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Contributions of the Plankton Community to Ecosystem Respiration, Tomales Bay, California

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This paper presents direct measurements of plankton community respiration for Tomales Bay, California, U.S.A., and compares these measurements with water column variables. These data were used to develop a regression model that predicts planktonic respiration and nutrient remineralization. Respiration was measured as change in dissolved O_2 in sealed, dark, 300 ml bottles. There was a consistent and linear decrease in O_2 concentrations over 35–48 h incubations. Chlorophyll *a* concentration ranged from 1 to 10 μg chl *a* l^{-1}. Bacterial counts were 2–11 × 10^6 cells ml^{-1} and leucine incorporation rates ranged from 200 to 1300 pmol l^{-1} h^{-1} over the period May 1992–July 1993. Respiration rates were 0·16–1·91 μmol O_2 l^{-1} h^{-1}, with an annualized average of 0·67 μmol O_2 l^{-1} h^{-1}. A multiple linear regression of O_2 consumption rate against the independent variables (chlorophyll concentration, temperature and particulate N concentration) explained 79% of the variation in the respiration rates. Modelled plankton community respiration rates for the period January 1988 to July 1993 ranged from <0·4 to >2·0 μmol O_2 l^{-1} h^{-1}. Over the same period, the average predicted areal respiration for inner Tomales Bay was 64·5 mmol O_2 m^{-2} day^{-1}. Mean predicted rates of N and P remineralization over the period of January 1988 to July 1993 were 9·8 and 0·6 mmol m^{-2} day^{-1}, respectively. Even in an embayment as shallow as Tomales Bay (mean z=3·1 m), planktonic respiration and remineralization are greater than benthic respiration and remineralization.

Keywords: respiration rates; plankton; estuaries; Tomales Bay

Introduction

Estuarine systems are often divided into two components; the benthos and the water column. Cross-ecosystem studies of respiration in shallow-water coastal systems indicate that ≈75% of respiration is planktonic (Nixon, 1981; Dollar *et al.*, 1991). Benthic respiration (and remineralization of nutrients) in inner Tomales Bay has been measured routinely since June 1987, and the first 2 years of these measurements have been reported by Dollar *et al.* (1991). Annual average benthic respiration, as indicated by the flux of dissolved inorganic carbon out of the sediment, is 21 mmol C m^{-2} day^{-1}. Smith *et al.* (1991) have estimated the net oxidation of organic matter as a whole in Tomales Bay to be 10 mmol organic C m^{-2} day^{-1}. Gross primary production in inner Tomales Bay is approximately 75 mmol C m^{-2} day^{-1} (Cole, 1989); therefore, total respiration of inner Tomales Bay is about 85 mmol C m^{-2} day^{-1} (Smith *et al.*, 1991). By difference, water column respiration in inner Tomales Bay should account for about 64 mmol C m^{-2} day^{-1}, or 75% of the total system's gross respiration. Of course, the errors associated with the estimates of each of these component fluxes are quite large (±25%), so any estimates of water column respiration by difference will also have a large uncertainty (Smith *et al.*, 1991).

Despite this budgetary evidence of the importance of the plankton community respiration, direct measurements of water column respiration have not been made for Tomales Bay. Measurement of volumetric water column respiration rates have been made for numerous coastal locations over the past 20 years, including recent work in Danish fjords (Jensen *et al.*, 1990; Sand-Jensen *et al.*, 1990); the English Channel (Holligan *et al.*, 1984; Iriarte *et al.*, 1991); Chesapeake Bay (e.g. Sampou & Kemp, 1994); the Georgia Bight (Hopkinson *et al.*, 1989, 1991); and the Gulf of Mexico (Pomeroy *et al.*, 1995). Incubations for

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determining plankton respiration rates are tedious and time-consuming, and as a result are rarely done as part of a routine monitoring programme; therefore, it is uncommon that measurements of volumetric respiration rates are integrated to provide estimates of the importance of water column respiration to ecosystem metabolism. Development of easily measured proxies for direct measurements of processes such as respiration and nutrient remineralization would increase our understanding of the spatial and temporal variation in these processes.

Many chemical and biological variables assessed in monitoring programmes measure aspects of the status of the plankton community, and may be useful as predictors of respiration rates. Temperature has a direct effect on the respiration rates or organisms. Pigment concentration and counts of bacteria directly estimate the biomass of the plankton assemblage. Rates of substrate (e.g. ^{3}H L-leucine, ^{3}-H thymidine) incorporation by bacteria measure aspects of the growth of bacterial cells. Concentrations of substrates of respiration pathways may also control respiration rates. Models relating these often-measured parameters to planktonic respiration rates would allow for assessment of the importance of planktonic respiration in ecosystems.

This paper presents direct measurements of plankton community respiration, and compares these measurements with commonly measured water column variables. These data are used to develop a regression model that predicts respiration, and this model is applied to assess the importance of plankton community respiration to the Tomales Bay system.

Methods and materials

Site description and sampling

Tomales Bay, CA, U.S.A., is a 20 km long and 1·4 km wide embayment with an average depth of 3·1 m and a maximum depth of 19 m (Figure 1). Since 1985, Tomales Bay has been the subject of an intensive study into the biogeochemistry of estuaries (e.g. Smith *et al.*, 1987, 1989, 1991; Cole, 1989; Dollar *et al.*, 1991; Hollibaugh *et al.*, 1991). A variety of water quality variables have been measured at 10 stations along the axis of Tomales Bay at intervals of 2 weeks to 2 months since the inception of the study (see Smith *et al.*, 1987, 1989). Water column respiration rates were determined at three stations in the inner portion of the bay (Figure 1, Stations 10, 12 and 14). Respiration measurements were made during bimonthly field trips between May 1992 and July 1993.

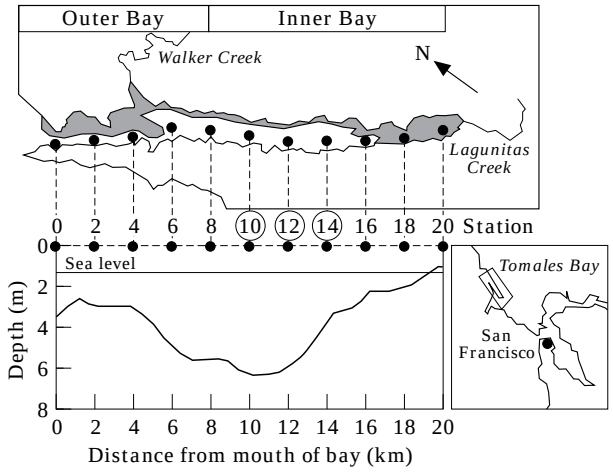

FIGURE 1. Tomales Bay in Northern California. Station designations correspond to distance in km from the mouth of the bay. Plankton community respiration measurements were made at Stations 10, 12 and 14 in the inner bay. Shaded areas are shoals <1 m deep. Depths are cross-sectionally averaged depth.

Water for respiration measurements was collected from the surface in 20 l carboys, and was returned to the laboratory immediately. Respiration rate measurements were begun within 2 h of sample collection.

Planktonic respiration measurements

Oxygen concentration of samples was adjusted to 90–95% of air saturation by gently sparging with N_2 (samples were generally supersaturated with O_2 with respect to air when they were collected). This water was gently siphoned into replicate opaque glass 300 ml biological oxygen demand (BOD) bottles, allowing 2 times the volumes of the bottles to overflow before capping. Carboys were stored in the shade at approximately *in situ* temperature between sampling and siphoning. The BOD bottles were incubated in the dark for *c.* 48 h in a temperature-controlled water bath set at field temperature ($\pm$ 0·5 °C). Three replicate bottles were sacrificed at the beginning of each incubation, and at intervals of 1–12 h throughout the incubation. The oxygen concentration of each bottle was determined using a stirred polarographic oxygen probe and meter (YSI models 5730 and 58, respectively). The meter and probe were calibrated using water-saturated air at the temperature of the incubation; the average precision of the replicate measurements, as indicated by the coefficient of variation of the oxygen concentration in triplicate BOD bottles, was 0·4%. Calibration was adjusted immediately prior to each set of measurements. The electrode was

placed in each bottle and allowed to equilibrate until a constant reading was obtained (generally 2–3 min).

Chemical and biological variables

Chemical variables measured routinely in Tomales Bay are: dissolved inorganic nutrients [nitrate+nitrite (henceforth referred to as N+N), NH_4^+, PO_4^{3-} (DIP), Si]; total dissolved N and P (TDN, TDP); dissolved organic C, N and P (DOC, DON, DOP); particulate organic C and N (POC, PON); particulate P; pH; total alkalinity (TA); salinity and temperature. Partial pressure of CO_2 was calculated from pH and TA. The methods are described in Smith *et al.* (1991). Chlorophyll *a* concentration was determined fluorometrically using DMSO:acetone:water (9:9:2;v:v:v, with 0·1% by volume of diethylamine) extracts of small volume samples (8–32 ml) collected on GF/F 2·5 cm filters.

Bacterioplankton were enumerated by epifluorescence microscopy (Porter & Feig, 1980). Bacterioplankton production was measured using the radiolabelled leucine (4,5-[^{3}H]- L-leucine) incorporation technique of Kirchman *et al.* (1985) as described in Hollibaugh and Wong (1992)).

Statistical analyses

Planktonic respiration rates were estimated using linear regression analysis of O_2 concentration against time as the independent variable. Pearson correlation coefficients were computed for the relationship between respiration and water column chemical and biological parameters. The significance of these correlations were computed using two-tailed probabilities. Stepwise multiple linear regression, using the water column chemical and biological parameters as independent variables, was used to determine the best predictors of planktonic respiration rates.

Modelling planktonic respiration

Respiration rates were converted from oxygen- to carbon-based units assuming a respiratory quotient (RQ; moles CO_2 produced:moles O_2 consumed) of 1. The RQ can be between 0·7 and 1·0, depending on the primary source of reduced carbon (Elliot & Davison, 1974); other investigators have assumed RQ of plankton communities to be between 0·85 and 1·0 (e.g. Williams, 1982; Pomeroy *et al.*, 1995). The multiple regression model developed for the relationship between the chemical and biological variables and respiration was used to predict water column respiration rates for the period from January 1988 to July 1993, using the monitoring data collected by the LMER programme over that time interval. These rates were converted to an areal basis using the bathymetric information in Figure 1.

Results

Planktonic respiration rate

Oxygen concentrations decreased linearly in the BOD bottles over the course of the 35–48 h incubations. *In vitro* O_2 consumption measurements, such as employed in this study, have been used to estimate the respiration rates of the planktonic community for decades (e.g. Riley, 1939). Criticisms of this technique are based on the possibility that artifacts are caused by holding a sample in a bottle during the extended time necessary to measure a change in oxygen concentration. Any artifacts introduced by bottle effects will most likely cause underestimates of true plankton community respiration rates (Williams, 1984). Although it has been argued that bottle effects should cause a change in the observed oxygen consumption rate through time, many authors have measured linear rates of oxygen consumption for incubations of at least 48 h (e.g. Williams, 1981; Pomeroy & Deibel, 1986; Hopkinson *et al.*, 1989). Similarly, the present data showed consistent linear decreases in oxygen concentration through up to 48 h of incubation. The regressions explained a minimum of 95% of the change in oxygen concentration through time for each incubation (r^2>0·95, Table 1). There was no pattern in the residuals of the regressions to suggest that the initial respiration rates were higher than rates measured later in an incubation. Oxygen consumption rates ranged from 0·16 to 1·91 μmol $O_2\,l^{-1}\,h^{-1}$ (Table 1). The average respiration rate obtained from all of the experiments was $0{\cdot}70 \pm 0{\cdot}39$ μmol $O_2\,l^{-1}\,h^{-1}$ ($\pm$ 1 SD).

Seasonal variation in respiration rate was examined by averaging all incubations conducted during a given month of the year. Data from 2 years of sampling (1992 and 1993) were averaged for May and July (Figure 2). There was relatively little seasonal variation. Maximum respiration rates occurred in July; however, this was largely influenced by the high respiration rate (1·91 μmol $O^2\,l^{-1}\,h^{-1}$) associated with a phytoplankton bloom at Station 12 on 11 July 1992 (Figure 6 and Table 1). Minimum respiration rates of $0{\cdot}21 \pm 0{\cdot}03$ μmol $O_2\,l^{-1}\,h^{-1}$ were measured in January, which was the only month significantly different from the others. The average annualized respiration rate, obtained by averaging the mean value for each month of the year, was 0·67 μmol $O_2\,l^{-1}\,h^{-1}$.

TABLE 1. Results of the regression analyses for all dark bottle incubations

Date	Station	Slope (μmol O_2 l^{-1} h^{-1})	Initial O_2 conc. (μmol l^{-1})	n	r^2
10 May 1992	12	1·00	221	13	0·98
9 July 1992	10	0·62	197	9	0·95
11 July 1992	12	1·91	198	9	0·99
13 July 1992	14	0·59	188	6	0·99
4 September 1992	10	0·94	225	7	0·99
6 September 1992	12	0·90	191	6	0·99
8 September 1992	14	0·37	230	4	0·98
5 November 1992	10	1·21	244	6	0·99
7 November 1992	12	0·58	213	6	0·99
9 November 1992	14	0·49	227	6	0·99
7 January 1993	10	0·25	285	6	0·99
8 January 1993	12	0·21	282	6	0·99
10 January 1993	14	0·16	298	5	0·99
3 March 1993	10	0·86	266	6	0·99
5 March 1993	12	0·56	268	6	0·98
7 March 1993	14	0·78	271	4	0·99
5 May 1993	10	0·67	228	5	0·99
7 May 1993	12	0·48	240	6	0·99
9 May 1993	14	0·43	248	5	0·99
7 July 1993	10	1·02	191	5	0·99
9 July 1993	12	0·87	198	5	0·99
11 July 1993	14	0·56	213	5	0·98

The number of observations (n) indicates the number of time intervals sampled. The means of triplicate bottles at each time were used in the analyses. Experiments were run for 35–48 h.

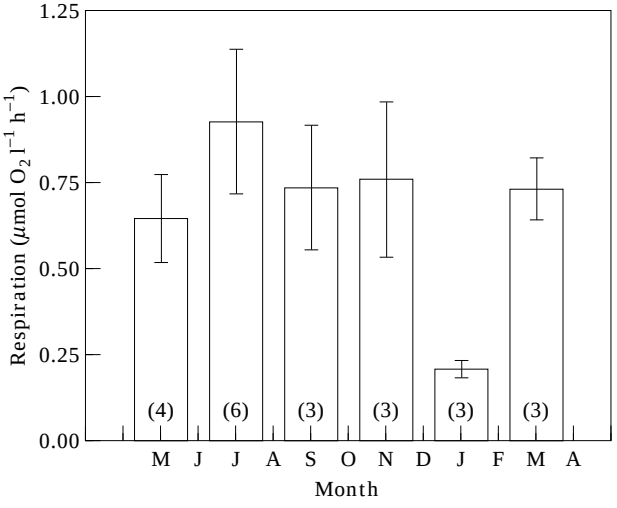

FIGURE 2. Summary of the measured plankton community respiration measurements by month of the year (mean ± 1 SD). The number in the bar is the number of observations.

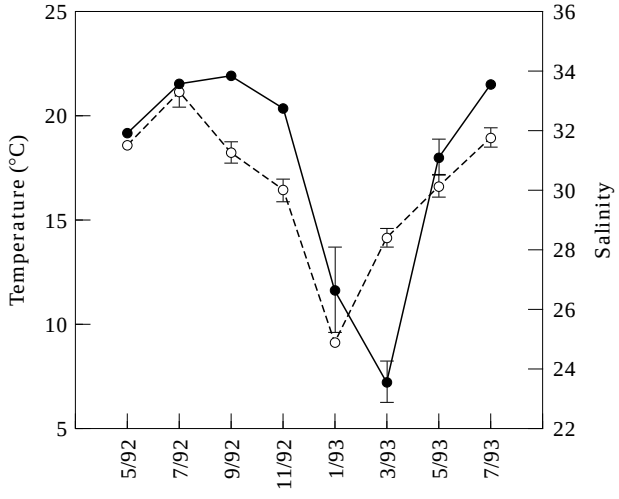

FIGURE 3. Variation in temperature (●) and salinity (○) at Stations 10, 12 and 14 in Tomales Bay for the plankton community respiration incubations. Symbols are means ± 1 SE for each sampling time.

Chemical and biological parameters

During the period respiration was measured, temperature and salinity in Tomales Bay followed the expected seasonal variation for a temperate, Mediterranean-climate estuary (Figure 3). Maximum temperatures were observed in July (22·3 °C), and minimum temperatures were observed in January

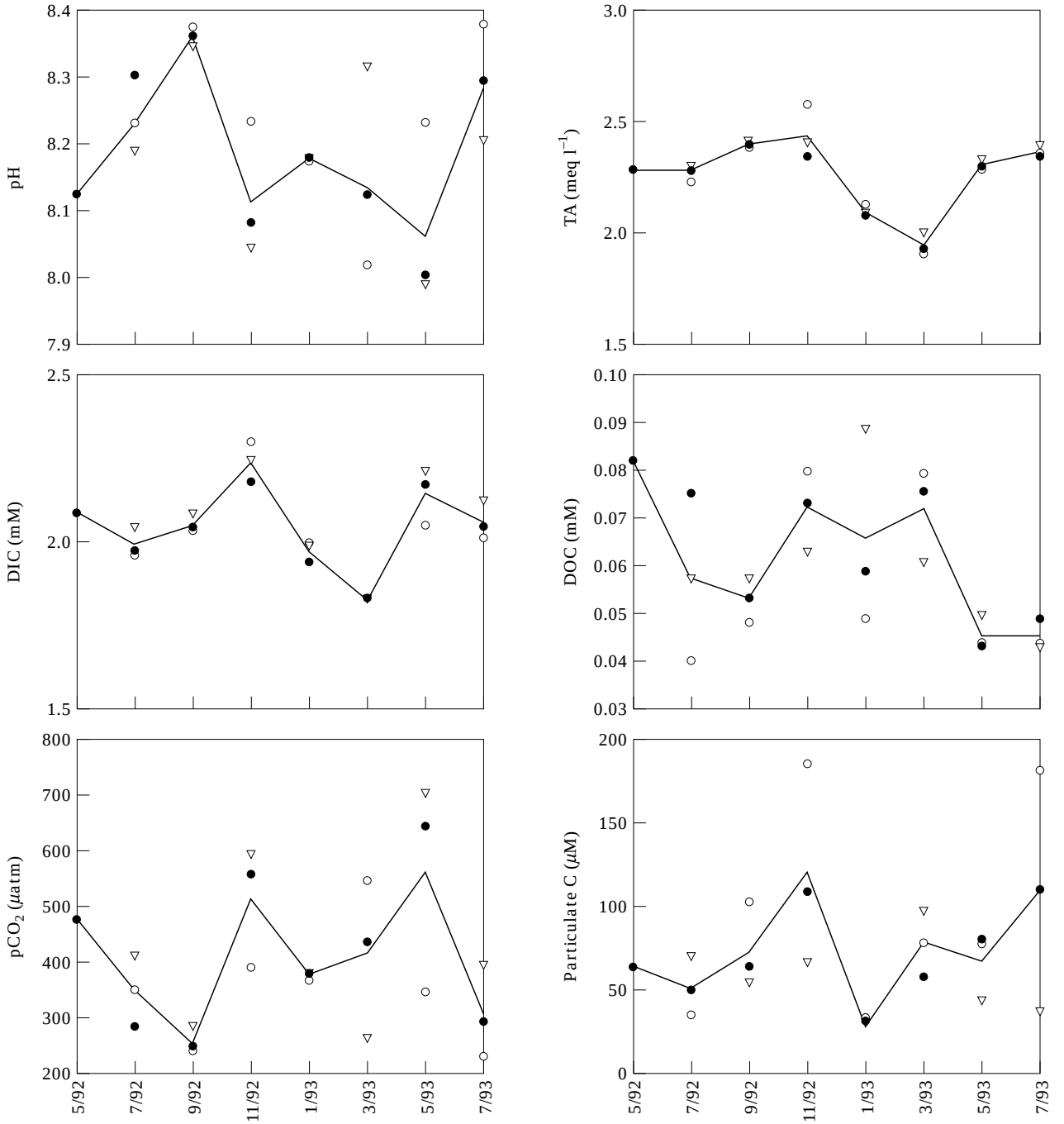

FIGURE 4. Variation in pH, total alkalinity (TA) and concentrations of carbon species for the plankton community respiration incubations. ○, Station 10; ●, Station 12; ▽, Station 14. The line connects the means at each sampling period.

(9·2 °C). Salinity was highest in July–September (34·2), with a winter minimum of 22·2. Winter runoff into Tomales Bay causes a decrease in pH, total alkalinity and dissolved inorganic carbon at the study sites (Figure 4; see also Smith *et al.*, 1991). There were no clear seasonal trends in the concentrations of dissolved organic or particulate carbon, or of the partial pressure of CO_2 (as calculated from pH and alkalinity, Figure 4).

There were pronounced seasonal trends in some of the nutrient concentrations (Figure 5). Si concentrations were 13–62 µmol l^{-1}, with a minimum in May 1993. Dissolved inorganic phosphate was the primary form of P in the water column, with

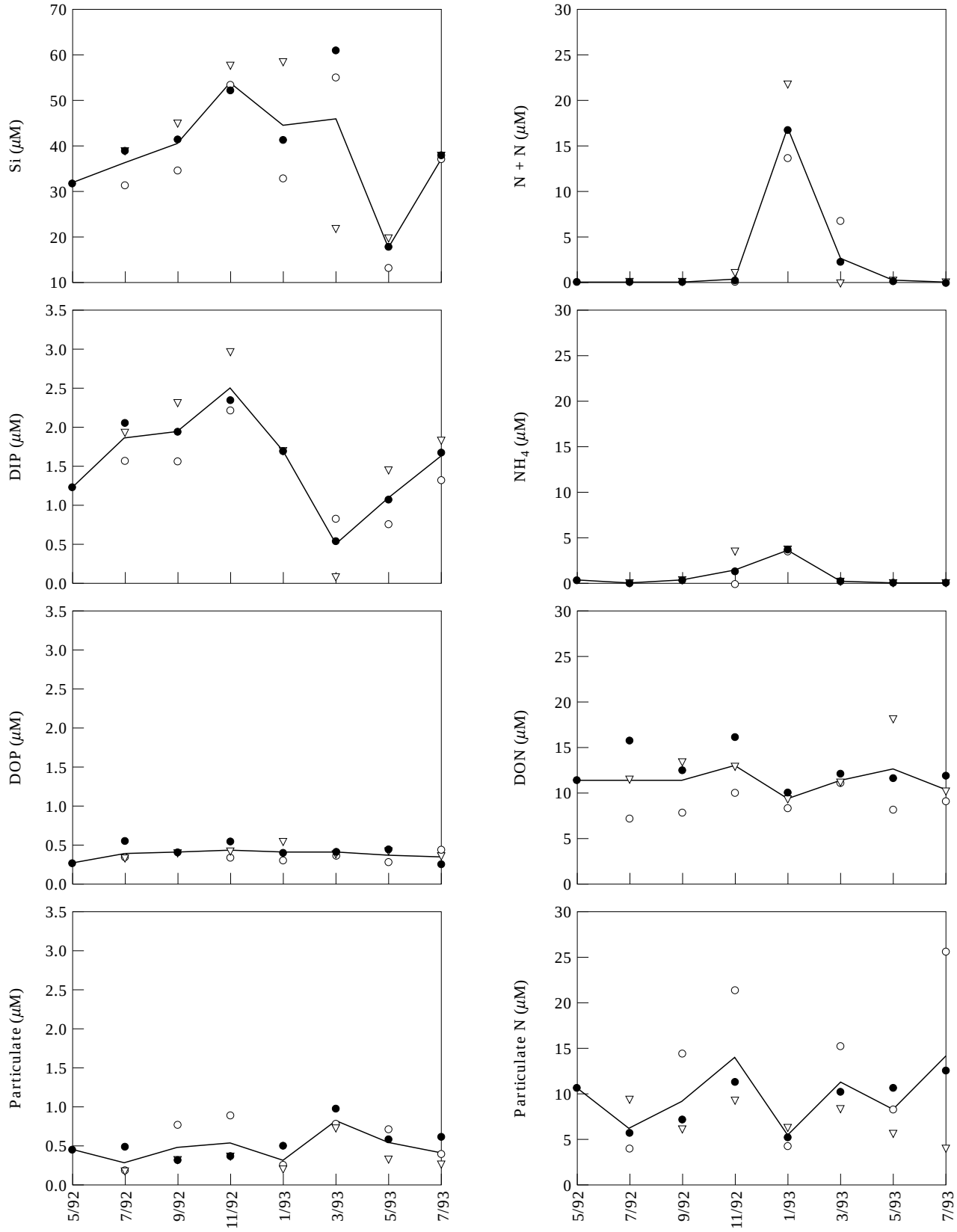

FIGURE 5. Variation in concentrations of silica, phosphorus and nitrogen species for the plankton community respiration incubations. ○, Station 10; ●, Station 12; ▽, Station 14. The line connects the means at each sampling period.

concentrations of 0·1–3·0 μmol l^{-1}. Dissolved organic phosphate concentrations were usually <0·5 μmol l^{-1}, and particulate P was generally <1·0 μmol l^{-1}. Dissolved inorganic phosphate concentrations peaked in late Summer to Autumn 1992, and were lowest in March 1993 (Figure 5). In contrast to P, concentrations of dissolved inorganic nitrogen forms (NH_4^+ and N+N) were generally low compared to DON and particulate N. Dissolved organic nitrogen was relatively constant through the year at concentrations of 6–18 μmol l^{-1}. Particulate N was more variable (4–26 μmol l^{-1}), but showed no clear seasonal pattern. Throughout most of the year, concentrations of inorganic nitrogen forms were below 0·5 μmol l^{-1}; however, there were peaks in both NH_4^+ and N+N concentrations in November 1992 (*c.* 5 μmol l^{-1} and 20 μmol l^{-1}, respectively).

Chlorophyll *a* concentration ranged from 1 to 10 μg chlorophyll *a* l^{-1}, with a minimum in January 1993 (Figure 6). Chlorophyll *a* concentration reached 24 μg l^{-1} during a phytoplankton bloom at Station 12 during July 1992. Bacterioplankton abundance ranged from 2 to 11×10^9 cells l^{-1} (Figure 6). Leucine incorporation rates ranged from 200 to 1300 pmol l^{-1} h^{-1}, but the three-station average for each sampling time was more constant (400–800 pmol l^{-1} h^{-1}; Figure 6).

Prediction of respiration rate

Seven of the measured chemical and biological parameters were significantly ($P \leq 0{\cdot}05$) correlated with respiration (Table 2): temperature, measures of dissolved nitrogen (N+N, NH_4^+, DIN and TDN), chlorophyll *a* and POC.

Stepwise multiple regression produced equations that predicted planktonic respiration as a function of chlorophyll concentration, temperature and PON (Table 3). A three-term regression equation (chl *a*, T and a constant) explained 75% of the variation in measured respiration rates. The addition of a PON term explained an additional 4% of the variation. This increase in explanatory power of the model was statistically significant, although small in magnitude. Both regression equations accurately predicted the pattern of measured respiration rates (Figure 7).

Modelling plankton community respiration in Tomales Bay

Owing the small increase in the goodness of fit of the regression model contributed by PON, the authors chose to model planktonic respiration using regression equation 1 from Table 3. Predicted plankton community respiration rates for the period January 1988 to

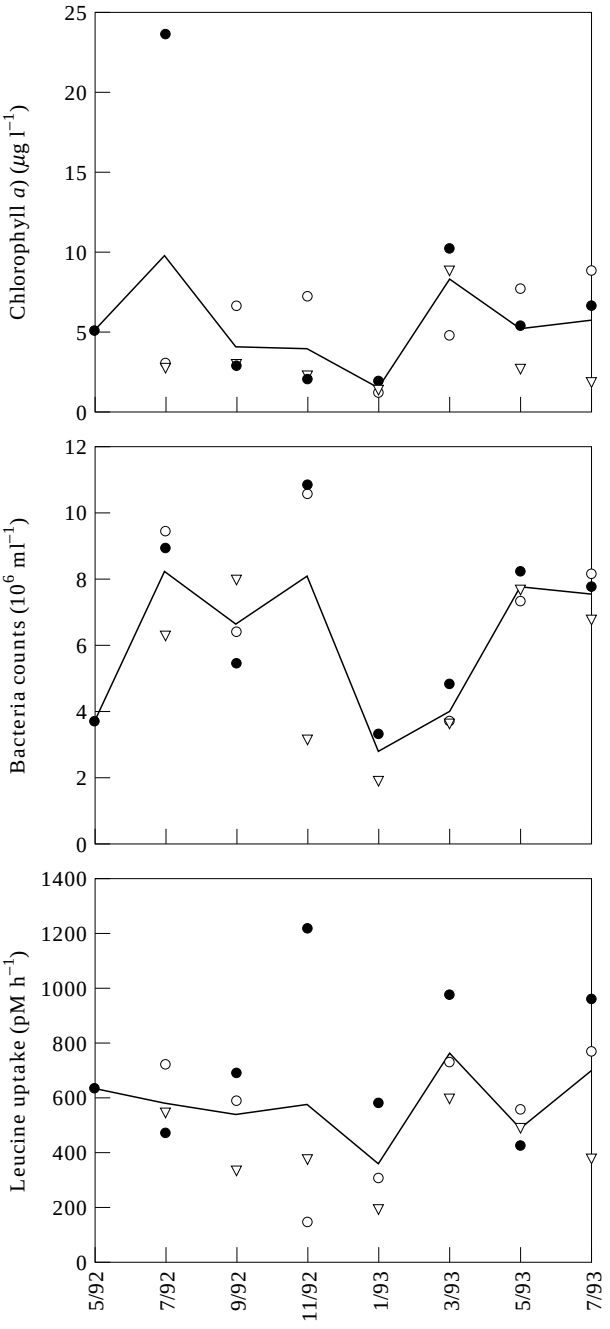

FIGURE 6. Variation in concentration of chlorophyll, bacterial counts and leucine incorporation rates for the plankton community respiration incubations. ○, Station 10; ●, Station 12; ▽, Station 14. The line connects the means at each sampling period.

July 1993 ranged from <0·4 to >2·0 μmol C l^{-1} h^{-1} [Figure 8(a)]. On an areal basis, maximum predicted plankton community respiration rates regularly occur in summer months, between 8 and 12 km from the mouth of the bay [Figure 8(b)]. Over the period from January 1988 to July 1993, the average predicted

TABLE 2. Pearson's correlation coefficients for the relationship between plankton community respiration and measured chemical, nutrient and biological variables in Tomales Bay, California

Chemical variables		Nutrient variables		Biological variables	
Temperature	**0·50 (0·018)**	DIP	0·00 (0·986)	Chlorophyll	**0·82 (<0·001)**
Salinity	0·34 (0·119)	DOP	− 0·02 (0·925)	Bacterial	0·40 (0·063)
pH	0·38 (0·077)	TDP	0·00 (0·996)	Counts	
TA	0·26 (0·234)	PP	0·33 (0·130)	Leucine	0·12 (0·607)
DIC	− 0·01 (0·964)	TP	0·14 (0·547)	Incorporation	
pCO_2	− 0·32 (0·150)	NN	**− 0·51 (0·015)**		
DOC	0·27 (0·221)	NH_4^+	**− 0·55 (0·008)**		
POC	**0·45 (0·037)**	DIN	**− 0·53 (0·011)**		
Secchi depth	0·12 (0·587)	DON	0·29 (0·194)		
		TDN	**− 0·45 (0·037)**		
		PON	0·40 (0·067)		
		TN	− 0·14 (0·542)		
		Si	− 0·03 (0·910)		

Numbers in parentheses are the two-tailed probabilities for the relationships. Correlation coefficients with $P \leq 0{\cdot}05$ are in bold type. See text for abbreviations.

areal respiration rate for inner Tomales Bay was 64·5 mmol C m^{-2} day^{-1}. There was substantial inter-annual variation in the areal respiration rates. For the years 1988–92, annual average daily planktonic respiration ranged from a low of 50·1 mmol C m^{-2} day^{-1} in 1990 to 84·0 mmol C m^{-2} day^{-1} in 1991.

Discussion

A multiple regression model, with independent variables describing the biomass of the planktonic community (chlorophyll *a*) and the rate of enzymatic reactions (temperature), was successful in predicting planktonic respiration in Tomales Bay. In Tomales Bay, temperature and the concentration of chlorophyll *a* in the water column provide enough information to describe 75% of the variation in planktonic respiration rates; a precision that is adequate for addressing many questions about the magnitude and variability of planktonic respiration in the system.

The rates of planktonic community respiration measured in this paper for Tomales Bay (0·16–1·91 µmol O_2 l^{-1} h^{-1}, Table 1) are comparable to rates measured in other temperature coastal water bodies. In a review of respiration rates of marine plankton, Williams (1984) cites a literature range of 0–0·84 µmol O_2 l^{-1} h^{-1}, with a mean of 0·16 µmol O_2 l^{-1} h^{-1}, for mostly open ocean samples. Subsequent work in coastal areas has produced somewhat higher estimates of respiration rates. In a eutrophic Danish fjord, spring to summer plankton community respiration was 0·29–5·18 µmol O_2 l^{-1} h^{-1} (Jensen *et al.*, 1990; Sand-Jensen *et al.*, 1990). For English Channel waters, Holligan *et al.* (1984) measured respiration rates of 0·03–2·24 µmol O_2 l^{-1} h^{-1} for stratified, frontal and tidally mixed water masses; Iriarte *et al.* (1991) report respiration rates of 0·52–0·79 µmol O_2 l^{-1} h^{-1}. In a mesohaline region of Chesapeake Bay, maximum summertime rates of plankton community respiration were between 1·2 and 2·2 µmol O_2 l^{-1} h^{-1} (Sampou & Kemp, 1994). Plankton community respiration from estuarine and marine areas of the Georgia coast ranged from 0·31 to 1·72 µmol O_2 l^{-1} h^{-1} (Hopkinson *et al.*, 1989, 1991). In the Gulf of Mexico, Pomeroy *et al.* (1995) found respiration rates as high as 1·4 µmol O_2 l^{-1} h^{-1} in the plume of the Mississippi River, and as low as <0·03 µmol O_2 l^{-1} h^{-1} in more oligotrophic areas.

Several variables that were found to be significantly correlated with the measured rate of plankton community respiration in Tomales Bay (Table 2) are often measured routinely in biogeochemical investigations of coastal water bodies. These included temperature, particulate carbon, DIN species and chlorophyll. Chlorophyll *a* concentration had the highest simple correlation to respiration rate, with $r = 0{\cdot}82$, $P < 0{\cdot}001$. Chlorophyll *a* concentration was very high for one sampling event (24 µg l^{-1}, Station 12, 11 July 1992). The effect of this one data point on the correlation between respiration rate and chlorophyll *a* was examined by removing that point and recomputing the correlation coefficient. The correlation between these variables for the remaining 21 cases was $r = 0{\cdot}67$, $P = 0{\cdot}001$, so even without the outlier point,

TABLE 3. Stepwise linear regression analysis of measured respiration rates of Tomales Bay planktonic communities as a function of water column chemical, nutrient and biological parameters listed in Table 2

Regression equation 1:

Respiration rate $=\beta_1$(chlorophyll)$+\beta_2$ (temperature)$+\beta_3$
Adjusted $r^2=0{\cdot}75$

Regression coefficients:

Variable	β	SE β	T	P
Chlorophyll *a*	0·059	0·009	6·54	>0·001
Temperature	0·033	0·012	2·79	0·012
Constant	− 0·178	0·197	− 0·90	0·378

Analysis of variance:

	d.f.	SS	MS	F	P
Regression	2	2489·2	1244·6	31·74	>0·001
Residual	19	745·0	39·2		

Regression equation 2:

Respiration rate $=\beta_1$(chlorophyll)$+\beta_2$ (temperature)$+\beta_3$(PON)$+\beta_4$
Adjusted $r^2=0{\cdot}79$

Regression coefficients:

Variable	β	SE β	T	P
Chlorophyll *a*	0·056	0·008	6·71	>0·001
Temperature	0·032	0·011	2·90	>0·01
PON	0·016	0·007	2·23	0·039
Constant	− 0·292	0·187	− 1·57	0·134

Analysis of variance:

	d.f.	SS	MS	F	P
Regression	3	2650·0	883·4	27·2	>0·001
Residual	18	584·1	32·4		

Respiration rate in μmol $O_2\,l^{-1}\,h^{-1}$, chlorophyll in μg l^{-1}, temperature in °C, and particulate organic nitrogen (PON) in μmol l^{-1}.

chlorophyll *a* had the highest simple correlation to respiration. In a eutrophic Danish fjord, phytoplankton biomass was also the best predictor of plankton community respiration rates (Jensen *et al.*, 1990). In the English Channel and the North Sea, chlorophyll concentration and plankton community respiration are also highly correlated (Iriarte *et al.*, 1991).

Temperature was also positively correlated with respiration rate, while measures of DIN were negatively correlated with respiration (Table 2). Note that temperature is negatively correlated with these measures of DIN ($r<-0{\cdot}77$, $P<0{\cdot}001$ for all comparisons), since high DIN occurs in the winter in Tomales Bay (Figures 5 and 7). The authors believe that the dependence of respiration on temperature, and the negative correlation between DIN and temperature, caused the observed negative correlation between plankton community respiration and DIN. Other studies have also shown a strong relationship between temperature and plankton community respiration in other systems (e.g. Iriarte *et al.*, 1991; Sampou & Kemp, 1994).

In contrast to these significant correlations, bacterioplankton abundance and activity (bacterial counts and leucine incorporation rate) were not significantly correlated with respiration in the authors' experiments (Table 2). Similarly, these parameters of bacterial activity were only weakly correlated in

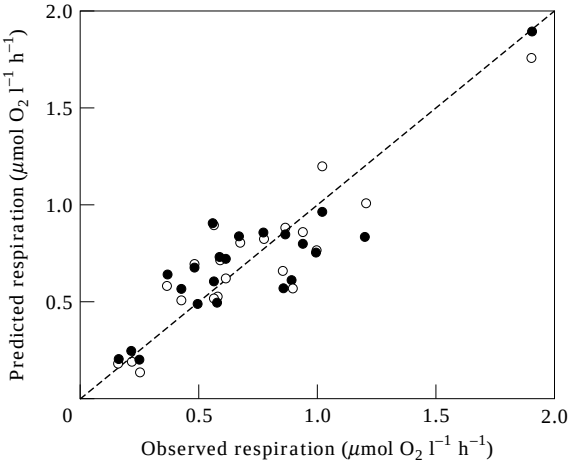

FIGURE 7. A comparison of measured and predicted rates of plankton community respiration, using the two regression equations in Table 3 to predict respiration. ● (chl, T) symbols are predictions from regression equation 1; ○ (chl, T, PN) are predictions from regression equation 2. The dashed line is 1:1.

seawater samples collected from 21 sites in the North Atlantic and Caribbean (Pomeroy *et al.*, 1994). The lack of significant correlation suggests that the contribution of bacterioplankton to plankton community respiration is small for Tomales Bay. Using the main L-leucine incorporation rate and empirical conversion factors, it is possible to estimate the contribution of the bacteria to total plankton community respiration. For a mean leucine incorporation rate of 600 pmol l^{-1} h^{-1} (Figure 6) and conversion factors of $6{\cdot}5 \times 10^{16}$ cells (mol leucine)$^{-1}$ (Hoch & Kirchman, 1993) and 20 fg C $cell^{-1}$ (Lee & Fuhrman, 1987; Hollibaugh *et al.*, 1991), mean bacterial production for the authors' experiments was 0·8 μg C l^{-1} h^{-1}. Assuming a net growth efficiency of 33% (Morita *et al.*, 1977; Pomeroy *et al.*, 1990), bacterial respiration would average 0·13 μmol C l^{-1} h^{-1}, or about 20% of the mean plankton community respiration rate of 0·7 μmol O_2 l^{-1} h^{-1}. Theoretically, L-leucine incorporation rate could be correlated with plankton respiration rate, even though bacterial respiration is not the dominant term in plankton respiration. A correlation would be expected if phytoplankton produce the organic matter used by bacterioplankton. However, variations in the coupling of C flow between phytoplankton and bacterioplankton (e.g. seasonal lags, Hoch & Kirchman, 1993; or variation in growth

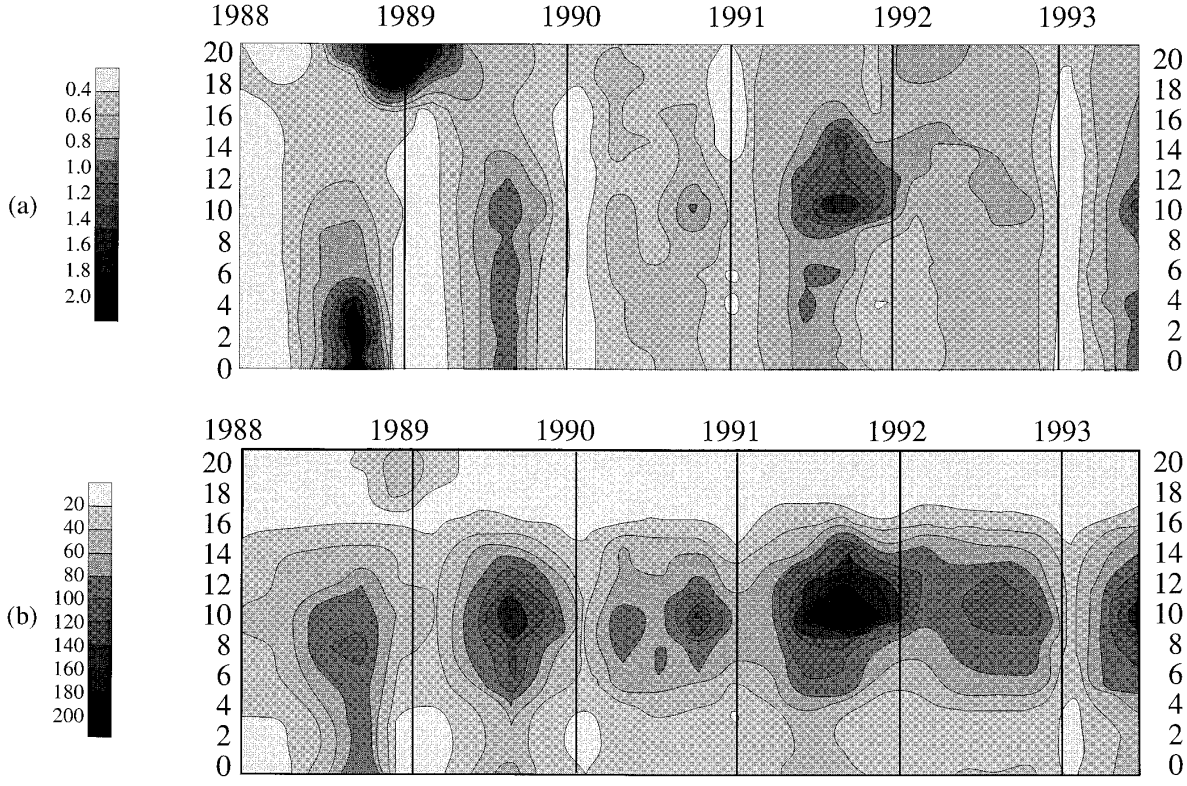

FIGURE 8. Contours of predicted plankton community respiration rates as a function of distance from the mouth of the bay and time for the period January 1988–July 1993. (a) Volume-specific rates (μmol l^{-1} h^{-1}). (b) Area-specific rates (mmol m^{-2} day^{-1}).

efficiency, Kirchman *et al.*, 1985; Hollibaugh, 1994) could remove the correlation, as could whole or partial dependence on other C sources. Jensen *et al.* (1990) found no significant correlation between bacterioplankton biomass and plankton respiration in a shallow Danish estuary, although Jensen *et al.* (1990) and Sand-Jensen *et al.* (1990) reported a correlation between plankton respiration and bacterioplankton production in the same estuary. There is only a weak correlation between bacterioplankton abundance or L-leucine incorporation rate and chlorophyll *a* concentration for Tomales Bay samples (Hollibaugh, unpubl. data), suggesting poor coupling in Tomales Bay. If the plankton community respiration measured in the present study is not due to bacterioplankton, it must be due to phytoplankton or protists. The contributions of mesozooplankton to plankton community respiration is usually quite small (Williams, 1981), and the biomass of zooplankton in Tomales Bay is low relative to other coastal water bodies (Kimmerer, 1993).

The chlorophyll-specific respiration rate of the plankton (β_1 in the regression model, Table 3) measured for Tomales Bay [59 nmol O_2 (μg chlorophyll *a*)$^{-1}$ h^{-1}] was similar to an average of 56 nmol O_2 (μg chlorophyll *a*)$^{-1}$ h^{-1} in English Channel waters (Iriarte *et al.*, 1991), but roughly double the rate of 24 nmol O_2 (μg chlorophyll *a*)$^{-1}$ h^{-1} found in a Danish estuary (Jensen *et al.*, 1990). Of course, included in the chlorophyll-specific respiration rate is the respiration of bacterioplankton and protists as well as the phytoplankton. Biomass-specific respiration rates of bacterioplankton are not very meaningful because of the strong dependence of bacterial respiration on growth rate and substrate (Novitsky & Morita, 1977), but unless the mean biomass-specific bacterioplankton respiration rate is much higher than that for phytoplankton, phytoplankton respiration should be more important than the bacterioplankton respiration in Tomales Bay. The mean rate of phytoplankton biomass to bacterioplankton biomass in Tomales Bay is 5·84 ± 0·186 (n=1115 samples taken between 1987 and 1995, Hollibaugh, unpubl. data). No estimates of protist biomass were available to evaluate their relative contribution to the plankton community respiration.

A potential problem with the application of the plankton community respiration predictive equation to all of Tomales Bay is spatial variability in the phytoplankton community composition. All of the water samples that were analysed for plankton community respiration in this study were collected from a 4-km section of inner Tomales Bay (Figure 1). Published data on the make-up of the phytoplankton community of Tomales Bay indicates that the outer and central reaches of the bay are often dominated by diatoms, while the southern reach is dominated by flagellates (Cole, 1989). This potential problem is minimized by the similarities in the communities from the central and outer reaches, which comprise 80% of the surface area of the bay, and by the relative shallowness of the southern reach as defined by Cole (1989). This shallowness controls the volume of the plankton community, and therefore the relative importance of the southern reach to baywide planktonic respiration [Figure 8(a,b)].

Another potential problem with using a regression approach to model system respiration arises with extrapolation beyond the range of the independent variables used to formulate the relationship. The temperature range over which the respiration incubations were made was 9·2–22·3 °C, which encompassed 95% of all observed temperature records from samples used to hindcast system respiration (1481 observations, range 4·8–23·5 °C). Only 12% of the historic chlorophyll *a* values (1481 observations, range 0·17–51·0 μg l^{-1}) fell outside of the range observed during respiration measurements (1·31–23·63 μg l^{-1}); most of the outliers were below 1·31 μg l^{-1}. Consequently, errors associated with extrapolation should be relatively small.

Model hindcasts of planktonic respiration in Tomales Bay indicated large inter-annual variability in the volume-specific respiration rate [Figure 8(a)]. This variability was largely driven by inter-annual variation in the concentration of chlorophyll *a*. Cooler winter temperatures caused a general decrease in the respiration rate during most winters, but the effect of temperature could be overwhelmed by winter phytoplankton blooms. In 1988, the model predicted maximum volume-specific respiration rates both near the mouth of the bay during late summer and at the head of the bay during the winter of 1988–89. During some years, such as 1990 and 1992, there were no distinct peaks in volume-specific respiration. The causes of the variability in biomass of phytoplankton that drive the water column respiration are presently being analysed (Hollibaugh, in prep.). The marked seasonal and spatial patterns in the hindcast volume-specific planktonic respiration would not have been predicted from the measured respiration rate data (Figure 2), because of the relative homogeneity of the chlorophyll concentration of the measured samples (Figure 6).

Areal rates of respiration were determined by integrating volumetric rates over the depth of the water column. This approach assumed that the chlorophyll-specific respiration rate is the same for all depths

in the water column. While respiration was not measured in samples collected deeper than 1 m in the water column, the water column of this shallow bay was generally well mixed, and chlorophyll concentration is generally not highly stratified. Thus, the authors feel that this assumption is reasonable. Owing to the bathymetry of Tomales Bay, most of the respiration of the planktonic community occurred in the deepest parts of the bay, between 5 and 14 km from the mouth of the bay [Figure 8(b)]. This finding is similar to Cole's (1989) estimations of phytoplankton productivity. which were highest in the deeper portions of Tomales Bay. There was substantial interannual variation in areal respiration rates. Hindcast annual daily average respiration was low in 1988 and 1990 (*c.* 50 mmol m^{-2} day^{-1}) and high in 1991 and 1992 (*c.* 80 mmol m^{-2} day^{-1}); the coefficient of variation (SD/mean) for annual mean daily respiration was 24%. The predictions for the first half of 1993 showed the formation of a large summer maximum, with rates up to 160 mmol m^{-2} day^{-1} 10 km from the mouth of the bay.

The average daily respiration rate of 64·5 mmol m^{-2} day^{-1} predicted by the model for the period 1988–93 was remarkably similar to the estimate of 64 mmol m^{-2} day^{-1} derived from a balance of the net ecosystem respiration of 10 mmol m^{-2} day^{-1} (Smith *et al.*, 1991), benthic respiration of 21 mmol m^{-2} day^{-1} (Dollar *et al.*, 1991), and primary production of 75 mmol m^{-2} day^{-1} (Smith *et al.*, 1991). For any one year, the authors' estimates of phytoplankton community respiration were from 50·1 to 84·0 mmol m^{-2} day^{-1}, or within 30% of the rate predicted using the budgetary approach.

It is fortuitous that the hindcast average plankton community respiration rate was so close to the predictions from net system stoichiometry, since the uncertainties on all of these estimates are quite large. Indeed, *Smith et al.* (1991) point out that one should not expect to be able to exactly predict the net behaviour of a system from a summation of component fluxes, due to the large uncertainties with all of the component flux estimates caused by spatial and temporal variation. Despite these caveats, arriving at an estimate for plankton community respiration close to the estimate predicted by system stoichiometry supports the utility of using system stoichiometry for describing the net behaviour of systems. Recent work suggests that the stoichiometric approach may overestimate net system heterotrophy by $\approx$30% due to export of terrestrially derived, inorganic P (Chambers *et al.*, 1995).

Even in a relatively shallow, heterotrophic system such as Tomales Bay, planktonic respiration accounts for the majority (76%) of the system's respiration. This finding corroborates the general pattern of about 25% of system respiration occurring in the benthos (Nixon, 1981). As respiration remineralizes nutrients as well as carbon, it is reasonable to assume that the majority of the nutrient regeneration in Tomales Bay also occurs in the water column.

Water column respiration releases N and P in proportion consistent with Redfield predictions (i.e. 106 C: 16 N; 1 P). This assumption was tested by monitoring nutrient concentrations during one incubation (Station 12 water collected on 7 November 1992). The rate of remineralization of N, as indicated by the accumulation of NH_4^+ during the incubations, was 89 ± 7 nmol l^{-1} h^{-1}; P remineralization was 4 ± 1 nmol l^{-1} h^{-1}. The rate of respiration of carbon during the incubation was 580 nmol l^{-1} h^{-1} (Table 1). These rates give ratios of $6{\cdot}5 \pm 0{\cdot}6$ mol C respired for each mol N remineralized, and 145 ± 36 mol C:mol P. This one-time estimate of remineralization stoichiometry was not significantly different from the Redfield ratio.

Using the estimated rates of respiration and Redfield C:N:P stoichiometry, the authors estimate a daily average remineralization of 9·8 mmol N m^{-2} day^{-1} and 0·6 mmol P m^{-2} day^{-1}, compared to fluxes from the benthos to the water column of 1·9 mmol N m^{-2} day^{-1} and 0·2 mmol P m^{-2} day^{-1} (Dollar *et al.*, 1991). N:P stoichiometry in the benthic flux deviates substantially from Redfield due to the importance of denitrification as a respiratory pathway in the sediments (Dollar *et al.*, 1991; Joye & Paerl, 1993), while there should be no important sinks of the N produced as a consequence of aerobic respiration in the planktonic community. Remineralization in the water column supplies 5 times the N and 3 times the P to phytoplankton as benthic flux. Assuming that phytoplankton production averages 60 mmol C m^{-2} day^{-1}, 9·1 mmol N m^{-2} day^{-1} and 0·6 mmol P m^{-2} day^{-1} are required by the phytoplankton. Plankton community nutrient remineralization can supply all of the N and P required for plankton community production in Tomales Bay. Even in a coastal system as shallow as Tomales Bay, planktonic processes may dominate the respiration and nutrient turnover.

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