sea (Antoine *et al*., 1995).

The rates of gross production, Chl concentrations and calculated photosynthetic indices [μmol $O_2$ $\mu g^{-1}$ Chl *a* $h^{-1}$ based on a 12 h photoperiod; (Williams and Purdie, 1991)] determined in the present study in the nearshore Aegean also compare favourably with open-ocean oligotrophic measurements. Williams and Purdie calculated a mean photosynthetic index of ~0.9 μmol $O_2$ $\mu g^{-1}$ Chl *a* $h^{-1}$ for phytoplankton in the North Pacific Ocean, where gross production was in the range 0.5–1.0 μM $O_2$ $kg^{-1}$ $day^{-1}$ and Chl *a* was <0.1 mg $m^{-3}$ (Williams and Purdie, 1991). The photosynthetic indices calculated in the present study were higher

(mean = 1.1, range 0.25–2, $n = 7$), reaching the calculated maximum photosynthetic efficiency of 2 μmol $O_2$ $\mu g^{-1}$ Chl *a* $h^{-1}$ (Falkowski, 1981) and so indicating a photosynthetically active population. Such large variability in photosynthetic index or assimilation number (μg C $\mu g^{-1}$ Chl *a* $h^{-1}$) within a single study has been reported for oligotrophic regions before [(Letelier *et al*., 1996), and references therein], and is attributed to (i) sporadic nutrient injection either as a result of deep mixing events or changes in nutrient regeneration rates, (ii) changes in ecosystem structure or (iii) a change of limiting nutrient [(Letelier *et al*., 1996), and references therein]. Unfortunately, nutrient analyses (e.g. nitrate and phosphate) were not carried out concomitantly with gross production measurements in the present study. However, ammonium concentrations as high as 900 mmol $m^{-3}$ in vent pore water and overlying water samples were measured in Palaeochori Bay (Robinson *et al*., 1997), indicating a substantial intermittent nutrient flux into the water column.

Two exceptions to the mean low plankton gross production rates occurred at Palaeochori Bay. The gross production of a sample collected from 7 m at an actively bubbling site in June 1996 was 26 mmol $O_2$ $m^{-3}$ $day^{-1}$, and the gross production of a sample collected at a depth of 8 m close to an active vent in June 1997 was 8 mmol $O_2$ $m^{-3}$ $day^{-1}$. These samples were collected within a few centimetres of the sediment and within the upward flow of liquid from the vent, hence suspension of benthic algae may be the cause of these high rates. Unfortunately, concomitant measurements of Chl *a* or POC are not available to corroborate this suggestion. However, surface sediment samples collected from the vent at which the high gross production measurements were made in June 1996 did contain substantial numbers of benthic diatoms of the genera *Nitzschia* and *Amphora* (Economou-Amilli *et al*., 1998). Therefore, the suspension of benthic algae by the upflow of water and gas movement from the vent is not inconceivable.

Contemporaneous measurements of plankton community respiration and bacterial numbers were not made in the present study. However, bacterial cell numbers in water samples immediately above the sediment at an adjacent vent in Palaeochori Bay lay in the range 3.2–9.5 × $10^5$ $ml^{-1}$ (Sievert *et al*., 1999). This compares well with concomitant measurements made previously in surface waters of the oligotrophic Arabian Sea where respiration rates lay between 2 and 4 mmol $O_2$ $m^{-3}$ $day^{-1}$ (Robinson and Williams, 1999), bacterial numbers were ~8 × $10^5$ $ml^{-1}$ (Pomroy and Joint, 1999) and Chl *a* was <0.1 mg $m^{-3}$ (Barlow *et al*., 1999).

The measured *in vitro* fluxes of dissolved oxygen reveal a dominance of microbial rate processes which consume oxygen rather than produce it (i.e. heterotrophy > autotrophy). There are two assumptions inherent in this statement. The first is that chemical oxidation of reduced compounds emanating from the vents did not measurably bias the oxygen uptake measurements. If chemical oxidation was substantial, then one would expect the measured uptake of oxygen to be considerably higher than the concomitant production of DIC. On the few occasions when concomitant oxygen and DIC flux measurements were made, DIC production was similar to or higher than oxygen consumption, indicating that chemical oxidation did not measurably bias the oxygen uptake measurements.

The second assumption is that aerobic chemoautolithotrophy by sulphur-oxidizing bacteria (SOB) was not a major component of the uptake of oxygen in the dark. Bacterial cell numbers in water samples overlying sediment cores taken from a vent in Palaeochori Bay lay in the range $3.2–9.5 \times 10^5$ ml$^{-1}$ (Sievert *et al.*, 1999). Mean probable number (MPN) estimates of chemoautolithotrophic SOB accounted for a maximum of 6% of total cell numbers either in the sediment or overlying water, and SOB only occurred in the overlying water samples, which included samples of the white precipitate (Sievert *et al.*, 1999). This suggests that the dark oxygen uptake rates determined in the water column are not measurably biased by rates of chemoautolithotrophy and are rates of heterotrophic processes. The suggested dominance of heterotrophy over autotrophy is therefore real. This may simply be a function of this particular habitat, i.e. shallow (<10 m), nearshore (<200 m offshore) and close (<30 m) to seagrass meadows (*Cymodocea nodosa* and *Posidonia oceanica*) (Aliani *et al*., 1998). Alternatively, this may correspond to recent findings by Estrada and Lykousis (Estrada and Lykousis, 1998) as discussed in Turley *et al*. (Turley *et al*., 2000) of an increased ratio of heterotrophic to autotrophic production along an increasing oligotrophic gradient from the West to East Mediterranean, and of Robinson and Williams (Robinson and Williams, 1999) of the increased dominance of heterotrophic processes over autotrophic processes with increasing distance offshore (and hence gradient of increasing oligotrophy) in the Arabian Sea.

*Influence of hydrothermal activity on plankton production and respiration*

The low gross production rates, coupled with the low precision of the measured rates, may have contributed to the lack of difference between plankton gross production at vent and non-vent sites over a range of 200 mmol C m$^{-3}$ in DIC concentration (Figure 4). However, the lack of any effect of DIC concentration (over a range of 800 mmol C m$^{-3}$) on the net or gross activity of sediment autotrophs (Wenzhofer *et al*., 2000) in Palaeochori Bay suggests that, in this environment, factors other than DIC concentration are limiting.

The lack of any difference in plankton production processes between hydrothermal and non-hydrothermal areas is in contrast to the work of Sorokin *et al*. (Sorokin *et al*., 1998). These authors report a significant increase in microplankton photosynthesis and bacterial chemosynthesis in shallow hydrothermal areas compared with adjacent oceanic waters in the Western Pacific, and significant inhibition of photosynthesis by sulphides and heavy metals at shallow hydrothermal sites in the caldera bay of Matupi Harbour, New Britain Island, Papua New Guinea. Since different vents, even within the same geographical region, can have substantially different chemical signatures (Dando *et al*., 1999) and such contrasting effects on plankton (Sorokin *et al*., 1998), there is no reason to believe that a significant measurable effect should be universal. In fact, as Tarasov *et al*. suggest, pronounced changes in plankton activity due to hydrothermalism may only occur in areas which are largely isolated from the open sea (Tarasov *et al*., 1999).

Sorokin *et al*. also note the variability in primary and bacterial production measured above shallow gasohydrothermal vents in the caldera bay of Matupi

Harbour, New Britain Island (Sorokin *et al.*, 1998). Primary production ranged from 0.3 to 14 mmol C $m^{-3}$ $day^{-1}$ in surface samples above active shallow vents, and was 16 mmol C $m^{-3}$ $day^{-1}$ at a control station away from volcanic influence. Bacterial production ranged from 1.13 to 1.95 mmol C $m^{-3}$ $day^{-1}$ in surface samples above the vents, and was 1.22 mmol C $m^{-3}$ $day^{-1}$ at the control station.

### *Influence of temperature on plankton production and respiration*

Palaeochori Bay does not exhibit the range in water temperature experienced by other hydrothermal coastal environments (30–75°C) (Acosta Pomar and Giuffrè, 1996; Tarasov *et al.*, 1999). However, local abrupt temperature changes of up to 2°C have been measured (P.Linke, personal communication), and the bay itself is 1–3.4°C warmer, for up to 7 months of the year, than a nearby non-hydrothermal bay (Aliani *et al.*, 1999). The temperature response curves of plankton processes here may give some indication of any hydrothermal adaptation or influence. Water samples were collected from various depths above gasohydrothermal vents, and the temperature response of dissolved oxygen production and consumption determined from temperature gradient incubations.

Gross production and respiration rates derived from the *in situ* productivity rig compared well with those determined at *in situ* temperature during the temperature gradient experiments, confirming that the plankton population was not in a shocked state due to experimental manipulation (Robinson and Williams, 1993) during the temperature gradient experiments. Time series temperature gradient experiments were undertaken to ensure a linear response of respiration rate over the incubation time.

In September 1996 and June 1997, the temperature response curve of plankton respiration was much more pronounced than that of gross production. In June 1997, the $T_{opt}$ for gross production occurred at <4°C above *in situ* temperature, whereas on both sampling occasions the $T_{opt}$ for respiration lay above the maximum incubation temperature (i.e. >6°C above *in situ* temperature). This differential effect of temperature on plankton gross production and respiration may indicate that the autotrophic plankton community is better adapted to the relatively stable temperatures of coastal Mediterranean waters, whereas the heterotrophic community appears to be able to flourish at temperatures at least 6°C higher than *in situ*. The caveat to this, of course, is that the measured plankton community respiration rates will include algal as well as bacterial respiration. Alternatively, due to the intermittent and variable force of venting, these mid-water plankton community samples may include a greater proportion of bacteria than algae that have originated from the hot surface of the hydrothermal sediment and so may be expected to be adapted to higher temperatures.

The temperature coefficients of plankton respiration calculated for a 10°C range (with the mean *in situ* temperature as the midpoint) ($Q_{10}$ = 6–7) were higher than the commonly accepted temperature coefficients of bacterial growth or community respiration ($Q_{10}$ = 2–3) (Figure 8). The use of the Arrhenius equation to determine the activation energy of processes such as respiration, which constitute a complex of reactions, is not ideal; however, it does provide a means

to compare studies. Lefèvre *et al*. attributed their high modal $Q_{10}$ (4–5) for shallow water temperate plankton respiration to the variation in temperature due to tidal activity (Lefèvre *et al*., 1994). The high $Q_{10}$ values measured in the present study may be a response to the small fluctuations in water temperature due to intermittent hydrothermal venting. Karl determined a significant temperature response of deep-sea hydrothermal vent microbes, with a 25-fold increase in the total rate of RNA synthesis for a 23°C temperature increase, i.e. an average $Q_{10}$ of 10.9 (Karl, 1985).

The complex geochemical environment of these shallow water (<9 m) hydrothermal vents therefore appears to have no consistent stimulatory or inhibitory effect on the magnitude of plankton biomass, gross production or dark community respiration. However, the higher than expected temperature coefficients of the plankton community respiration measured here may be a response to the temperature fluctuations in these environments.



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